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L. Francon[1*], C. Corona[1], I. Till-Bottraud[1], P. Choler[2], B. Carlson[3], G. Charrier[4,5], T. Améglio[4,5], S. Morin[6], N. Eckert[7], E. Roussel[1], J. Lopez-Saez[8], M. Stoffel[8,9,10]

[1]Université Clermont Auvergne, CNRS, Geolab, F-63000 Clermont-Ferrand, France
[2] Université Grenoble Alpes, Université Savoie Mont-Blanc, CNRS, LECA, F-38000 Grenoble, France
[3] Centre de Recherches sur les Ecosystèmes d'Altitude (CREA), Observatoire du Mont-Blanc, 74400 Chamonix, France
[4] Université Clermont Auvergne, F-63000 Clermont-Ferrand, France
[5] INRA, PIAF, F-63000 Clermont-Ferrand, France
[6] Météo-France – CNRS, CNRM UMR 3589, Centre d'Études de la Neige, Grenoble, France
[7] Université Grenoble Alpes, Irstea, UR ETGR, F-38000 Grenoble, France
[8] Climate Change Impacts and Risks in the Anthropocene (C-CIA), Institute for Environmental Sciences, University of Geneva, Geneva, Switzerland.
[9] Department of Earth Sciences, University of Geneva, Geneva, Switzerland.
[10] Department F.-A. Forel for Environmental and Aquatic Sciences, University of Geneva, Geneva, Switzerland.
*Contact information: loic.francon@etu.uca.fr

Abstract

Enhanced shrub growth in a warming alpine climate has potential far-reaching implications, including soil nutrient cycling, carbon storage, or water and surface energy exchanges. Growth ring analysis can yield mid- to long-term, annually resolved records of shrub growth, and thereby offer valuable insights into how growth is driven by interannual climate variability. In the European Alps, dendroecological approaches have shown that dwarf shrub productivity is influenced by interannual variations of growing season temperature but results also point to a negative effect of winter precipitation on radial growth. However, as past work lacked snow cover data, links between snow cover duration, growing season length, energy availability and inter-annual shrub growth remain poorly understood.

In this paper, we combined multi-decadal shrub-ring series from 49 individuals sampled at three sites along a 600-m elevational gradient in the Taillefer massif, located in the French Alps to assess growth sensitivity of long-lived and widespread *Rhododendron ferrugineum* shrubs to

both snow cover dynamics and temperature changes. To this end, we computed structural equation models to track the response of shrub radial growth to extending growing season at 1800, 2000 and 2400 m above sea level and for two time periods (i.e. 1959-1988 and 1989-2016). The second period is marked by a significant advance in snow melt-out resulting in a regime shift highlighted at the end of the 1980s by a breakpoint analysis.

At the high-elevation site, our results demonstrate a positive effect of increasing growing season length on shrub growth, which is strongly dependent on snowpack depth and snow cover duration. Conversely, at lower elevations, earlier melt-out dates and associated late frost exposure are shown to lead to radial growth reduction. Moreover, the climate signal in ring-width chronologies of *R. ferrugineum* portrays a weakening since 1988 – similar to a phenomenon observed in series from circumpolar and alpine tree-ring sites and referred to as "divergence".

By analyzing long-term records of radial growth along an elevation gradient, our work provides novel insights into the complex responses of shrub growth to climate change in alpine environments. This paper demonstrates that *R. ferrugineum*, as a dominant alpine shrub species, behave as an ecological indicator of the response of alpine ecosystem to global warming.

Keywords

dendrochronology; dendroecology; shrub expansion; dwarf shrubs; *Rhododendron ferrugineum*; Structural Equation Model; divergence; elevation gradient; frost; snow cover

Introduction

Temperatures in Arctic and Alpine regions have been increasing twice as fast as the global average over the last decades (Stocker et al., 2013), with potential far-reaching consequences for ecosystem functioning due to feedbacks between vegetation and climate (Bjorkman et al., 2018, 2020; Pearson et al., 2013). Rapid climate warming is also driving changes in the structure and composition of cold ecosystems and has been associated with changes in plant

phenology, diversity and richness (Boscutti et al., 2018; Grabherr et al., 1994; Myers-Smith et al., 2019; Steinbauer et al., 2018), poleward and upslope shifts in species geographic distribution (Chen et al., 2011; Elsen and Tingley, 2015; Lenoir et al., 2008; Parmesan and Yohe, 2003; Walther et al., 2002) and thermophilization (Dolezal et al., 2016; Elmendorf et al., 2015; Gottfried et al., 2012). At high-latitude sites, increasing vegetation productivity (Pearson et al., 2013) associated with a widespread shrub expansion (Elmendorf et al., 2015; Sturm et al., 2001; Tape et al., 2006) has resulted in a greening trend, characterized by increasing canopy cover, height, abundance, and biomass (Forbes et al., 2010; Hollesen et al., 2015; Myers-Smith et al., 2011, 2015a, 2020). Conversion of tundra to shrubland is driven by ongoing warming, and modulated by soil moisture (Ackerman et al., 2017; Elmendorf et al., 2012), but also by changes in snow cover duration (Gamm et al., 2018; Niittynen et al., 2018; Weijers et al., 2018a; Young et al., 2016). Recent warming and related shrubification (i.e. increasing shrub cover and biomass) in Arctic systems has also been shown to drive climate feedbacks, for instance by altering surface albedo, energy, water balance, or permafrost (Blok et al., 2011; Chapin, 2005; Liston et al., 2002; Sturm et al., 2001). Although comparable changes can be expected at high altitudes, shrubification has hitherto received very little consideration in temperate mountain systems.

In the European Alps, documentation of upslope advancement of shrub species remains scarce and spatially limited (Anthelme et al., 2007; Cannone et al., 2007; Dullinger et al., 2003; Malfasi and Cannone, 2020). At the regional scale, Carlson et al., (2017) provided remote sensing-based evidence linking the observed greening of alpine vegetation (increased productivity) to increasing air temperatures and decreasing snow cover duration. Snow manipulation experiments, designed to simulate the expected advance of melt-out dates in a warmer climate (Gerdol et al., 2013; Rixen et al., 2010; Wipf and Rixen, 2010) confirm the strong control of snowpack duration on shrub phenology and growth via indirect effects on soil

temperature, nutrient availability and frost exposure. Despite the indisputable value of these studies to improve understanding of climate–growth linkages, experimental studies typically cover relatively short periods (1-2 years; Wipf and Rixen, 2010) and cannot capture longer-term shrub growth responses to climate change.

By contrast, growth-ring analyses have the potential to provide uninterrupted mid- to long-term, annually-resolved records of shrub growth, thereby revealing responses to interannual climate variability (Bär et al., 2006; Buchwal et al., 2013; Forbes et al., 2010; Hantemirov et al., 2000; Hollesen et al., 2015; Weijers et al., 2010; Young et al., 2016 and Myers-Smith et al., 2015b for an exhaustive review). Still underused in high-altitude environments, the limited number of existing dendroecological studies tends to confirm that dwarf shrub productivity is influenced by interannual variations of growing season temperature (Francon et al., 2017; Franklin, 2013; Liang et al., 2012; Liang and Eckstein, 2009; Lu et al., 2015; Pellizzari et al., 2014). In the Alps, initial results point to a negative effect of winter precipitation on the radial growth of shrubs (Carrer et al., 2019; Francon et al., 2017; Pellizzari et al., 2014; Rixen et al., 2010), a phenomenon that has been observed only rarely in circum-Arctic tundra ecosystems (Bär et al., 2008; Hallinger et al., 2010; Ropars et al., 2015; Zalatan and Gajewski, 2006; but see Schmidt et al., 2010, who found snow to correlate negatively with *Salix arctica* growth). Several hypotheses have been proposed to explain this phenomenon, such as the detrimental effect of late-persisting snow on the onset of cambial activity, growing season length or soil temperatures (Pellizzari et al., 2014). In the Alps, the positive effects of longer and warmer growing seasons could be offset by the negative effect of increased late-frost exposure due to earlier melt-out dates (Jonas et al., 2008; Rixen et al., 2012). Most of the previous dendroecological studies, however, relied on monthly-resolved meteorological time series and lacked snow cover data, thereby precluding a precise assessment of the relationships between snow cover duration, growing season length and energy availability during the snow free period. In addition, in the

Alps, existing dendroecological studies addressing the sensitivity of shrubs to climate have largely ignored the role of topography, and even more so changes along elevational gradients. We argue that by ignoring the impact of changes in snow cover alongside temperature at different elevations, shrub ring–climate studies focusing on plant growth in temperate mountain ecosystems will likely dismiss an obvious mechanistic pathway, which could potentially regulate shrub growth in response to winter snow accumulation. This knowledge gap is particularly pressing given the wealth of studies documenting a warming-induced decrease of snow cover duration in temperate alpine regions of North America (Mote et al., 2005) and Europe (Beniston et al., 2018; Hantel et al., 2000, 2012; López-Moreno, 2005). Ongoing and future climate change will likely accelerate warming, but also favor earlier melt-out dates and decreased snowpack depths at altitudes comprised between 1500 and 3000 m above sea level (asl; Beniston et al., 2018; Marty et al., 2017; Steger et al., 2013; Verfaillie et al., 2018).

Here, we investigate long-term relationships between snow cover dynamics and the growth of *Rhododendron ferrugineum* in the Taillefer massif where shrub growth is expected to be influenced by snow cover dynamics (Francon et al., 2017) and where plants are likely to be vulnerable to climate change. We use individuals sampled at three sites along a 600-m elevational gradient. In order to test the hypothesis that shrub growth is directly positively influenced by the accumulation of degree days received after the snow melt-out date (SFGDD), we (i) developed multidecadal shrub-ring series from long-lived *Rhododendron ferrugineum* individuals; (ii) evaluated recent climatic trends in atmospheric temperature, snow cover and SFGDD obtained from a locally calibrated meteorological model, specifically designed for the mountain environment and spanning the period 1958-2016 (Durand et al., 2009a, 2009b) and (iii) investigate climate–growth relationships using structural equation models (SEMs) designed to disentangle the effects of the above-mentioned climate variables on radial growth.

We computed SEMs for the periods 1959-1988 and 1989-2016 to test for the potential change in shrub sensitivity to climatic drivers in the context of recent climate changes.

Material and methods

Study species

Rhododendron ferrugineum L. is the dominant mountain shrub of the subalpine belt in the siliceous Alps (Ozenda, 1985). It is distributed from about 1600 to 2500 m asl, where it can form large heathlands or grow in localized patches (Escaravage et al., 1997). The high local abundance of the species can be attributed to complementary sexual and vegetative reproductive strategies (Doche et al., 2005) which enable *R. ferrugineum* to outcompete other plants (Pornon and Doche, 1996) and to reach a 90–100% cover after 150–250 years (Pornon and Doche, 1995). *R. ferrugineum* provides an ideal model to study the long-term effects of climate on radial growth due to its high longevity, estimated to be up to three centuries (Escaravage et al., 1998), as well as its clearly identifiable annual rings discriminated by a band of radially aligned, thick walled latewood fibers, flattened along the ring boundary (Francon et al., 2017).

Study area

The study area is situated in the northern French Alps (Fig. 1), on a northwest-facing slope in the Taillefer massif. At Taillefer, *R. ferrugineum* is the dominant species (80–100% cover) of above-treeline dwarf shrub heathlands. The species developed on abandoned pastures between 1900 and 2100 m asl and is intermixed with *Sorbus* sp. and *Vaccinium* sp. along with scattered *Picea abies* and *Pinus uncinata* trees. Beyond this altitude, heathlands become more fragmented and are mixed with patches of alpine meadows and scree. Isolated patches of *R. ferrugineum* are observed up to ~2500 m asl. Shrub individuals were sampled along an elevational gradient,

157 at three sites located at (i) 1800-1850 m (SAL1800), (ii) 1950-2050 m (SAL2000) and (iii)
158 2300-2500 m asl (CN2400). SAL1800 and SAL2000 are located at the Côte des Salières (SAL,
159 45°02′N, 5°52′E, Fig. 1) on a northwest-facing slope with slope angles ranging from 23° to 33°.
160 CN2400 is located in the Combe Nord (3 km east of SAL, 45°02′N, 5°55′E, Fig. 1) on a north-
161 facing slope (25°). At SAL1800 and SAL2000, bedrock consists of amphibolite and gneissic
162 gabbro (Doche et al., 2005). SAL1800 and SAL2000 heathlands have developed on stony,
163 ochre-brown humic acidic soils (Pornon et al., 1997). At CN2400, *R. ferrugineum* individuals
164 grow on shallow and discontinuous soils developed on talus slopes and weathered rock
165 outcrops.

166 Climate of the Taillefer massif reflects a transition between the wet oceanic Pre-Alps
167 (Chartreuse, Vercors) and the intra-alpine Oisans massif, with the latter being characterized by
168 a more continental climate with drier summers (Pautou et al., 1992). Daily reanalysis from the
169 SAFRAN meteorological system (Durand et al., 2009a) was used to characterize climatic
170 conditions along the elevational gradient (Fig. 1B). Over the period 1959-2016, mean annual
171 air temperatures were 4.2°C, 3.3°C, and 1.4°C at SAL1800, SAL2000 and CN2400,
172 respectively. The melt-out date occurred on average on May 2 at 1800 m asl, and roughly one
173 month later at 2400 m asl (June 6).

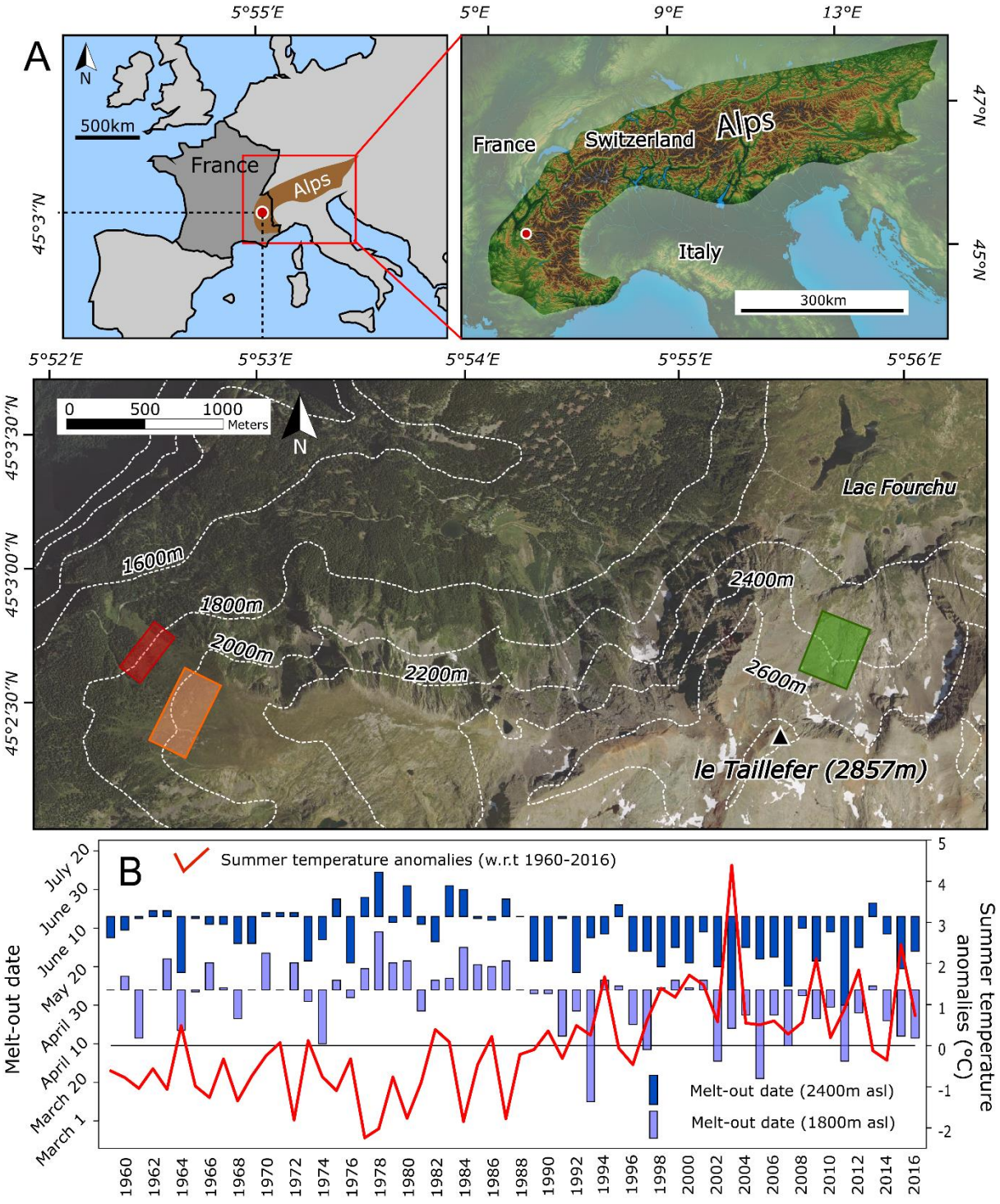

Figure 1: (A) Location of the study sites, Côte des Salières (SAL1800, red; SAL2000, orange) and Combe Nord (CN2400, green) in the Taillefer massif (French Alps). (B) Summer (May-August) temperature anomalies (1959-2016) as well as melt-out dates at 1800 (light blue) and 2400 m asl (dark blue) for the 1959-2017 period. Meteorological data were extracted from the SAFRAN-Crocus re-analysis datasets (Durand et al., 2009a, 2009b).

Sample collection and preparation

A total of 80 randomly selected *R. ferrugineum* individuals were sampled at the three sites: 36 at SAL2000 in October 2015, 17 at SAL1800, and 27 at CN2400 in October 2016. Individuals were sampled at a minimum distance of four meters from each other to avoid the sampling of the same clone (Escaravage et al., 1998). Locations were recorded with metric precision using a Trimble GeoExplorer GNSS (Global Navigation Satellite System) unit. Three to six wood sections were cut per individual on the main stems, starting at the root collar and then every 10-20 cm to the stem extremity. This approach was used in order to apply the serial-sectioning method, consisting of repeated growth-ring width measurements and cross dating at the intra-stem level (Kolishchuk, 1990).

To ensure precise detection of all rings, 20 µm thick cross sections were prepared from each sample using a slide microtome. Cross sections were then stained using Safranin and Astra Blue, and permanently fixed on microslides with Canada balsam (Schweingruber et al., 2011). High-resolution digital pictures were taken using a Carl Zeiss Axio Observer Z1 coupled to a Zeiss AxioCam MR R3 camera under 40–100 magnification. Individual images were merged automatically to cover the whole cross-sections by using the Zen 2011 software.

Crossdating and chronology development

Width of individual growth rings were measured from digital images with CooRecorder 7.6 (CYBIS Elektonik & Data AB) along three radii of the cross-sections to detect wedging rings. Radial measurements along the chosen radii were supplemented by careful visual inspection of each cross section to eliminate annual growth underestimation caused by partially missing rings. Cross-dating was based on a three-step procedure involving a comparison of growth curves (i) between three radii measured within a single cross section, (ii) among the mean growth curves of all sections within individual plants, and finally (iii) between the mean growth

curves of all shrubs of a given site. The output of visual crossdating was statistically checked with COFECHA (Holmes, 1994).

After cross-dating, each individual mean series was standardized (Cook and Kairiukstis, 1990; Fritts, 1976) with a double-detrending process in ARSTAN (Cook, 1987). We first selected a negative exponential function to eliminate non-climatic trends (e.g. age-related growth trend and other potential biological effects) referred to as Neg-Exp chronologies. In addition, we fitted a cubic smoothing spline, preserving 50% of the variance at a wave-length of 32 years so as to remove the effect of localized disturbance events (Cook and Peters, 1981) hereafter referred to as detrended chronologies. In both approaches, outputs referred as growth indices were averaged by year using a bi-weighted robust mean aimed at reducing the influence of outliers and at developing mean standardized site chronologies (Cook and Peters, 1981). The resulting growth indices are referred to as ring-width indices (RWI).

Several descriptive statistics were then applied to detrended chronologies using the *dplR* package, including standard deviation (SD), first-order autocorrelation (AC), mean sensitivity (MS), mean inter-series correlation (Rbar), and expressed population signal (EPS; Bunn, 2008) in R 3.3.2 (R Core Team, 2016). Running Rbar and EPS were computed at each site using a 30-year moving window with a 29-year overlap to illustrate changes in the strength of common patterns of radial growth over time. We used the commonly applied quality threshold of EPS $\geq$ 0.85 to determine the reliability of our chronologies. As shrubs may potentially retain climate-driven, low frequency variations in the raw data (decadal growth variations), Neg-Exp chronologies were used to detect potential impacts of decadal-scale climatic fluctuations on radial growth. Indices from the double-detrending procedure were used for climate-growth correlations and climate-growth modeling in relation to high-frequency (interannual) growth variations.

Meteorological series

At each plot, daily meteorological and snow time series were obtained from the SAFRAN-Crocus coupled snowpack-atmosphere model. The SAFRAN reanalysis combines *in-situ* meteorological observations with synoptic-scale meteorological fields to provide continuous time series of meteorological variables at hourly resolution and for elevation bands of 300 m within areas, referred to as "massifs" (Oisans in the case of this study), assumed to be horizontally homogenous (Durand et al., 2009a). The dataset extends back to 1958. SAFRAN meteorological fields are used to drive a land surface model, the ISBA-Crocus soil and snowpack model. This tool provides corresponding reanalysis of snow conditions and underlying ground temperature for the same time span as SAFRAN reanalysis (Durand et al., 2009b; Vionnet et al., 2012). To quantify ground temperature, we extracted values for the uppermost soil layer with a thickness of 1 cm.

SAFRAN meteorological fields corresponding to the sampling sites were extracted according to their elevation, aspect, and slope angles (Lafaysse et al., 2013). Meteorological data were interpolated from the neighboring 300-m elevation bands, and incoming shortwave radiation data was adjusted by using the prevailing aspect and slope angle. The ISBA-Crocus models runs were performed specifically for the sites. Vegetation was represented in a simplified manner in the simulations, assuming grassy conditions so as to simulate typical snow conditions and underlying ground temperature for open areas, therefore neglecting small-scale interactions between vegetation, topography, and snowpack. We then extracted hourly air temperature and precipitation sums as well as daily snow depth and uppermost ground layer temperatures (6:00 UTC) for the period 1959-2017. The data were carefully visually checked to detect extreme temperature events that could be linked with marked growth reduction. Monthly minimum, mean, and maximum air temperature, monthly precipitation sums, snow depth, and duration, melt-out date, sum of snow-free growing degree days (SFGDD) and daily uppermost ground

254 layer temperature series were computed from the same datasets. The snow melt-out date was
255 defined as the last day when snow cover reached the mean height of the shrub canopy at *c.* 50
256 cm for SAL1800 and SAL2000, and at *c.* 30 cm for CN2400. SFGDD were calculated for
257 periods with snow-free ground and daily air mean temperatures above zero degrees. SFGDD
258 series were calculated from melt-out date to August 31.
259 Given that previous work identified a shift toward earlier snow melt-out in the study region
260 occurring during the late 1980s (Dedieu et al., 2016); we applied a breakpoint analysis to the
261 time-series of melt-out dates. This preliminary analysis points to a significant tipping point in
262 1988, which is consistent with regional-scale studies (Reid et al., 2016). At 2400 m asl, the
263 melt-out date thus advanced on average from June 14 (1959-1988) to May 28 (1989-2016). At
264 the same time, mean May temperatures increased from 1.7°C to 3.5°C. At 1800/2000m, a shift
265 of 19 days is observed for the melt-out date and an increase of 25% in SFGDD is observed. As
266 a consequence, climate-growth analyses were systematically performed separately for the
267 subperiods 1959-1988 and 1989-2016.

268 *Statistical analysis of climate-growth relationships*

269 Structural Equation Models (SEMs, Grace, 2006; Kline, 2011) enable (i) decomposition of total
270 effects into direct and indirect types, and (ii) comparison of alternative models using indices of
271 goodness of fit (Kline, 2011; Mitchell, 1992). SEMs have been used in previous ecological
272 studies to investigate e.g. the impacts of shrub expansion on species richness and plant diversity
273 (Boscutti et al., 2018), the relation between climate and mountain plant productivity (Choler,
274 2015; Jonas et al., 2008; Madrigal-González et al., 2017, 2018) or the relation between tree-
275 ring width and sea surface temperature in Mexican dry forests (Brienen et al., 2010). Although
276 SEMs have been used quite rarely in dendroecology to date, they can indeed improve our
277 understanding of the concurrent effects that snow cover climatic variables have on growth. The
278 following two-step procedure was used to build models for each site: (Fig. 2):

(i) bootstrapped correlation functions (BCFs) between the detrended chronologies, mean monthly air temperature (°C), monthly precipitation sums (mm), melt-out dates, and SFGDD series were computed with the *Treeclim* package (Zang and Biondi, 2015) in R (R Core Team, 2016) to identify climate variables that are significantly correlated ($P< 0.05$) with radial growth. To identify direct and indirect drivers of radial growth, we also computed partial correlation functions (PCFs); and

(ii) SEMs were developed with the "*Lavaan*" package (Rosseel, 2012) in R. The structure of the hypothetical SEM path structure (see Fig. 2) requires the incorporation of available *a priori* knowledge (Pérez-de-Lis et al., 2016). In this study, direct effects are given as standardized path or partial regression coefficients. According to the hypothesis formulated in the introduction, we considered SFGDD as a direct driver of radial growth, while melt-out timing was incorporated as an indirect parameter through its mediating effect on growing season length. The latter parameters formed the backbone of the SEMs at each site, while additional climatic variables significantly correlated ($p<0.05$) with radial growth (steps 1-2) were added as explanatory variables. To derive comparable estimates, we standardized all quantitative predictors to a mean of zero and to a standard deviation of one. To prevent any effect of multicollinearity among explanatory variables, we used variance inflation factors (VIF). Collinearity was assessed with a cut-off value of 3 (Zuur et al., 2010). To compare the competing models, each model was first evaluated with the Akaike Information Criterion (AIC, Akaike, 1981) for which lower values correspond to more parsimonious models. We thereafter employed the Chi-square (χ^2) difference statistic to control the overall fit and to verify whether the model was consistent with the data covariance matrix (p cut-off ≥ 0.05) (Kline, 2011). In addition, we computed the CFI (Comparative Fit Index, Bentler, 1990) with a CFI cut-off $\geq$ 0.90. Assumptions of normality and homogeneity of variance were controlled for every

endogenous variable in the SEMs using qq-plots and standardized residuals vs. fitted values plots (see Fig. S1 in supplementary material).

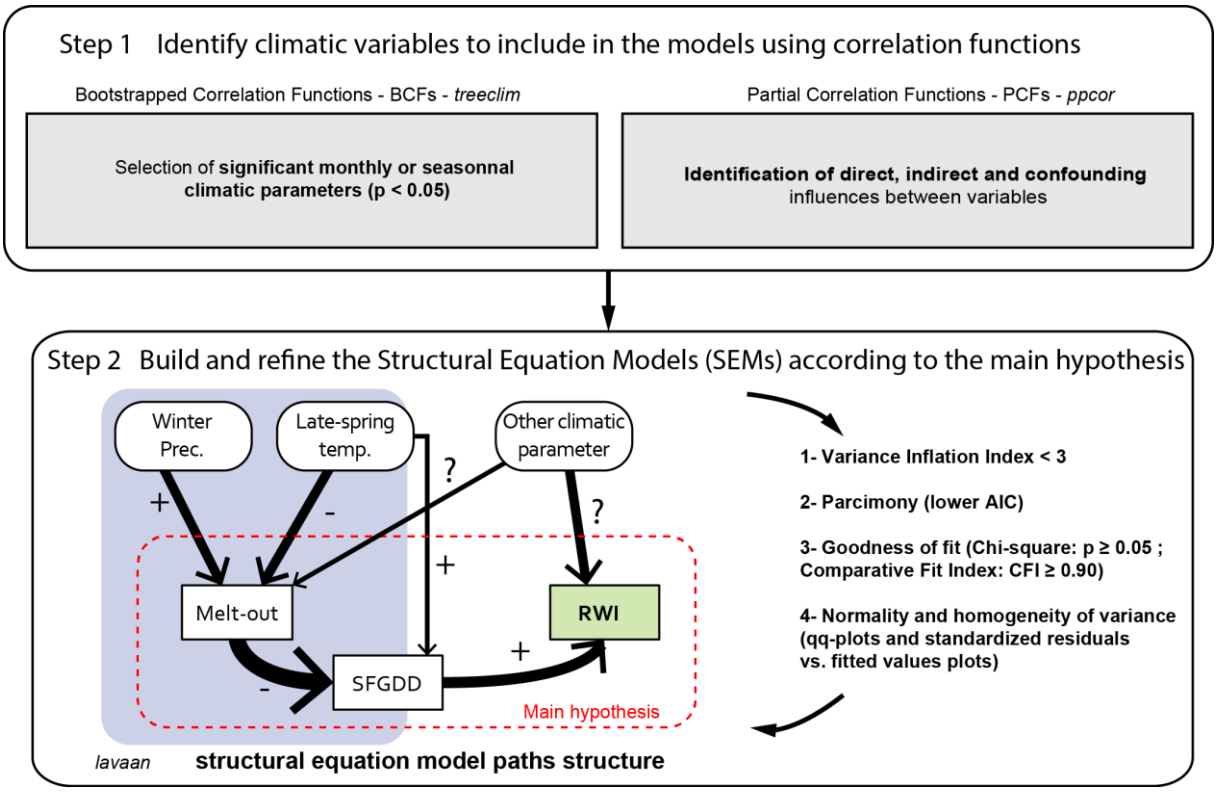

Figure 2: Diagram of the 2-step procedure adopted for the development of the Structural Equation Models (SEMs). First (step 1), Bootstrapped Correlation Functions (BCFs) are used to identify climatic variables that potentially have a direct or indirect effect on Ring-Width Indices (RWI) at the monthly or seasonal scales. Relationships with SFGDD and Melt-out dates were also tested. Climatic variables were then tested using Partial Correlation Functions (PCFs) for direct, indirect or confounding effects on RWI. Second (step 2), SEMs are built according to the main hypothesis (Melt-out timing → SFGDD → RWI) and with other climatic parameters selected in step 1. Collinearity, parsimony, goodness of fit and main assumptions (normality and homogeneity of variance) were controlled and the SEM structure was potentially refined.

Results

Chronology statistics

A total of 11, 24, and 14 *R. ferrugineum* individuals were included in the SAL1800 (1826-2016), SAL2000 (1821-2015) and CN2400 (1896-2016) chronologies, respectively (Fig. 3 A, B) corresponding to rejection rates (e.g. the percentage of misdated individuals) of 35, 33, and 48% of the samples. Cross-correlations between standardized chronologies over the period

1960-2016 yielded r values of 0.80 (SAL1800-SAL2000), 0.46 (SAL2000-CN2400) and 0.30 (SAL1800-CN2400). Wood productivity – estimated as the mean annual growth between cambial age 20 and 39 – was 0.17 mm at SAL1800, 0.16 mm at SAL2000, and thus significantly larger than the values obtained at CN2400 (0.12 mm, ANOVA $p<0.001$). Descriptive statistics computed for the detrended chronologies (Fig. 3B) are given in Table 1. Mean sensitivity values were comparable at SAL1800 (0.34) and CN2400 (0.31), but lower at SAL2000 (0.26). The highest inter-series correlations (Rbar = 0.41), EPS (0.94) and AC values (0.22) were observed at SAL2000. At SAL1800 and CN2400, lower Rbar and EPS values (slightly below the 0.85 threshold at CN2400) were found for the period covered by meteorological series (1959-2016), thereby pointing to higher inter-individual ring-width variability.

Table 1: Characteristics of *R. ferrugineum* raw ring-width chronologies: length, mean age, median ring-width. Statistics computed for detrended chronologies: standard deviation (Std. dev.), signal strength (Rbar and EPS, computed only from 1959 onwards), mean sensitivity (MS) and first order autocorrelation (AC).

	Raw ring-width chronologies				**Detrended ring-width chronologies**				
Chronology	First year	Last Year	Mean age	Median ring-width	Std. dev.	Mean Rbar (1959-2016)	Mean EPS (1959-2016)	MS	AC
SAL1800	1862	2016	81	0.171	0.281	0.321	0.86	0.338	0.136
SAL2000	1821	2015	86	0.159	0.246	0.412	0.94	0.257	0.221
CN2400	1896	2016	56	0.117	0.265	0.278	0.82	0.314	0.008

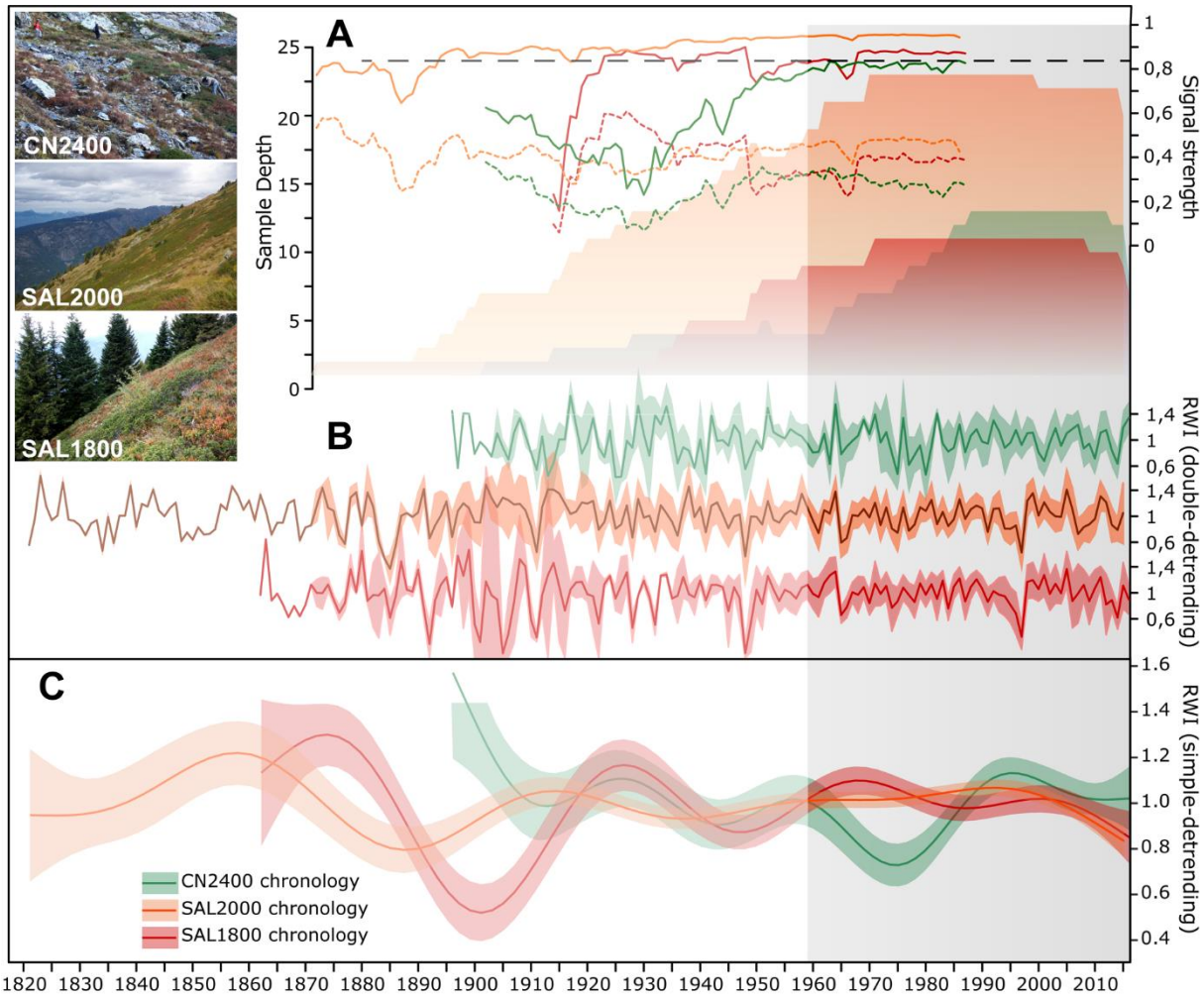

Figure 3: (A) Sample depth (colored areas) and running detrended chronologies signal strength: Expressed Population Signal (EPS, solid lines) and common variance between single growth-ring series in a chronology (Rbar, dotted lines) were computed using a 30-year moving window. Colored areas indicate sample depth. The EPS threshold (0.85) is shown by the black dotted line. (B) Standard growth-ring chronologies of *R. ferrugineum* with ribbons designating Ring-Width Indices (RWI) ± 1 SD. (C) Neg-Exp chronologies smoothed with a GAM-smoothing, ribbons indicate the 95% confidence intervals. The grey area corresponds to the period analyzed.

Bootstrapped correlation functions (BCFs) and partial correlation functions (PCFs)

Results from the bivariate bootstrapped correlation function analyses are summarized in Fig. 4. May temperatures (year N; r = 0.33, 0.34, 0.40 at 1800, 2000, and 2400 m asl, respectively, all with $p<0.05$) were the only statistically significant climatic driver of radial growth observed in all *R. ferrugineum* chronologies. More generally, positive correlations (albeit not significant) were observed between summer temperature of year N (June, July, and August) and radial growth at each site. Similar BCF profiles were observed at SAL1800 and SAL2000,

characterized by positive significant correlations with September (year N-1) temperatures (r = 0.26 and r = 0.35, p<0.05) and April precipitation sums (r = 0.28, r = 0.28, p<0.05). By contrast, at CN2400, the response to fall (N-1) temperature was delayed to October (r = -0.28, p=0.06) and November (r = -0.30, p<0.05). The response of *R. ferrugineum* to snow melt-out date and SFGDD was particularly acute at 2400 m asl. The correlation between ring-width indices and SFGDD increased from low to high elevation sites, with r = 0.18 (p=0.18) at SAL1800, r = 0.28 (p<0.05) at SAL2000, and r = 0.51 at CN2400 (p<0.001). Radial growth also appeared to be more limited by melt-out date at CN2400 (r = -0.56, p<0.001) and winter precipitation (r = -0.41, p<0.01) as compared to r = 0 at SAL1800 (Fig. 4).

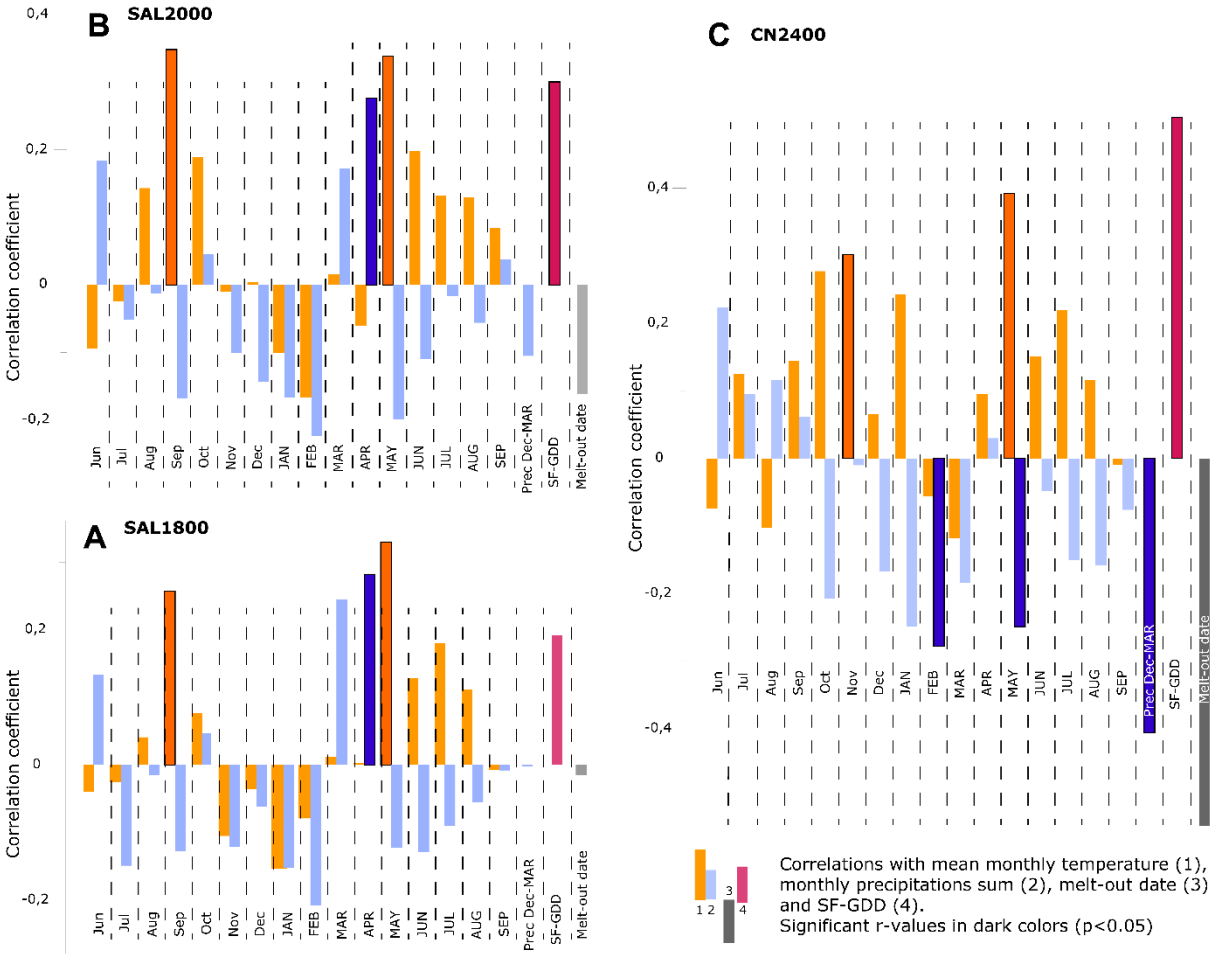

Figure 4: Monthly bootstrapped correlation functions (BCFs) analysis between *R. ferrugineum* radial growth chronologies at SAL1800 (A); SAL2000 (B); and CN2400 (C), monthly mean temperatures, monthly precipitation sums, previous December to current March precipitation sums (Prec dec-MAR), SFGDD and snow melt-out date for the period 1959–2016. Months of the year preceding ring formation

(N-1) are given with lowercase letters, and months of the year (N) of ring formation are shown with capital letters.

At our study sites, melt-out timing, late winter precipitation and May temperature are correlated, therefore partial correlations between tree-ring growth and the latter variables were performed. At CN2400, PCFs computed between radial growth, May temperature and precipitation or winter precipitation were not significant when melt-out timing was included as a control variable (Table 2). In other words, this indicates that the latter climatic variables have no impact on radial growth when melt-out-timing is held constant. Conversely, at SAL1800 and SAL2000, correlations between shrub chronologies, May temperature and March/April precipitation totals remain highly significant in the absence of melt-out timing fluctuations (Tab. 2). One can thus conclude that the correlations between our shrub ring width chronology and May temperature and late winter precipitation totals are 0.33 and 0.47 ($p<0.05$), respectively at SAL1800 if adjusted for the effects of melt-out timing. At SAL2000, the partial coefficients reveal the critical influence of May temperature ($r=0.32$, $p<0.05$) and Mar-Apr precipitation ($r=0.48$, $p<0.001$) on radial growth.

Table 2: Partial Correlations Functions (PCFs) and their significance computed between climatic parameters and ring width indices (RWI) at SAL1800, SAL2000 and CN24000 controlling for melt-out timing. Significant relationships ($p<0.05$) are given in bold. "na" means that the partial correlation was not computed, as no effect on radial growth was detected in the Bootstrapped Correlation Functions for the corresponding climatic variable.

	SAL1800		SAL2000		CN2400	
Effect	Corr.	Signif.	Corr.	Signif.	Corr.	Signif.
May temperature	**0.33**	**0.01**	**0.32**	**0.02**	0.03	0.84
March + April precipitation	**0.47**	**0.00**	**0.48**	**0.00**	na	na
Winter precipitation	na	na	na	na	-0.10	0.45
May precipitation	na	na	na	na	-0.08	0.56

Structural equation modeling

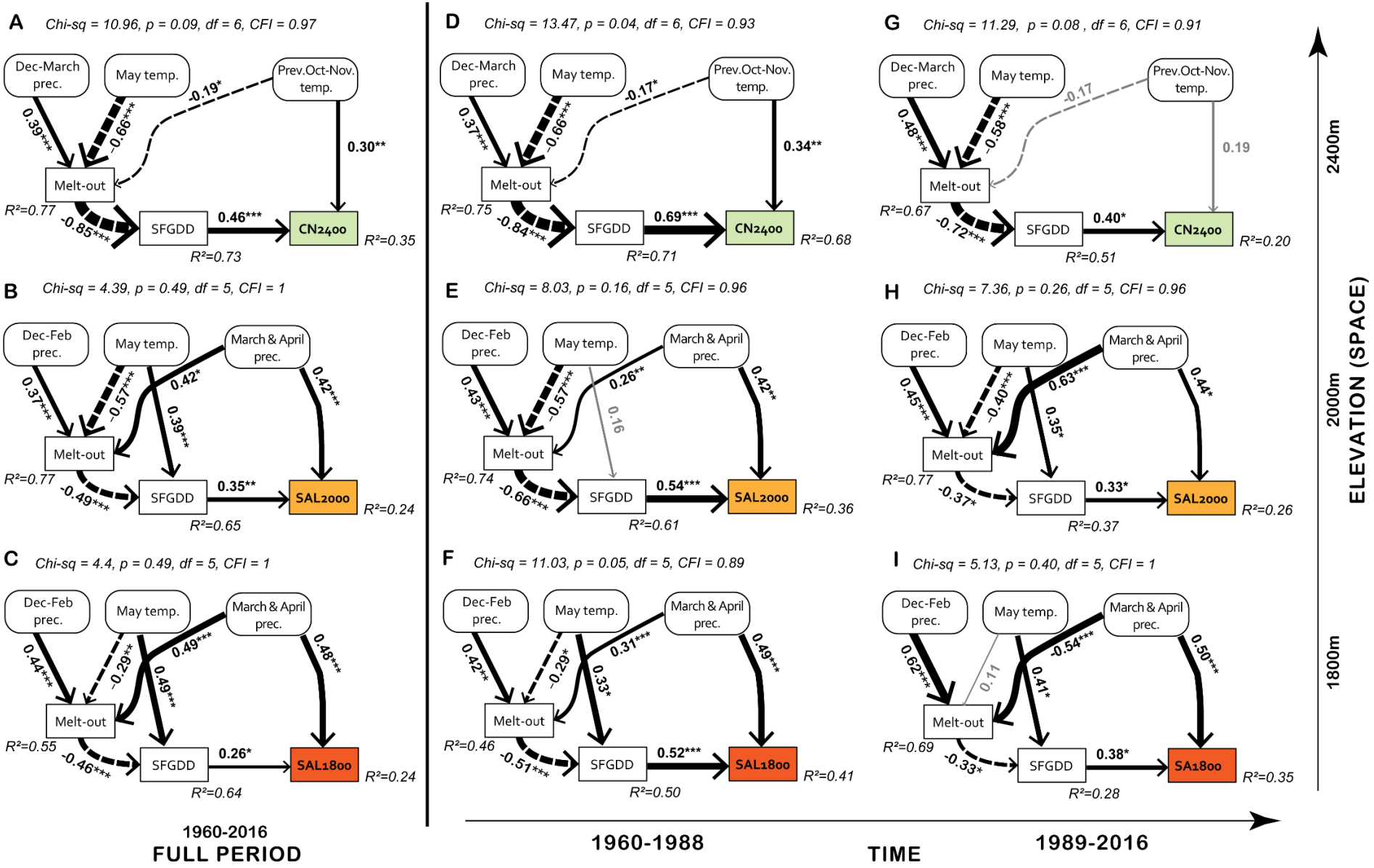
A
Chi-sq = 10.96, p = 0.09, df = 6, CFI = 0.97
Dec-March prec.
May temp.
Prev.Oct-Nov. temp.
Melt-out
SFGDD
CN2400
0.39***
-0.66***
-0.19*
0.30**
0.46***
-0.85***
R²=0.77
R²=0.73
R²=0.35
B
Chi-sq = 4.39, p = 0.49, df = 5, CFI = 1
Dec-Feb prec.
May temp.
March & April prec.
Melt-out
SFGDD
SAL2000
0.37***
-0.57***
0.42*
0.39***
0.42***
0.35**
-0.49***
R²=0.77
R²=0.65
R²=0.24
C
Chi-sq = 4.4, p = 0.49, df = 5, CFI = 1
Dec-Feb prec.
May temp.
March & April prec.
Melt-out
SFGDD
SAL1800
0.44***
-0.29**
0.49***
0.49***
0.48***
0.26*
-0.46***
R²=0.55
R²=0.64
R²=0.24
D
Chi-sq = 13.47, p = 0.04, df = 6, CFI = 0.93
Dec-March prec.
May temp.
Prev.Oct-Nov. temp.
Melt-out
SFGDD
CN2400
0.37***
-0.66***
-0.17*
0.34**
0.69***
-0.84***
R²=0.75
R²=0.71
R²=0.68
E
Chi-sq = 8.03, p = 0.16, df = 5, CFI = 0.96
Dec-Feb prec.
May temp.
March & April prec.
Melt-out
SFGDD
SAL2000
0.43***
-0.57***
0.26**
0.16
0.42**
0.54***
-0.66***
R²=0.74
R²=0.61
R²=0.36
F
Chi-sq = 11.03, p = 0.05, df = 5, CFI = 0.89
Dec-Feb prec.
May temp.
March & April prec.
Melt-out
SFGDD
SAL1800
0.42**
-0.29*
0.31***
0.33*
0.49***
0.52***
-0.51***
R²=0.46
R²=0.50
R²=0.41
G
Chi-sq = 11.29, p = 0.08 , df = 6, CFI = 0.91
Dec-March prec.
May temp.
Prev.Oct-Nov. temp.
Melt-out
SFGDD
CN2400
0.48***
-0.58***
-0.17
0.19
0.40*
-0.72***
R²=0.67
R²=0.51
R²=0.20
H
Chi-sq = 7.36, p = 0.26, df = 5, CFI = 0.96
Dec-Feb prec.
May temp.
March & April prec.
Melt-out
SFGDD
SAL2000
0.45***
-0.40***
0.63***
0.35*
0.44*
0.33*
-0.37*
R²=0.77
R²=0.37
R²=0.26
I
Chi-sq = 5.13, p = 0.40, df = 5, CFI = 1
Dec-Feb prec.
May temp.
March & April prec.
Melt-out
SFGDD
SA1800
0.62***
0.11
-0.54***
0.41*
0.50***
0.38*
-0.33*
R²=0.69
R²=0.28
R²=0.35
1960-2016
FULL PERIOD
1960-1988
1989-2016
TIME
ELEVATION (SPACE)
2400m
2000m
1800m

Figure 5: Results of structural equation models (SEMs) exploring the effects of spring snow-cover duration (Melt-out) on Snow-Free Growing Degree Days (SFGDD), and the effects of SFGDD and other climatic parameters (March and April precipitation totals at SAL1800/2000, previous September temperature at SAL2000 and previous October-November temperature at CN2400) on shrub ring width indices (RWI) at different sites (A, D, G: 1800 m asl, SAL1800; B, E, H: 2000 m asl, SAL2000 and C, F, I: 2400 m asl, CN2400). SEMs were performed for the period 1960-2016 (A, B, C) and two sub-periods: 1960-1988 (D, E, F) and 1989-2016 (G, H, I). Winter precipitation totals and May temperature effects on Melt-out timing as well as the direct effect of May temperature on SFGDD are also represented. Colored boxes represent measured RWI, white boxes represent intermediate climate parameters and rounded white boxes represent monthly or seasonal meteorological data. Black solid (or dotted) arrows indicate unidirectional positive (negative) significant relationships (at $p<0.05$) among variables. Grey arrows indicate non-significant relationship ($p>0.05$). The thickness of the paths was scaled to the magnitude of the standardized regression coefficient (shown besides the arrows). Multiple R^2 are given next to the box of the respective response variable. Significance levels are denoted by *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$). Chi-square and CFI values indicate goodness of fit.

Results from BCFs and PCFs were used to determine the direction and strength of correlations between climate variables and the shrub ring chronologies implemented in the path diagrams of each structural equation model over the period 1960-2016 (Figs. 5A-C). At each site, as stated in our initial hypotheses (Fig. 2), path diagrams were designed to disentangle the respective impacts of SFGDD, melt-out timing, winter precipitation and spring temperatures on shrub radial growth. In addition to the latter variables, fall temperatures (N-1, CN2400, SAL2000) and spring precipitation (SAL1800, SAL2000), significantly correlated to shrub ring records (BCFs), were added as direct predictor variables. SEMs computed for the periods 1960-2016 displayed Chi-square p-values above 0.05 and CFI higher than the 0.9 cut-off. At the three sites, the proportion of the variance in the dendrochronological series that could be explained by the climatic variables increased with elevation (R^2= 0.35, 0.24, 0.24 at CN2400, SAL2000 and SAL1800, respectively). However, the effect of SFGDD on shrub ring records increased from 0.26 standard deviation units as a result of change of one standard deviation in SFGDD at 1800 m ($p<0.05$) to 0.35 ($p<0.01$) at 2000 m and to 0.46 ($p<0.001$) at 2400 m asl. Significant relations between climatic variables and radial growth differed along the elevational gradient. At CN2400, SFGDD variability is the main driver of radial growth, which is significantly related to melt-out-timing (path coefficient of -0.85, $p<0.001$). Melt-out was in turn directly

conditioned by May temperature (-0.66, $p<0.001$), winter precipitation (0.39, $p<0.001$) and – to a lesser extent – by previous late-autumn temperature (-0.19, $p<0.05$).

At SAL2000, SFGDD, spring precipitation and previous fall temperature show comparable, statistically significant impacts on shrub radial growth. Interannual variability of SFGDD remains dependent on melt-out timing but is also directly driven by May temperature (Fig. 5B). Finally, at 1800 m asl, the SEM differs from those obtained for the higher elevation sites. Albeit significantly related to radial growth at SAL1800, SFGDD is not the main driver for shrub ring width which appears to depend more strongly on March-April precipitation totals (0.48, $p<0.001$). At this elevation, SFGDD is driven by melt-out timing and May temperature (-0.46, $p<0.001$ and 0.49, $p<0.001$, respectively).

Stationarity of radial growth-climate relationships over time

To evaluate the stationarity and consistency of radial growth-climate relationships, SEMs were computed for the two sub-periods 1960-1988 and 1989-2016 (Fig. 5 D-I). The SEMs presented good overall performances by passing the goodness of fit cutoffs of Chi-square $p>0.05$ and CFI >0.90 except for the SEMs computed at CN2400 and SAL1800 for the period 1960-1988 (χ^2 = 13.47, p=0.04, CFI = 0.93 at CN2400 and χ^2 = 11.03, p=0.05, CFI = 0.89 at SAL1800).

Strikingly, we observe a loss of the explanatory powers of the SEMs for the recent period, especially at CN2400 where the amount of variance in radial growth explained by climatic variables decreased from 0.69 for the period 1960-1988 to 0.20 between 1989 and 2016. For both subperiods, the dependence of radial growth on SFGDD thus decreased from 0.69 ($p<0.001$) to 0.40 ($p<0.05$), from 0.54 ($p<0.001$) to 0.33 ($p<0.05$), and from 0.52 ($p<0.001$) to 0.38 ($p<0.05$) at 2400, 2000, and 1800 m asl, respectively. In addition, the models illustrate nicely that the dependence of SFGDD on melt-out dates and May temperatures remain highly significant ($p<0.001$) at CN2400, whereas their influence strongly decreased at SAL2000 and

SAL1800 after 1988. Similarities exist between the SEM computed at SAL2000 for the period 1960-1988 and at CN2400 for the period 1989-2016 (Fig. 5 E, G), especially with respect to the correlations between May temperatures, melt-out timing, SFGDD and radial growth. Similarly, comparable impacts of winter precipitations and May temperatures on melt-out dates were observed in Fig. 5F and 5H. This evolution suggests a 200-400 m shift of the climatic conditions and, to a lesser extent, of radial growth response to climate over the last 30 years.

Discussion

In this paper, we disentangled the impact of recent climate change, especially of earlier snow melt-out, on radial growth in the widespread mountain shrub species *Rhododendron ferrugineum* by sampling a total of 80 stems along an elevation gradient. The three multi-decadal growth-ring chronologies developed from individuals sampled at 1800, 2000, and 2400 m asl (referred to as SAL1800, SAL2000, and CN2400) provide a unique perspective on mountain shrub responses to climate variability in the context of recent climate changes (Myers-Smith et al., 2015). We used Structural Equation Models (SEMs), rarely used in dendroecological studies so far, to disentangle direct and indirect drivers of radial growth. Our results clearly demonstrate an elevation-dependent response of *R. ferrugineum* to snow cover duration and provide evidence for a divergence of radial growth responses to climate during recent decades, given that climate-growth correlations have weakened since 1988. This study also benefits from the hourly-resolution of meteorological as well as snow series from the SAFRAN-Crocus dataset. The latter data, available at the elevations of the three study plots for the period 1960-2017, are of a precision that is only rarely equaled in any previously published alpine or arctic dendroecological study.

Radial growth responses along the snow melt-out timing gradient

At CN2400, results support the initial hypothesis that the amount of growing degree days during the snow-free period (SFGDD) would impact *R. ferrugineum* radial growth strongly whereas melt-out dates would act only as an indirect limiting factor on radial growth by conditioning the length of the growing season. Results from SEMs show that SFGDD – controlled by melt out dates – explained about 46% of radial growth variability over the period 1960-2016 and about 70% of the variability between 1960 and 1988. At this elevation, the growing season is short (85 days on average prior to August 31) and SFGDD totals are low (823°C on average for the period 1959-2016). Snowmelt frequently occurs between early and mid-June and coincides with peak annual temperatures and photoperiod, i.e. when the carbon gain of a single bright day is at its maximum. Consequently, any variation in melt-out dates, even by a few days, can affect SFGDD totals strongly, and can thus also explain the strong correlation between both variables ($r = -0.85$, $p<0.001$).

R. ferrugineum is an evergreen shrub that has developed an opportunistic growth strategy, able to photosynthesize within two hours after snow removal (Larcher and Siegwolf, 1985). We can therefore reasonably assume that the species will also benefit from an earlier growing season, consistent with the correlation between SFGDD and radial growth. Our results are in line with numerous studies from Arctic and Alpine environments, which demonstrated that the accumulation of temperature above a certain threshold is 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). Results are also consistent with (i) dendrochronological studies that demonstrated the negative effect of snowpack duration on radial growth at the upper shrub limit in the Alps (Carrer et al., 2019; Francon et al., 2017; Pellizzari et al., 2014) and (ii) manipulation experiments (Stinson, 2005; Wheeler et al., 2016) showing increased productivity in case of artificial snow removal at sites where melt-out dates occurred after late-May (Wipf and Rixen, 2010). Results from the Alps

differ from the wealth of studies in the Arctic, where a positive effect of snowpack was highlighted. We can explain this discrepancy by the fact that, in the Arctic, the positive winter precipitation effect is mostly related to snowpack thermal insulation, which protects plants from the harsh external conditions but also promotes higher winter soil surface temperatures with greater decomposition and nutrient release (Chapin, 2005; Hallinger et al., 2010). Furthermore, Alpine snowpack tends to be deeper and winter temperatures milder compared to the Arctic, and accordingly soil temperatures less sensitive to a slight change in snow accumulation. In the context of our study sites, root and vegetative shrub tissues are likely more protected from persistent negative temperatures in the Alps than in the Arctic (Domine et al., 2016; Ernakovich et al., 2014).

By contrast, at the lower sites (SAL1800, SAL2000), our results indicate that the weaker effects of (i) snow cover duration on SFGDD and (ii) SFGDD on ring width can be explained by earlier melt-out dates, occurring at these elevations between early and mid-May, when daily temperatures (4.9°C and 6.4 °C in May on average for the 1960-2016 period at 2000 and 1800m asl, respectively) and solar radiation have not yet attained peak values and are insufficient for shrub growth. In addition, SFGDD at SAL1800 and SAL2000 (1316°C on average) are significantly higher than those estimated at CN2400 and thus certainly less constraining for plants to complete the phenological cycle and a complete carbon storage at the end of the growing season. These hypotheses are consistent with experiments showing neutral to negative impacts of early (i.e. late-April) artificial snow removal (Dorrepaal et al., 2006; Wipf et al., 2006, 2009) at sites where natural early melt-out date would occur before mid-May. Wipf et al. (2009) found a general decrease in shoot growth in mountain shrub species (*Empetrum nigrum*, *Vaccinium myrtillus* and *V. uliginosum*) under earlier melt-out dates due to higher frost exposure. In the specific case of *R. ferrugineum*, Malfasi and Cannone (2020) found that the recruitment rate was favored by prolonged snow cover occurrence. In our case, the positive

effect of a longer growing season on radial growth can be similarly offset by the detrimental impact of spring frost (Choler, 2015; Jonas et al., 2008) or drought (Wheeler et al., 2016). Accordingly, we hypothesize that the positive correlations observed between low-elevation chronologies and March-April precipitation sums could either reflect (i) the positive effect of early spring precipitation on nutrient supply at the beginning of the growing season by enhancing decomposition and nitrogen mineralization right after snow melt-out (Baptist et al., 2010; Ernakovich et al., 2014) or (ii) the protective effect of late snowfalls against late frost (Choler, 2015; Jonas et al., 2008), irradiation (Neuner et al., 1999) or limited drought stress during the subsequent growing season (Buchner and Neuner, 2003; Daniels and Veblen, 2004).

In the case of the Taillefer massif, a detailed analysis of meteorological conditions and radial growth in 1997 is relevant in order to illustrate the detrimental effects of late frost. According to the SAFRAN-Crocus reanalysis, melt-out occurred on approximately April 14 at lower elevations (SAL1800 and SAL2000,) and on May 31 at CN2400. At lower elevations, spring 1997 was the coldest since 1959 at the ground level. Immediately after melt-out, two cold episodes with two extreme freezing periods occurred between April 14 and 24 and between May 6 and 9. Ground level temperatures reached their absolute minimum on April 17 at -7.3°C. The same year, a majority of *R. ferrugineum* individuals from the two lower elevation sites formed extremely narrow rings, whereas no significant growth reduction was observed at 2400 m asl where plants were still under snow. This suggests that very low productivity at SAL1800 and SAL2000 is linked to cellular damage associated with intense late frost which likely damaged fine roots, leaves, buds, and the cambium (Inouye, 2000; Wipf et al., 2006; Wipf and Rixen, 2010). However, the absence of other events comparable to 1997 in meteorological or ring width series does not allow inference of robust relationships between late frost and radial growth. Here, experimental testing using ecophysiological monitoring could be used to further explore the effects of frost events on radial growth (Charrier et al., 2017).

Climate warming, trend analysis and the divergence problem

Our study demonstrates diverging effects of growing season length and snowmelt timing on radial growth along the elevational gradient. At CN2400, the decadal growth trend follows that of SFGDD, in line with findings from the Arctic (Myers-Smith et al., 2015a). In addition, at lower elevation sites, our results also point to a divergence of radial growth as radial growth did not track the SFGDD increase during more recent decades. These results concur with the growth decline detected since the 1990s in shrub rings of *B. nana* and *S. glauca* from Western Greenland, where reduced ring width was attributed to increasing moisture limitation (Gamm et al., 2018). In the Taillefer massif, a weakening of the climatic signal is observed in shrub-ring chronologies after 1988, a year that can be considered as a tipping point in the meteorological series. Interestingly, comparable trends were reported for *B. nana* and *E. hermaphroditum* in the central Norwegian Scandes, where the positive influence of summer conditions was replaced by a negative response to May temperatures, over the last decades (Weijers et al., 2018a, 2018b). These findings echo the "divergence problem" reported in trees growing at circumpolar, northern latitudes (Briffa et al., 1998; D'Arrigo et al., 2008; Driscoll, 2005) and high-elevation sites (Büntgen et al., 2006, 2008). This body of evidence suggests more complex and nonlinear growth responses of trees to a changing climate, thereby leading to a decrease in year-to-year sensitivity of tree growth (i.e. "non-stationarity") in previously temperature-limited sites (D'Arrigo et al., 2008; Vaganov et al., 1999; Wilmking, 2005; Wilmking et al., 2020). Potential causes for this divergence include warming-induced thresholds of tree growth (D'Arrigo et al., 2004; Jochner et al., 2018), limitation of growth by nutrient availability (Fajardo and Piper, 2017) or drought stress (Büntgen et al., 2006) or interactions between these factors. In the case of low-stature alpine vegetation, frost damage (Phoenix and Bjerke, 2016; Treharne et al., 2019) could also be assumed as a cause divergence, and merits further investigation.

Conclusion

In this paper, we analyze annually resolved, statistically solid multi-decadal chronologies of 49 *R. ferrugineum* shrubs sampled along an elevational gradient in the French Alps. Results show that a clear, elevation-dependent climatic signal exists in the growth-ring series covering the period 1959-2016. Comparison of the SEMs along the elevational gradient shows that SFGDD and, by extension, melt-out dates are the main drivers of radial growth at 2400 m asl. By contrast, at lower elevations, melt-out dates have a limited effect on SFGDD, as the latter only barely limit radial growth. In addition, meteorological and snowpack series from the model SAFRAN-Crocus point to a breakpoint in 1988. In fact, since the late 1980s, melt-out dates have advanced by an average of 17 to 19 days depending on elevation. Since 1988, our study provides evidence of a recent divergence in radial growth, insofar as the increase in SFGDD results in a weakening of the climatic signal in shrub ring-width chronologies, similar to the divergence observed in trees at circumpolar and alpine sites. Moreover, at lower elevations (1800 and 2000 m asl), an extremely narrow ring was formed in 1997 following a late frost event. Albeit unique in the dendrochronological series, it illustrates the potential detrimental effects of early melt-out dates on productivity. Accordingly, 1997 might well be an example of extreme events that can be expected to become more frequent in a warmer climate. This non-stationarity of climate-growth relationships suggests strong threshold effects in terms of temperature and melt-out timing in a context of global warming.

This study shows that *R. ferrugineum* is particularly sensitive to local meteorological conditions such as snow cover or frost events. For this reason and given its large occurrence above the treeline in the Alps and Pyrenees (Francon et al., 2017; Gracia et al., 2007), we believe that this species represents a valuable dendroecological indicator to document the response of alpine vegetation to global warming over the last centuries. As such, *R. ferrugineum* could be used easily to complement *Juniperus nana* in future dendroecological studies, even more so as both

595 species are characterized by a wide distribution above treeline and a life span of more than a
596 century (Carrer et al., 2019; Pellizzari et al., 2014, 2016). Yet, unlike *J. nana*, whose radial
597 growth is mainly driven by regional climate variability (Carrer et al., 2019), *R. ferrugineum*
598 seems to be very sensitive to fine-scale climatic variations induced by topography.

599 To further improve our understanding of the processes governing shrub growth in mountain
600 environments and to precisely define the values of the above-mentioned climatic thresholds,
601 including the potential impact of extreme climatic events, we recommend that future research
602 be directed in two directions. Firstly, more populations growing in contrasting topoclimatic
603 situations across the Alps should be sampled and compared with topoclimatic data. Secondly,
604 we plead for future work to combine field-based eco-physiological and microclimatic
605 monitoring (see e.g. Charrier et al. 2017), with remote sensing of landscape-scale vegetation
606 dynamics in alpine regions (see e.g. Carlson et al., 2017; Bayle et al. (2019).

607 ## Acknowledgments

608 This research was supported by the program ProXyCliM (2016–2017) funded by the CNRS
609 (Mission interdisciplinarité - RNMSH) and by the french national grant EC2CO-
610 Biohefect/Ecodyn//Dril/MicrobiEen, SNOWSHRUB. We wish to thank all who contributed to
611 the meteorological series data used in the analyses, especially Carlo Maria Carmagnola (Météo-
612 France - CNRS, CNRM, CEN). We are particulartly grateful to Brigitte Girard (INRA, PIAF)
613 for her much appreciated help during the tedious phase of the laboratory. We acknowledge
614 Olivier Voldoire (GEOLAB, CNRS) for technical support. Rhododendron shrubs were sampled
615 with the help of Séverine Finet, and Robin Mainieri. We are also grateful to Frida Piper and
616 Jaime Madrigal González for insightful feedback on the manuscript. CNRM/CEN,
617 Irstea/ETNA and LECA are part of LabEX OSUG@2020.

618

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