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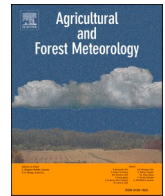
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Alpine shrubs have benefited more than trees from 20th century warming at a treeline ecotone site in the French Pyrenees

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ABSTRACT

Mountain ecosystems are particularly sensitive to climate change, which in part causes encroachment of woody plants at the treeline ecotone, with repercussions on treeline advance and ecosystem carbon balance. Yet, studies investigating the long-term trends in radial growth as well as year-to-year response of several tree and shrub species to climate change are scarce, especially in the Pyrenees where dendroecological studies are hitherto critically lacking. Here, we estimate and compare the long-term growth trends of two shrub (*Rhododendron ferrugineum* and *Juniperus communis*) and one tree (*Pinus uncinata*) species, and investigate their year-to-year growth response to changing climatic conditions and advancing snow melt-out timings. We used the Age-Class Isolation method (ACI) to derive growth trends from the ring width series of trees and shrubs. Climate-growth relationships were evaluated using fixed- and moving-window bootstrap correlation functions with the aim to determine the effects of changing climate and snowpack on shrub and tree growth. Overall, our results show that all species at our site, especially shrubs, have grown increasingly well over at least the last century, probably in response to increasing temperatures during the growing season and earlier snow melt-out dates. Nevertheless, the two shrub species differ quite strongly in their response to climate. Whereas the climate signal of *J. communis* has been relatively stable in recent decades despite the persistent and significant warming trend, *R. ferrugineum* shows a strong shift in climate sensitivity and is increasingly affected negatively by climate change. Altogether, our results address the different climate sensitivity of the two most common shrubs in the Pyrenees. They also contribute to a better understanding of vegetation dynamics in the Pyrenean treeline ecotone in the context of global change.

1. Introduction

High elevation ecosystems have faced unprecedented warming in recent decades, leading to accelerated changes in their productivity and functioning (Carlson et al., 2017; Choler, 2015; Choler et al., 2021; Filippa et al., 2019; Rumpf et al., 2022). Shrub encroachment at the treeline ecotone and beyond, a landscape-scale phenomenon, has been observed on the Tibetan Plateau and in the Himalayas (Brandt et al., 2013; Klein et al., 2014; Lehnert et al., 2016), in the Rocky Mountains (Formica et al., 2014), Scandes (Hallinger et al., 2010; Kullman, 2002; Rundqvist et al., 2011), European Alps (Cannone et al., 2007; Dullinger et al., 2003) and the Pyrenees (Grau et al., 2019; Montané et al., 2007;

Urbina et al., 2020). Specifically in the Pyrenees, shrub and tree encroachment has been found to be triggered primarily by land abandonment after centuries to millennia of intense agro-silvo-pastoral activities and by climate change (Améztegui et al., 2016; Améztegui et al., 2010; Galop and Jalut, 1994; Gartzia et al., 2014). Shrub encroachment has direct effects on surface albedo, vegetation roughness, snowpack dynamics and litter input, which in turn has various impacts on alpine tundra carbon balance by increasing ecosystem carbon uptake and altering ecosystem respiration (Mekonnen et al., 2021; Urbina et al., 2020). In the Pyrenees, shrub encroachment plays a complex but important role in the first stage of tree re-colonization at treelines. Treeline advance is mainly driven by *Pinus uncinata* establishment

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(Améztegui et al., 2010; Camarero and Gutiérrez, 2004), in interaction with the spread of *Juniperus communis* and/or *Rhododendron ferrugineum* dominated heathlands (Angulo et al., 2019; Batllori et al., 2009; Gartzia et al., 2014; Pasche et al., 2004; Urbina et al., 2020). Indeed, scattered shrubs have a beneficial effect on tree establishment by sheltering seedlings, but dense, encroached heaths inhibit their development (Angulo et al., 2019; Batllori et al., 2009; Camarero and Gutiérrez, 1999). Even if land abandonment plays a key role for the establishment of new individuals, climatic conditions are also responsible for the success of the initial recruitment and the velocity of subsequent shrub encroachment dynamics through vegetative growth (Formica et al., 2014). However, the exact climatic factors that determine the growth of co-occurring tree and shrub species at the treeline ecotone remain poorly understood.

Dendroecology, the analysis of growth rings of woody plants, has been widely used to fill this knowledge gap (Forbes et al., 2010; Mekonnen et al., 2021; Myers-Smith et al., 2015b), because growth rings contain information on the response of trees and shrubs to climatic variables at different timescales. Variations in ring width over decades or centuries reflect the effects of gradual changes in environmental factors that limit growth (e.g. temperature, precipitation, CO₂ concentration), but also biological and geometric age-related growth trends (Peters et al., 2015). Studies on long-term growth trends have been used

in different contexts to detect growth changes and biomass increase (Bouriaud et al., 2005; Nehrbass-Ahles et al., 2014; van der Sleen et al., 2015), but were only rarely employed to analyze encroaching alpine environments (see Šenfeldr et al., 2021).

Interannual variations in temperature, precipitation and snow cover drive short-term variations in ring widths (i.e. year-to-year variations). Dendroecological studies show that trees occurring at their uppermost distribution margin are cold-limited and therefore highly sensitive to summer temperature (Körner, 2012). Alpine dwarf shrubs, on the other hand, do not only exhibit a summer temperature signal but also a snowpack signal, with the latter determining growing season length (Carrer et al., 2019; Francon et al., 2020a). Yet, we are not aware of any study that investigated climatic drivers of growth of structuring co-occurring long-lived dwarf shrub species to compare them with those of neighboring trees in European mountains. Furthermore, few studies have performed combined analyses of short-term climate-growth relations and long-term growth trends in shrubs (Pellizzari et al., 2016; Šenfeldr et al., 2021), which we hypothesize could facilitate understanding of the missing link between shrub encroachment and climate signals retrieved from growth rings (Babst et al., 2014; Nehrbass-Ahles et al., 2014).

In this paper, we attempt to fill this gap and to explore, for the first time in the Pyrenees, the climate-growth responses of three shrub and

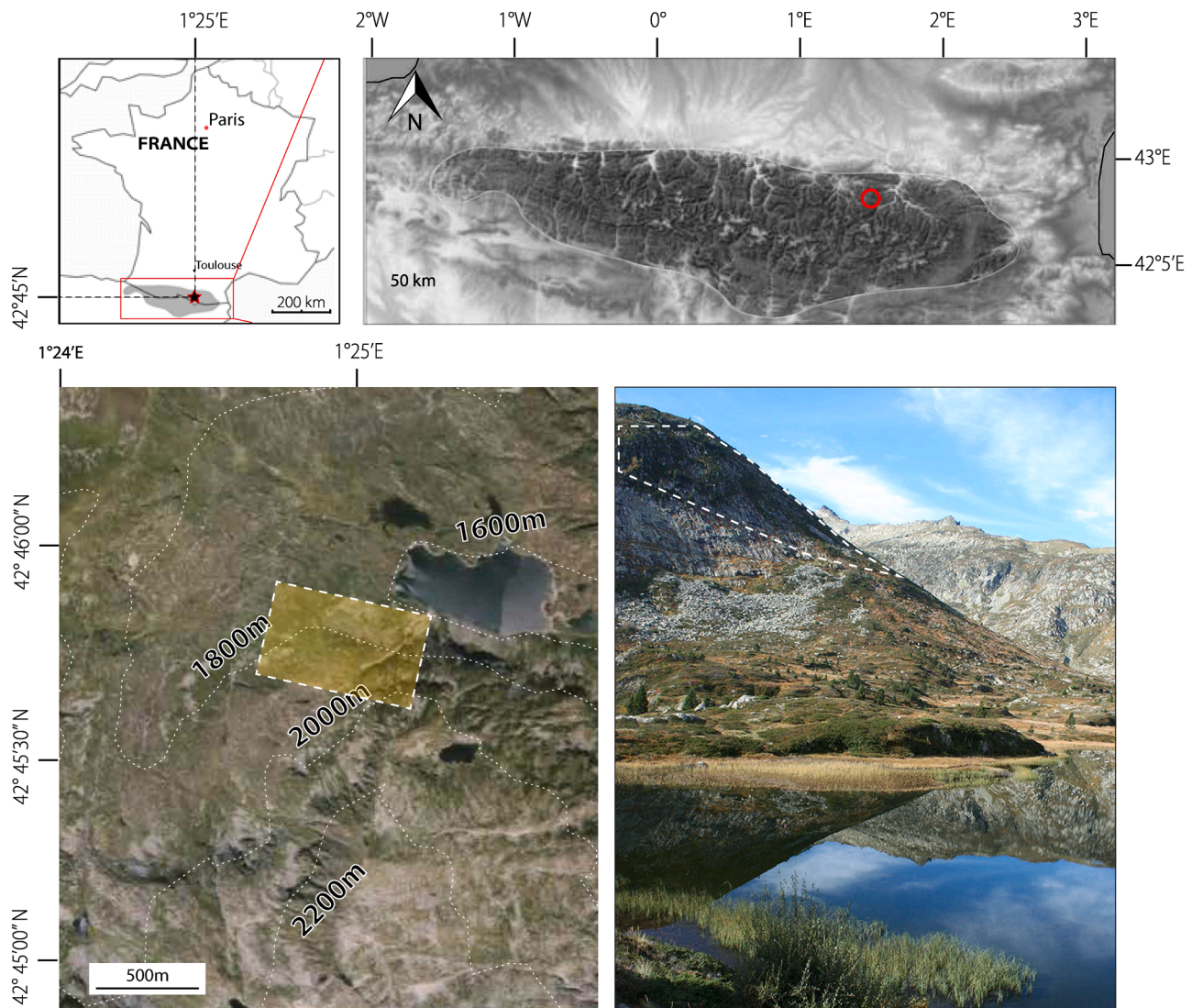


Fig. 1. Location and overview of our study site located at 1800 m asl in the Bassiès valley (French Pyrenees).

tree species co-occurring at a site where intense encroachment is ongoing. Our objective is twofold, namely: (1) to estimate, in the longer term, the evolution of shrub and tree woody biomass by investigating growth trends over the last decades/centuries; and (2) to compare growth responses of *R. ferrugineum* and *J. communis* shrubs and *P. uncinata* trees to year-to-year climate variability.

2. Methods

2.1. Study site

Our study site (42°45'30"N, 1°24'50"E, Fig. 1) is located in the central-eastern part of the French Pyrenees, in the hanging Bassiès valley, a tributary of the Ariège basin. Bedrock at Bassiès valley (15 km²) consists mostly of granitic *roches moutonnées* that were formed during the last glaciation (Delmas et al., 2011). Microtopography at the sampling site is rugged and consists of medium-sized rocks covering the talus slopes. Vegetation consists primarily of subalpine meadows and dwarf shrubs (65%), whereas forest and tall shrubs occupy 5% and 2% of the valley surface, respectively. Vegetation-free rock and bare soils occupy 25% and water 3% of the surface (Marti et al., 2016; Szczypta et al., 2015). Since the 1950s, successional processes involving tree (*P. uncinata* and *Betula pendula*) and shrub (*Calluna vulgaris*, *R. ferrugineum* and *J. communis*) encroachment of open grasslands occur rapidly across the valley and are driven by changing pastoral practices and under-grazing (Galop et al., 2011). At 1800 m asl, average annual temperature over the period 1981–2010 was 5.3 °C (June–August mean temperature was 12.3 °C) and mean annual precipitation was 1245 mm (May is the moistest month with 133 mm and July the driest, with 73 mm precipitation) according to the SAFRAN-Crocus dataset (Durand et al., 2009). Precipitation falls as snow generally as of November–December (Marti et al., 2016) and snow melt-out timing occurs around the second week of May (See Fig. S1).

2.2. Study species

Pinus uncinata Ram. (Pu) is a tree species growing in the subalpine belt of the central and eastern Pyrenees, where it forms most treelines. At our site, the treeline has been lowered due to past human activities. A few remaining groups of trees form the current treeline, which is below 2000 m asl. Pu is a shade-intolerant species occurring in different soil and slope aspects. *P. uncinata* is the main contributor to vegetation encroachment in the Pyrenees (Ameztegui et al., 2016; Ameztegui et al., 2010; Ninot et al., 2008), it also is the most widely investigated taxa in dendrochronological studies from the Pyrenees (Büntgen et al., 2008; Diego Galván et al., 2015; Reid and Wilson, 2020; Sangüesa-Barreda et al., 2018; Sanmiguel-Valladolid et al., 2019). *Juniperus communis* (L.) (Jc) and *Rhododendron ferrugineum* (L.) (Rf) are both long-lived, late-successional, multi-stemmed dwarf shrub species (Cannone et al., 2022), widely distributed in the European high mountains, in the subalpine and alpine belt. Both species have been shown to be able to rapidly invade meadows, and ultimately form dense closed heathlands (Escaravage et al., 1997; Pasche et al., 2004). While *R. ferrugineum* occurs mainly on north-facing slopes in the Pyrenees, *J. communis* is more tolerant and occurs on slopes of varying aspect (Gracia et al., 2007). Both species have been shown to be suitable for dendrochronological analyses (Carer et al., 2019; Francon et al., 2017), although no studies have compared their growth response to climate at a site where they co-occur. In the Alps, *J. communis* shows high sensitivity to snowpack, which is consistent across contrasting topoclimatic sites (Ninot et al., 2008). *R. ferrugineum*, on the other hand, shows a more complex response to climate and snowpack, varying considerably along environmental gradients (Francon et al., 2020a; Francon et al., 2021).

2.3. Sample collection and preparation

A total of 22 *R. ferrugineum* and 21 *J. communis* were sampled in the Bassiès valley at a site where they co-occur, on a north-facing slope, at an elevation between 1800 and 1900 m asl (Fig. 1). For each species, we sampled shrubs at a minimum distance of four meters from each other to avoid sampling the same clone. Two to three sections were sampled from each shrub, starting at the root collar if accessible, or as low as possible on the main stem. Sampling was designed to perform a serial-sectioning approach in which ring widths are measured at different stem levels to detect missing rings and improve cross-dating, i.e. assigning exact calendar years to the formation of each ring (Kolishchuk, 1990). However, after successful cross-dating, we retained only the lower section for climate signal extraction as recommended by Ropars et al. (2017). Since sufficiently old individuals of *P. uncinata* were not found in large numbers in the closed heath where we sampled the shrubs, we collected tree samples that were growing on the same slope and at the same elevation, but c. 200 m away from the shrub sampling site where they occur in larger numbers due to the presence of a less closed heath. Finally, 21 *P. uncinata* trees were cored at breast height (two cores per tree) using an increment borer.

For *R. ferrugineum*, 20 µm-thick micro-sections were obtained using a rotary microtome. Each section was stained with safranin and astra blue dyes to enhance ring boundaries and finally mounted on slides (Schweingruber and Poschold, 2005). High-resolution digital pictures were captured by a Carl Zeiss Axio Observer Z1 coupled to a Zeiss AxioCamMR R3 camera. The images were merged automatically with the Zeiss Zen 2011 software to cover entire cross-sections. Because ring widths are roughly three times larger in *J. communis* than in *R. ferrugineum*, the preparation of microsections is not necessary and we simply air-dried sections and sanded them with gradually finer sandpapers according to standard procedures used in dendrochronology (Bräker, 2002). Similarly, for *P. uncinata*, increment cores were air-dried and sanded. Subsequently, sections and increment cores were scanned with a resolution of 1200 dpi using a high-resolution Epson 11000XL scanner.

2.4. Ring-width chronologies

For all species, growth rings were measured from digital images with the CooRecorder 7.6 software (CYBIS Elektronik & Data AB). For shrubs, ring widths were measured at three radii to detect partial rings. Cross-dating was done with Cdendro (CYBIS Elektronik & Data AB) following the three-step procedure described in Francon et al. (2017) for shrubs and the traditional dendrochronological protocol for trees (Bräker, 2002). Visual cross-dating was statistically validated using COFECHA (Holmes, 1994). Only carefully dated sections were retained for further analysis. Individual tree and shrub-ring series were standardized using the R (R Core Team, 2016) dplR package (Bunn, 2008) to eliminate non-climatic trends (e.g., age related growth trends, effects of natural or human-induced disturbances) and to maximize climatic information. We used a cubic smoothing spline with a 50% frequency response at 25 years (Cook and Peters, 1981) to detrend each series. Besides the standardized series, we also calculated residual (or pre-whitened) time series where auto-correlation was removed. After standardization, ring-width indices (RWI) were averaged for each individual with a bi-weighted robust mean so as to reduce the influence of outliers (Cook and Peters, 1981).

Descriptive statistics including standard deviation (SD), mean sensitivity (MS), and autocorrelation (AC) were computed using the R (R Core Team, 2016) dplR package (Bunn, 2008) for the three chronologies. In addition, the subsample signal strength (SSS), expressed population signal (EPS; Wigley et al., 1984) and mean inter-series correlation (rbar) were computed using dplR to evaluate their robustness. The SSS statistic quantifies the strength of the common climate signal in the tree-ring proxies by calculating how well a finite subsample represents

the reference chronology – and a theoretical infinite sample in the case of EPS (Buras, 2017; Wigley et al., 1984). We used a SSS threshold >0.85 to determine the period over which each chronology is reliable. Finally, we computed Pearson correlations between the three mean residual chronologies over this period.

2.5. Trend analysis

We used the Age-Class Isolation (ACI) method to derive growth trends from tree and shrub ring-width series (Peters et al. 2015). This method compares growth rates within fixed age classes, thereby removing age trends from the raw growth rates. In our case, we used 20-year age classes. For each individual, we calculated the average raw ring width in each age class, centered on the 10-, 20-, 30- etc. cambial age. We discarded age classes as soon as the number of individuals included in the age class dropped below 10. To detect significant positive or negative growth trends by age class, we calculated linear regressions and Pearson's correlation coefficients between time and mean ring width (significance level $p < 0.05$, see Cook and Peters, 1981). We also used linear mixed models (LMMs) available from the R (R Core Team, 2016) nlme package (Pinheiro and Bates, 2000) to test the significance of trends among age class. Year was used as a fixed effect, and we chose individual ID as a random factor. We calculated a pseudo- R^2 of the selected models following Nakagawa and Schielzeth (2013), which comprises marginal (R^2_m) and conditional (R^2_c) R^2 values. R^2_m accounts for the proportion of variance explained by the fixed factors, and R^2_c accounts for the proportion of variance explained by the whole model, i.e. fixed plus random factors. Statistical analyses were realized with R (R Core Team, 2016).

2.6. Year-to-year climate-growth relationships

To identify effects of interannual climate variability on year-to-year ring-width variability in the three species, we computed bootstrapped correlation functions (BCFs) between the spline-detrended and residual chronologies on the one hand and mean monthly air temperature ($^{\circ}\text{C}$), precipitation totals (mm) and melt-out dates on the other hand using the R (R Core Team, 2016) Treeclim package (Zang and Biondi, 2015). In addition, we computed a 30-year moving window only for the monthly/seasonal climate parameters that were found to be significant in the BCF to determine possible changes in the strength, sign and significance of correlations among themselves. We extracted monthly meteorological and snowpack variables from the SAFRAN-Crocus reanalyses dataset for the period 1959–2017 (S2M, Durand et al. 2009; Vionnet et al. 2012). This dataset combines *in situ* meteorological observations with synoptic scale meteorological fields to provide continuous time series of meteorological variables at hourly resolution for elevation bands of 300 m, different slope aspects and angles within spatial units referred to as "massifs" (i.e. Couserans in our case). In addition, S2M also provides snow depth values. Vegetation and microtopography are simplified in the simulations and a continuous grass cover is assumed to simulate typical snow conditions for open areas (Vionnet et al., 2012). The simulated snow depth was found to be very comparable to observations in a recent S2M evaluation (Vernay et al., 2022), ensuring reliable snow data for our study.

We included monthly predictors from June of the year preceding ring formation ($n-1$) to October of the year of actual growth (n). We also considered mean temperature of the vegetative period (i.e. the period without snow cover, starting around May and ending in October), mean temperature of the growing season (around July and August, based on unpublished dendrometric data) and precipitation accumulated from December to February, falling mainly in the form of snow, as indicators of snow accumulation. Finally, we derived snow melt-out dates from S2M according to elevation, slope aspect and slope angle at the study sites. Melt-out dates correspond to the date by which thickness of continuous snowpack falls below 10 cm (see Fig. S1). All climate data

were detrended using the same approaches as for ring widths (see Chapter 2.4), as the focus of this analysis was on the interannual radial growth response to climate.

3. Results

3.1. Chronology statistics

A total of 15, 13, and 20 individuals were included in the chronologies of *R. ferrugineum* (hereafter referred to as Rf), *J. communis* (Jc) and *P. uncinata* (Pu), respectively, corresponding to rejection rates (i.e. the percentage of misdated individuals) of 32, 38, and 5%. The average ring widths are 0.16, 0.47 and 1.31 mm for Rf, Jc, and Pu, respectively (Table 1). The oldest individual sampled was a 212-year-old Rf shrub. Signal strength statistics computed for the standardized, residual chronologies (mean intercorrelation, Rbar, EPS and SSS) show lower values for the Rf and Jc chronologies as compared to the Pu chronology (Table 1, Fig. 2). For instance, the Rbar amounts to 0.26 for both shrub chronologies, and to 0.37 in the case of Pu. Yet, between 1960 and 2017, that is the period for which climate data is available, all species exceed the 0.85 SSS threshold. Mean sensitivity (MS) is higher in the case of Rf (0.53) than in Jc (0.24) or Pu (0.19). On the contrary, first-order autocorrelation (AR1), computed before pre-whitening, was much higher in Pu (0.74) than in the shrubs (Rf: 0.27 and Jc: 0.34). The Pearson correlation coefficient ($p < 0.05$) between Jc and Pu, Rf and Jc, as well as Rf and Pu are 0.49, 0.25 and 0.00, respectively.

3.2. Long-term growth trends

Results obtained from the growth trend analysis show a general increase in woody biomass for the different species. In Fig. 3A–B, ACI indicates that trends for each 20-years age classes are positive in all cases, but not always significant. For Rf, individuals being younger than 40 show the strongest positive trends, whereas older individuals exhibit weaker trends. For Jc, we could not find any trend differences between age classes. Very young Pu individuals (c. 10 years old) and individuals aged 60+ show stronger positive trends than individuals aged 20–50. Linear mixed-effects models computed between age-classes for each species separately confirm the significance of the positive temporal trends for each species (Table 2, Fig. 3C). Specifically, Jc shows the strongest growth increase, followed by Rf and Pu (Fig. 3C). The proportion of variance explained by fixed effects (R^2_m) reaches 100% for Jc, while it is lower for Rf and particularly for Pu, where random effects explain most of the variance.

3.3. High frequency climate-growth response

Correlations computed with the monthly and seasonal climate variables and snow melt-out timing over the period 1960–2017 are shown in Fig. 4. Overall, we observe that Pu and Jc respond similarly to year-to-year climate variability and that their response to snow melt-out timing is significant: years with early melt-out dates are indeed significantly related with larger rings in Jc ($-0.52, p < 0.05$) and, to a lesser extent, also in Pu ($-0.41, p < 0.05$). Both species also show a bimodal response to monthly temperature in the year of ring formation, as Pu is positively and significantly correlated with May ($0.36, p < 0.05$) and September ($0.25, p < 0.05$) temperatures, whereas ring formation in Jc is controlled by April ($0.39, p < 0.05$), May ($0.33, p < 0.05$), September ($0.27, p < 0.05$) and October ($0.23, p < 0.05$) temperatures. However, Pu, which is positively affected by temperature in previous November and negatively by temperature in previous August, is overall more sensitive to conditions in the previous year than Jc. In addition, we find that wet conditions in early summer of the year preceding ring formation ($n-1$) have a positive effect on Pu growth, whereas they have a negative effect if occurring in late summer of the year of ring formation (n). Rf, on the other hand, reacts somewhat differently to climate: whereas growth correlates

Table 1
Characteristics of *R. ferrugineum* (Rf), *J. communis* (Jc) and *P. uncinata* (Pu) ring-width chronologies: mean ring-width (RW), chronology length (calendar years), number of individuals (Nb.), mean intercorrelation between individual series, signal strength (Rbar and EPS calculated for the entire chronology and for 1960–2017, respectively), first year in which SSS > 0.85 (and number of individuals included in the chronology), first order autocorrelation (AR1) and mean sensitivity (MS). Values (except for mean RW) refer to chronologies after detrending.

Chrono. (mean RW)	Length	Nb.	Mean inter-corr	Rbar	EPS	Rbar (1960–2017)	EPS (1960–2017)	Year SSS >0.85 (Nb.)	AR1	MS
Rf (0.16)	1805–2017	15	0.42	0.26	0.65	0.30	0.85	1928 (7)	0.27	0.53
Jc (0.47)	1879–2017	13	0.45	0.26	0.68	0.25	0.80	1951 (7)	0.34	0.24
Pu (1.31)	1859–2017	20	0.56	0.37	0.88	0.38	0.92	1892 (7)	0.74	0.19

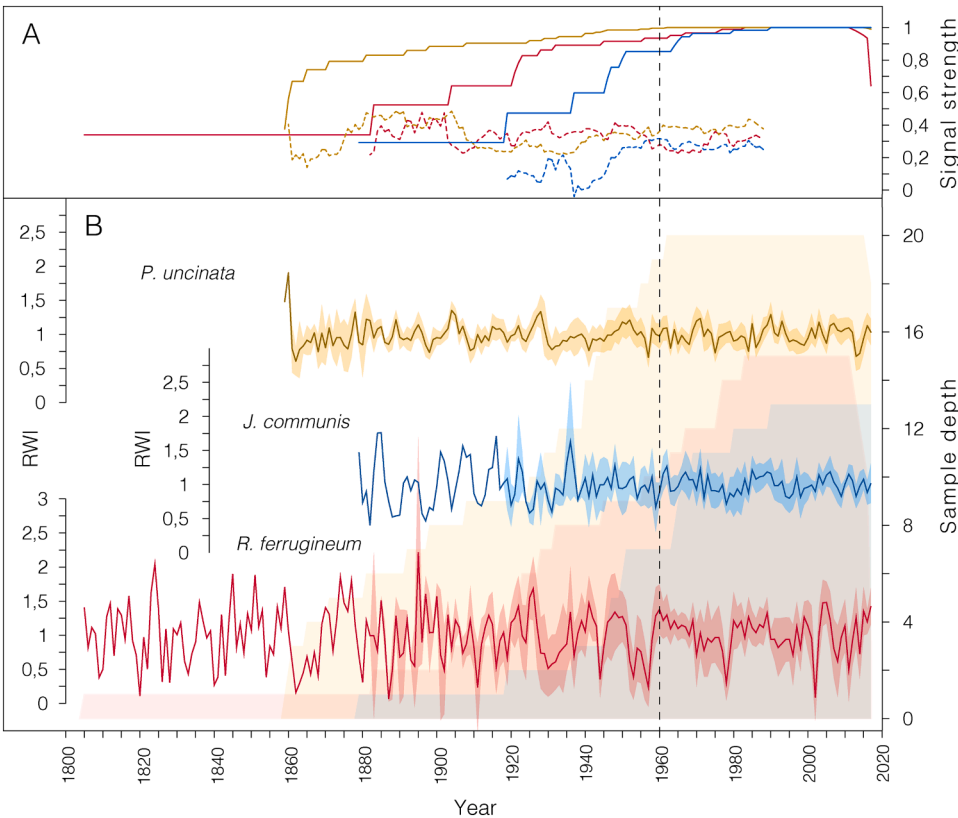


Fig. 2. Detrended *Pinus uncinata* (yellow), *Juniperus communis* (blue) and *Rhododendron ferrugineum* (red) ring-width chronologies (Panel B) with their confidence intervals (± 1 SD) and their respective subsample signal strength (SSS, solid lines) and mean inter-series correlation (rbar, dashed lines) (panel A) computed with a 30-year moving window. The vertical dashed line indicates 1960, the starting year for climate–growth analyses. Colored background surfaces represent sample depth on panel B.

positively as well with temperatures during the vegetative season (May–October), the climatic signal is clearly strongest during the warmest summer months (July and August, $r = 0.41$, $p < 0.05$). Rf also correlates positively with previous June, September and November temperatures, but is negatively influenced by current February mean temperature.

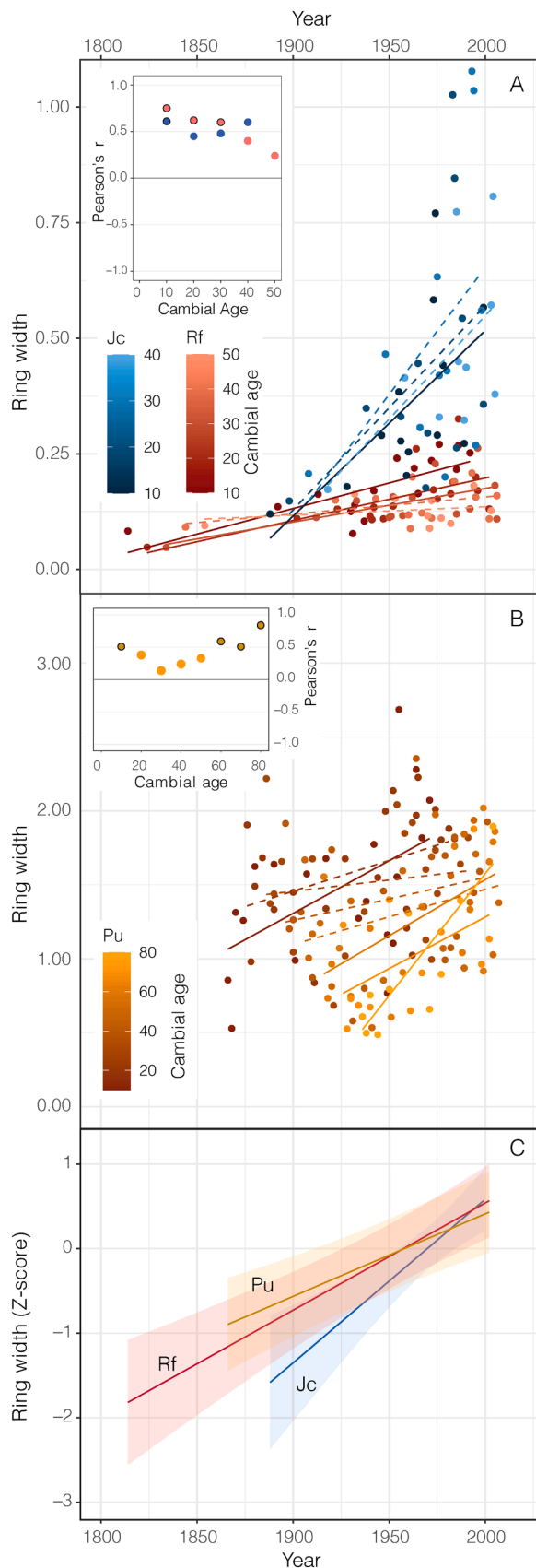
The moving-window correlations between radial growth and climate parameters show a significant change for Pu and especially for Rf since the 1990s (Fig. 5A and C). We observe a negative effect of January and February temperature on Rf, which only becomes significant from the period 1979–2008. Furthermore, correlations between winter precipitation, melt-out timing and Rf gradually change from negative to positive over the period of analysis. We observe no change in the correlation sign for Pu, but note an increasing negative effect of winter temperature and an increasing positive signal of previous year’s growing season (June–October) precipitation. In comparison, Jc shows a very strong, stable signal of the melt-out timing over the entire period (Fig. 5B), whereas correlation with growing season temperature is declining and not significant anymore since the 2000s.

4. Discussion

4.1. Chronology quality

In this study, we established two robust shrub-ring and one tree-ring chronologies to compare growth of different species from the same environment. In the case of shrubs, cross-dating was especially complex in the specific case of *J. communis* (Jc) due to its narrow, partial and missing rings as well as eccentric or lobed growth (Buras and Wilmking, 2014; Francon et al., 2017). *R. ferrugineum* (Rf) has thinner rings than Jc and *P. uncinata* (Pu) at our site. In the case of both shrub species, mean ring width is slightly higher than in those collected in the Alps (for Rf see Francon et al., 2017, 2020b; for Jc see Carrer et al., 2019). In addition, we counted 212 annual rings on one of the Rf specimens, making it the oldest dated individual of *R. ferrugineum* found so far. It exceeds the 202 years of an individual sampled in the Central Alps (Schweingruber and Poschold, 2005) and opens perspectives for multi-centennial climate reconstructions.

Yet, both shrub chronologies (1) also have high rates of rejection and (2) a lower common signal strength than Pu. The rejection rates of both shrubs chronologies are comparable or even lower than those of other studies (Carrer et al., 2019; Francon et al., 2020a). Likewise, the signal strength over the whole period is rather low in shrubs when compared to



(caption on next column)

Fig. 3. Results of the Age-Class isolation (ACI) analysis of long-term growth trends on ring-width series of *R. ferrugineum*, *J. communis* (Panel A) and *P. uncinata* (Panel B). Trends are presented for different age classes (20-years age-classes) centered on the 10-, 20-, 30- etc. cambial age. For growth trends, significant linear trends and Pearson's correlation coefficients between time and mean ring width (significance level $p < 0.05$) are indicated with solid lines and circled dots (dashed lines and simple dots if $p > 0.05$). Panel C shows linear mixed models of each species mean ring-width within 20-years age-classes as a function of the year.

trees. We speculate that this could probably be due to the low stature of shrubs and the related, stronger influence of microclimate as compared to erect trees for which mesoscale conditions play a decisive role (Francon et al., 2021; Šenfeldr et al., 2021). At our site, it seems that microsite effects are critical as chronologies were built from samples that were growing on a highly heterogeneous and rugged topography consisting primarily of scree. Nevertheless, the EPS statistic shows that all chronologies are robust for dendroecological analyses over the period 1960–2017 for which climate data is available (Wigley et al., 1984). Lower MS and higher AR1 for Pu suggest that the tree species is less sensitive to interannual climate fluctuations than shrubs. Its lower position relative to the potential tree line and higher needle longevity (Chropeňová et al., 2016) relative to Jc and Rf (Pornon and Lamaze, 2007) are potential explanations.

Strong interspecific differences in growth patterns are evidenced by the low correlations between the three chronologies, especially between Rf and Pu. The reasons for these contrasts between chronologies might be related to differences between shrubs and trees (Šenfeldr et al., 2021) on the one hand, and between conifer and broadleaf evergreen (Martínez-Vilalta et al., 2016) growth forms on the other hand. Indeed, shrubs differ from trees in how they distribute carbon between and along the stems (Blok et al., 2011; Götmark et al., 2016; Li et al., 2013; Wilmking et al., 2012) and in how they balance radial and apical growth (Myers-Smith et al., 2019). Furthermore, due to their low stature, shrubs are more directly tied to microclimatic conditions than to regional climate, which may explain the contrasting species-specific growth patterns further (Buras and Wilmking, 2014; Šenfeldr et al., 2021). Leaf longevity between the three species could also explain diverging growth patterns (Poljanšek et al., 2015). Finally, conifers also differ from evergreens in the way they use their reserves throughout the year (Martínez-Vilalta et al., 2016).

4.2. Growth trends

Our results provide clear evidence of increased secondary growth and woody biomass of two dwarf shrub and a co-occurring tree species in the French Pyrenees, at least over the 20th century, thereby supporting global observations of shrub encroachment into the tundra biome (Myers-Smith et al., 2011) and, more particularly, into the Pyrenees (Galop et al., 2011; Pasche et al., 2004). Increased growth rates for co-occurring shrubs and trees have also been reported by Šenfeldr et al. (2021) in the High Tatras and by Pellizzari et al. (2016) in the Alps. Such an increased secondary growth has previously been associated with shrub biomass accumulation and vertical growth, which eventually allows them to become dominant and encroach the landscape (Bret-Harte et al., 2002; Hallinger et al., 2010). Moreover, increased growth rates are also likely to impact tree and shrub net carbon uptake (Eldridge et al., 2011; Mekonnen et al., 2021; Peters et al., 2015), but will also affect soil carbon stocks by altering ecosystem respiration (Doche et al., 2005; Mekonnen et al., 2021) or slowing down biogeochemical cycles (Urbina et al., 2020), depending on plant traits, local climate, and soil conditions (Collins et al., 2020). In the specific case of *R. ferrugineum* and *J. communis* encroachment in the Pyrenees, Urbina et al. (2020) highlight their role in increasing carbon sequestration at the treeline ecotone.

Rising temperatures during the 20th century probably explains most

Table 2
Fixed effect coefficients (value) and Student's t values of the linear mixed-effects models predicting *R. ferrugineum*, *J. communis* and *P. uncinata* growth trends. Conditional R^2 (R^2_c), marginal R^2 (R^2_m) are given for each model. All variables are scaled. *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$) indicate the level of significance.

	<i>R. ferrugineum</i> $R^2_c=0.40$; $R^2_m=0.27$		<i>J. communis</i> $R^2_c=0.28$; R^2_m $=0.28$		<i>P. uncinata</i> $R^2_c=0.39$; $R^2_m=0.11$	
Parameter	value	t-value	value	t-value	value	t-value
Intercept	-0.03	-0.17	0.00	1.00	-0.10	6.37
Year	4.54***	5.56	3.56***	4.16	4.25***	4.60

of the increasing growth trends for all three species investigated at the study site. Global warming has been described by Šenfeldr et al. (2021) and Pellizzari et al. (2016) as the main cause of increasing radial growth trends in shrubs and trees in the Alps and High Tatras. The positive effect of increasing temperatures is also supported by climate-growth relations evidencing that growing season temperatures will positively influence radial growth year-to-year variability in all species. In addition, the observed positive effect is consistent with several studies showing a warming-triggered increase in growth of tundra shrubs both in the Arctic (Myers-Smith et al., 2015a; Tape et al., 2006) and in alpine environments (Carlson et al., 2017; Francon et al., 2017; Pellizzari et al., 2016).

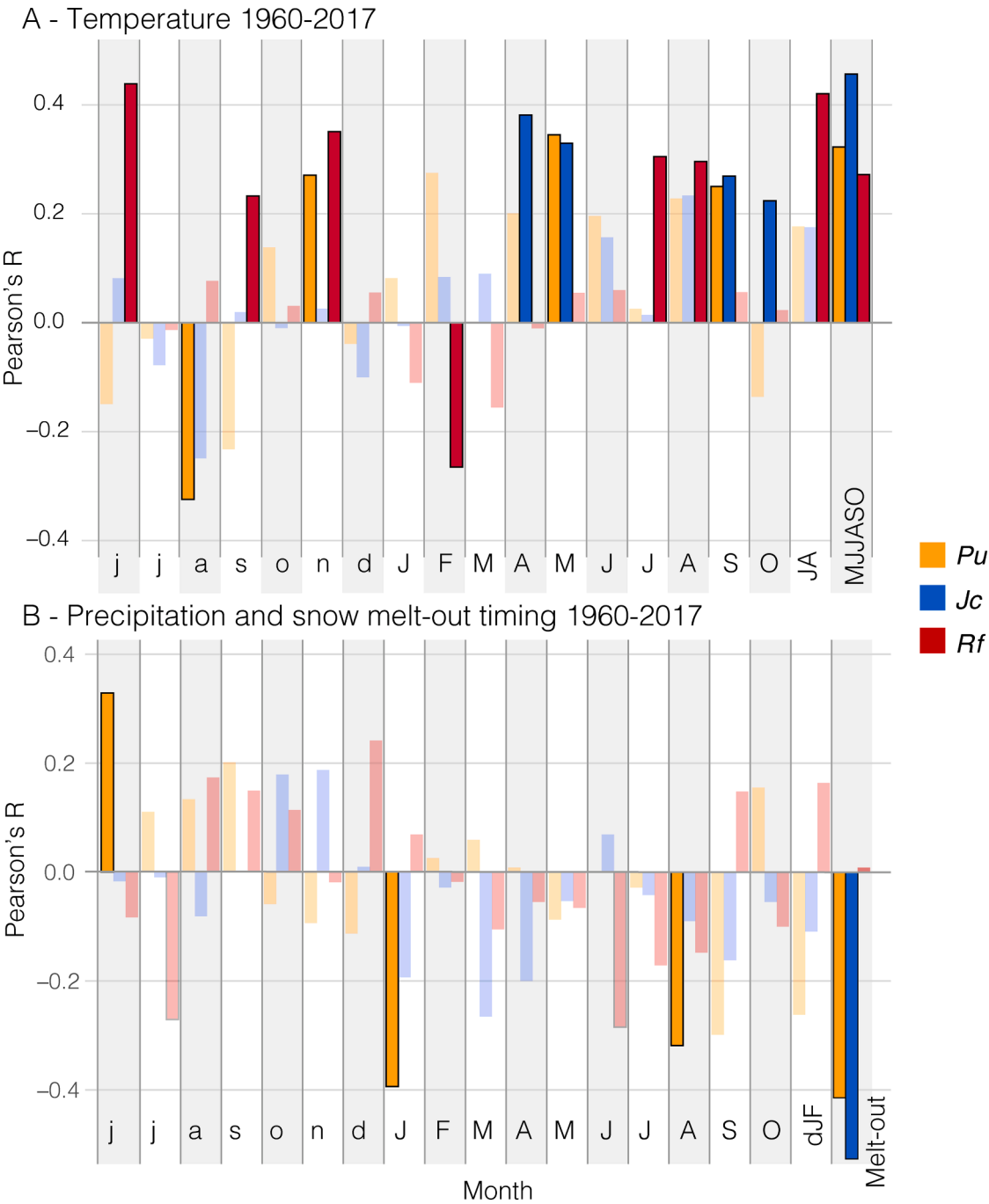


Fig. 4. Bootstrapped correlations computed between *R. ferrugineum* (Rf, red), *J. communis* (Jc, blue) and *P. uncinata* (Pu, yellow) detrended chronologies and monthly (seasonal) mean temperatures (Panel A) and precipitation sums, snow melt-out dates (Panel B) for 1960–2017. Months of the year prior to ring formation are shown with lowercase letters; current year periods are shown with capital letters.

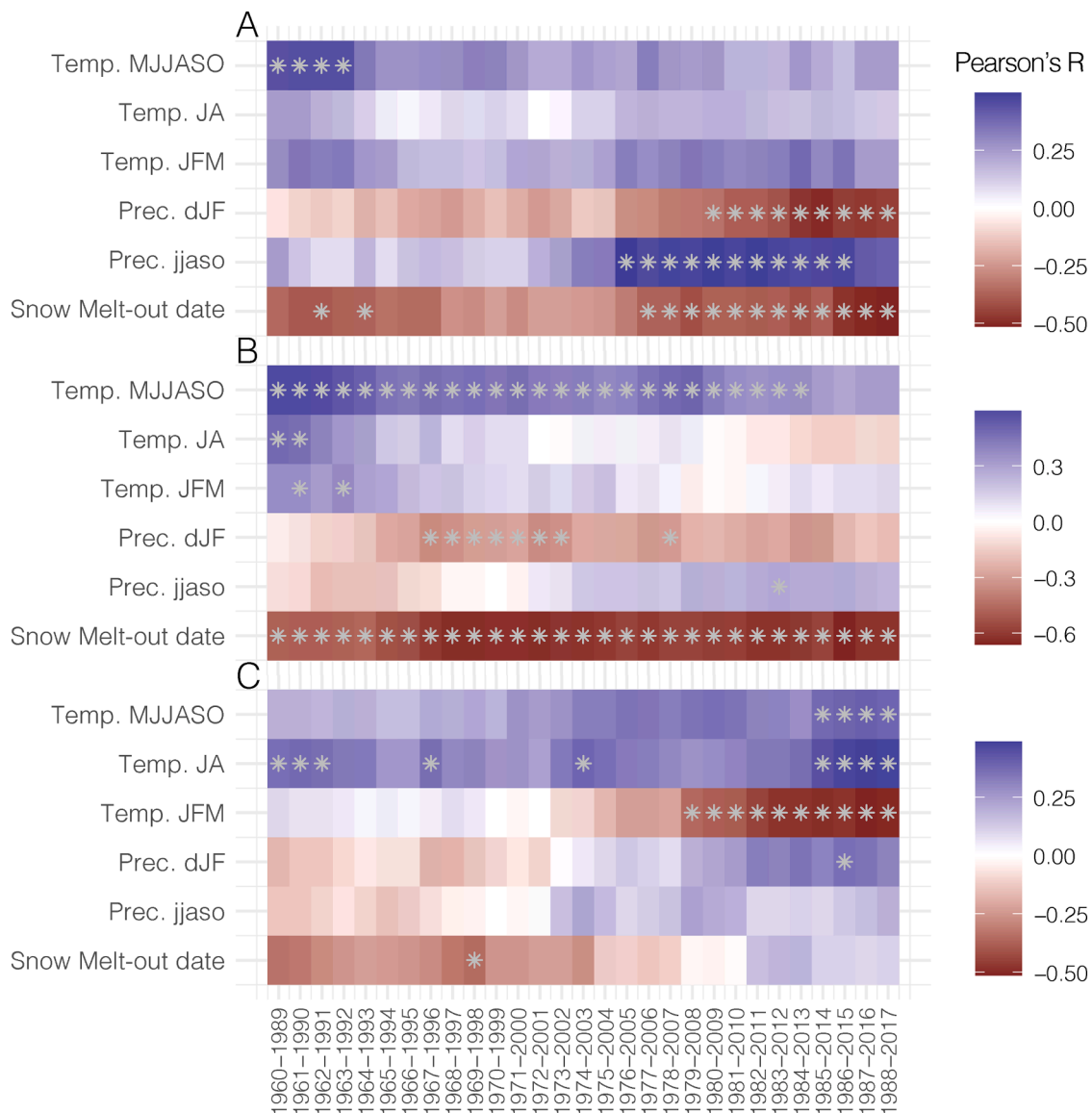


Fig. 5. Bootstrapped 30-years moving-windows correlations computed between *P. uncinata* (Panel A), *J. communis* (Panel B) and *R. ferrugineum* (Panel C) detrended chronologies and seasonal mean May–October temperature (Temp. MJJASO), July–August temperature (Temp. JA), January–March temperature (Temp. JFM), previous December–current February precipitation (Prec. dJF), previous June–October precipitation (Prec. jjaso) and snow melt-out dates. * ($p < 0.05$) indicates the level of significance.

Besides rising temperature, we also hypothesize that the growth rate increase over the last century may have been triggered by rising CO₂ concentrations and changing competition level. We tend to exclude any anthropogenic influence through land abandonment, as none of the species studied is grazed by livestock, which probably influences the establishment of woody plants (Améztegui et al., 2010; Galop et al., 2011), but not the radial growth of already established individuals (Vuorinen et al., 2022). Yet, uncertainties remain about possible changes in the level of competition between plants in a context where shrubs have been favored over herbaceous species in the past. Regarding the potential effects of CO₂ increase, some studies at high-elevation sites have shown evidence of growth stimulation of some plant species under CO₂ enrichment (Dawes et al., 2015, 2011, 2010) through increased water use efficiency (Camarero et al., 2015; Lara et al., 2020; Song et al., 2019), while other studies have not found such a growth response (Hättenschwiler and Körner, 1997; Inauen et al., 2012; Körner et al., 1997). Anadon-Rosell et al. (2018) show that CO₂ enrichment has a smaller impact on *Vaccinium myrtillus* shrub growth in the Alps than has a temperature increase. Secondly, competition for water, light and

nutrients is likely to have increased during the last century as a result of shrub and tree encroachment at the site (Pornon et al., 2000). However, higher competition levels have usually negative impacts on plant growth and productivity (Coomes and Allen, 2007; Fernández-de-Uña et al., 2017; Sánchez-Salguero et al., 2015), and thus may have rather hampered than boosted tree and shrub growth trends. Nevertheless, positive feedback loops can also occur in encroaching shrub heathlands: in fact, Doche et al. (2005) evidenced that Rf can improve edaphic and microclimatic conditions in closed heathlands, thereby promoting stem growth. Such a positive feedback loop could have promoted not only the growth of Rf at our site, but also that of co-occurring Jc, which also – like Rf – follows a colonization strategy via vegetative propagation. However, it may also have hindered the growth of Pu seedlings due to competition for light and nutrients (Angulo et al., 2019) and due to the high concentration of growth-inhibiting phenolic compounds in the leaves of Rf (Doche et al., 2005; Pellissier, 1994). Consequently, the lower growth rate prevalent in Pu (compared to Rf and Jc) could be explained by the development and closure of the shrub heath. This would also explain the low growth rates of young Pu trees (see Fig. 3B,

Angulo et al., 2019).

4.3. Shrubs and trees year-to-year climate signal

4.3.1. Temperature signal

For the first time we compare the climatic response of Jc, Rf and Pu coexisting at the same site. In general, the year-to-year response of these shrub and tree species to climate is clearly positive and reflective of effect of increasing temperatures and/or growing season length on radial growth. This finding agrees with large-scale studies on the climate sensitivity of shrubs in the Arctic (Myers-Smith et al., 2015a), but also a large body of literature focused on the response of the three species to climate change in the Alps and Pyrenees (Büntgen et al., 2008; Carrer et al., 2019; Galván et al., 2015; Francon et al., 2021; Pellizzari et al., 2014). More generally, our results are in line with numerous studies from Arctic and alpine environments showing that the accumulation of positive daily temperatures is indeed a key factor driving growth through cell division and differentiation (Hoch, 2015; Körner, 2003; Wheeler et al., 2016; Wipf, 2010) and phenological transitions (Kudo and Suzuki, 1999; Molau et al., 2005).

Jc and Pu respond positively to warmer than average September temperature (and October in the case of Jc), but not in July and August. A comparable signal was detected by Galván et al. (2015) for Pu in the Pyrenees and by García-Cervigón et al. (2018) for *Juniperus sabina* in the southeastern Sierra Nevada, Spain. The latter authors interpret this signal as an evidence for the shrubs' ability to benefit from an extension of the growing seasons beyond the meteorological summer for wood formation. We find that Rf shows a different climate sensitivity than the two conifers. The vegetative season signal is concentrated over the warmest summer months (July and August). This result is consistent with dendroecological studies realized with several alpine *Rhododendron* sp. (Francon et al., 2020a; Liang and Eckstein, 2009) and Arctic dwarf shrub species such like *Salix* sp., *Betula* sp., *Alnus* sp., or *Empetrum nigrum* (Forbes et al., 2010; Myers-Smith et al., 2015a). In addition, we find positive effects of above-average temperatures during the growing season of the year preceding ring formation, possibly leading to high photosynthetic rates in the year prior to ring formation. This could then lead to high carbon storage and thus increased growth in the following year (Babst et al., 2012; Fritts, 1976). Moreover, while summer temperature-growth relations have remained quite stable for Rf since the 1960s, we observe a gradual loss in temperature sensitivity in the case of the two conifers. This can probably be explained by an increasing moisture limitation driven by the temperature increase in recent decades, in line with a previous study showing the importance of summer drought as a new limiting factor of pine growth in the Pyrenees (Galván et al., 2015). The increasingly positive effect of previous year precipitation for Pu and Jc supports this hypothesis. Comparable shifts in the limiting factor from temperature to moisture availability for tree and shrub growth were observed at several sites in cold environments (D'Arrigo et al., 2008; Francon et al., 2020; Jochner et al., 2018; Juday et al., 2015).

4.3.2. Snowpack signal

We found a prominent snow melt-out timing signal in ring width variability of Jc and to a lesser extent also of Pu. Moreover, the signal is stable, even in recent years, despite the recent trend towards earlier melt-out dates. This result is consistent with dendroecological studies on Jc in the Alps (Carrer et al., 2019) and Pu in the Pyrenees (Sanmiguel-Valladolid et al., 2019) but also in line with findings for other tree (see Franke et al., 2017; Kirilyanov et al., 2003; Vaganov et al., 1999) or shrub species (Francon et al., 2020a; Schmidt et al., 2010). Whereas Carrer et al. (2019) show a spatially consistent and temporally stable winter snowpack signal in Jc, Sanmiguel-Valladolid et al. (2019) evidence that the effect of snowpack might depend on topoclimate in the specific case of Pu. Delayed melt-out timing in late spring and early summer, when air temperature and photoperiod peak – by decisively

shortening the growing season – has strong effects on growing degree days and eventually on shrub or tree cambial initiation, cell division and growth (Carrer et al., 2019; Francon et al., 2020a; Franke et al., 2017; Hoch, 2015; Kirilyanov et al., 2003; Schmidt et al., 2010; Vaganov et al., 1999; Wheeler et al., 2016). Finally, we interpret the May temperature signal, also found at our site for Jc and Pu, by the rushing effect of higher spring temperatures on melt-out dates (Carrer et al., 2019; Durand et al., 1999; Francon et al., 2017; Klein et al., 2016). However, as a tree species, Pu has vegetative parts that are not covered by snow in winter (unlike Jc). Therefore, potentially increased cambial activity remains possible as a direct response to warm temperatures in May in addition to the effect of snow (Galván et al., 2014; Tardif et al., 2003).

In contrast to Jc and Pu, Rf shows no significant correlation with winter precipitation and snow melt-out timing. Similarly, the sensitivity of Rf to climate shifts towards more negative effects of warming and less snowy winters, which have become more frequent since the 1990s due to global change. This absence of snowpack sensitivity observed at Bassiès contrasts with the response of Rf individuals sampled above the treeline but are in line with Rf responses observed at comparable elevations (1800 m asl) in the Alps (Francon et al., 2020a). Rf is a species that lives at sites characterized by deep, long-lasting winter snowpack, which protects the plant from late frost, winter drought and irradiation (Gracia et al., 2007; Larcher and Wagner, 2004). Increasingly negative impacts of decreasing snowpack on Rf have also been found in response to climate change in the Alps (Francon et al., 2021; Francon et al., 2020ab). In the latter studies, Rf growth is reported to be negatively affected if melt-out dates occur too early in spring, which in our case could have offset the positive effect of extending growing season length. In addition, the negative response of Rf growth to February temperature is likely an indirect effect of winter temperature on Rf growth through changes in snowpack properties. One interpretation of this result could be that warmer temperature episodes in winter will lead to snow melt which in turn would reduce the insulating properties of the snowpack (Domine et al., 2016) and hence exacerbate hazardous frost events in winter and spring (Choler, 2015; Jonas et al., 2008).

5. Conclusions

This study represents the first dendroecological investigation comparing *R. ferrugineum* and *J. communis*. The two most widespread shrub species in the high mountains of Western Europe are studied together and compared with *P. uncinata* trees growing nearby. Overall, our results show that all species have increased their wood productivity over the last century, probably in response to increasing temperatures during the growing season, as shown by year-to-year climate-growth relations. Specifically, we hypothesize that shrubs appearance could have been favored more by global warming than that of trees due to positive feedback loops favoring them over trees in closed subalpine heathlands. At the interannual scale, shrubs show a stronger response to summer temperature than trees. Nevertheless, the two shrub species differ quite strongly in their response to climate, especially to snow melt-out dates, confirming the results of previous dendroecological studies in the European Alps (Carrer et al., 2019; Francon et al., 2020a).

In contrast to *J. communis*, *R. ferrugineum* seems to be increasingly negatively affected by the acceleration of climate change observed since the 1990s and the resulting impacts on snowpack characteristics and melt-out dates. These results are consistent with the non-linear relationships observed between *R. ferrugineum* growth and snowpack duration in the Alps since the 1990s (Francon et al., 2021). The effects of this shifting climate sensitivity of *R. ferrugineum* have not yet influenced growth trends of the species (mainly driven by summer temperature rather than a snowpack decrease), but could reflect a transitory state and affect growth trends in the future. Further investigation of shrub and tree growth trends using a more extensive sample size with the aim of exploring diverging growth trends would be a valuable research question to explore in future studies.

Supplementary material

Fig. S1: Snow melt-out dates (in day of year, D.O.Y.) evolution since 1959 at our study site in the Bassiès valley. A spline function was fitted to the data to represent the decadal trend (grey line).

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.

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Supplementary materials

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