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LETTER

Shrub growth in the Alps diverges from air temperature since the 1990s

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Supplementary material for this article is available online

Abstract

In the European Alps, air temperature has increased almost twice as much as the global average over the last century and, as a corollary, snow cover duration has decreased substantially. In the Arctic, dendroecological studies have evidenced that shrub growth is highly sensitive to temperature—this phenomenon has often been linked to shrub expansion and ecosystem greening. Yet, the impacts of climate change on mountain shrub radial growth have not been studied with a comparable level of detail so far. Moreover, dendroecological studies performed in mountain environments did not account for the potential modulation and/or buffering of global warming impacts by topography, despite its possible crucial role in complex alpine environments. To fill this gap, we analyzed a network of eight sites dominated by the dwarf shrub *Rhododendron ferrugineum*. The sites selected for analysis represent the diversity of continentality, elevation and slope aspect that can be found across the French Alps. We quantified annual radial increment growth for 119 individuals, assembled meteorological reanalyzes specifically accounting for topographic effects (elevation, slope and aspect) and assessed climate-growth relations using a mixed modeling approach. In agreement with a vast majority of dendroecological work conducted in alpine and arctic environments, we find that the number of growing degree days during the snow-free period snow-free growing degree days (SFGDDs) is a strong and consistent driver of *R. ferrugineum* growth across all sites since 1960 until the late 1980s. We also document a marked loss of sensitivity of radial growth to increasing SFGDD since the 1990s, with this decoupling being more pronounced at the driest sites. Our observations of the spatial and temporal variability of shrub sensitivity to limiting factors can be compared to the 'divergence' problem observed in tree-ring series from circumpolar and alpine regions and, accordingly, sheds light on possible future trajectories of alpine shrub growth in response to ongoing climate change.

1. Introduction

Mountainous and Arctic regions are experiencing a temperature increase that is about two times larger than the global average; as a corollary, observations also show a general decline in snow cover (IPCC 2019). In the Arctic, higher temperatures during summer lead to intense greening and increased shrub productivity and cover, which ultimately drive climate feedbacks (Myers-Smith *et al* 2015a, Berner *et al* 2020). Likewise, the ongoing shrub expansion has been shown to modify a range of ecosystem processes (Myers-Smith *et al* 2011) by altering surface albedo, snowpack depth, energy, water balance, or permafrost conditions (Sturm *et al* 2001, Liston *et al* 2002, Chapin 2005). By analyzing a network of circumpolar shrub rings, Myers-Smith *et al* (2015a) suggested that increasing summer temperature have enhanced shrub radial growth. Several arctic studies also showed that topography may have a positive buffering effect on changing summer temperatures by modifying soil moisture conditions (Myers-Smith *et al* 2015a). Ropars *et al* (2015) and Ackerman *et al* (2017) thereby demonstrated that the response of shrub individuals to climatic parameters can be strongly modulated by local topography. However, Bär *et al* (2008) and Ackerman *et al* (2018) did not detect any inconsistent responses of shrubs sampled in contrasting topographic situations to ongoing climate warming.

In the European Alps, increasing vegetation productivity and denser shrub cover above treeline have been documented through remote sensing or resurveys of vegetation plots (Dullinger *et al* 2003, Cannone *et al* 2007, Carlson *et al* 2017, Filippa *et al* 2019, Malfasi and Cannone 2020). Dendroecological studies have highlighted the negative role of winter precipitation and subsequent, delayed melt-out dates on radial growth of shrubs, but have also demonstrated the positive effect that increasing summer temperatures can have on shrub growth (Pellizzari *et al* 2014, Francon *et al* 2017). In the Italian Alps, a study suggested a positive, spatially consistent and stable effect of increasing growing season length on shrub radial growth (*Juniperus communis nana*; Carrer *et al* 2019). By contrast, two recent, albeit spatially-limited studies emphasized that elevation and slope aspect can significantly modulate *Rhododendron ferrugineum* growth response to increasing temperature significantly (Francon *et al* 2020a, 2020b). Slope aspect, as a local topographic factor, can mimic temperature differences of large elevational or latitudinal gradients over distances of just a few meters (Scherrer and Körner 2009) by modulating solar incidence angles, frost exposure and soil moisture conditions (Riihimäki *et al* 2017). Additionally, within mountain ranges, rain-shadow effects—controlling precipitation sums and aridity—were demonstrated to be of paramount importance for plant interactions and growth (Michalet *et al* 2003). However, no dendroecological study has so far specifically investigated the impacts of topoclimatic variability (defined as the local scale of a few hectares, where climate is driven by variations in topography; Aalto *et al* 2017) on shrub growth in mountain regions. This research gap is critical given that (a) topoclimatic heterogeneity in alpine environments (Dobrowski 2011) is likely to buffer the response of shrubs to global warming; and that (b) strong moisture gradients that exist over short distances due to the presence of rugged terrain (Scherrer and Körner 2011) could potentially modulate the productivity and performance of alpine vegetation more markedly than in the Arctic (Ernakovich *et al* 2014). Recent shrub growth and expansion in the European Alps is a critical and understudied topic, considering the various ecosystem 'disservices' expected to be conferred by the replacement of alpine meadows by dense shrub canopies, including: modifications of the microclimate (Mekonnen *et al* 2021) localized reductions in vascular plant diversity (Anthelme *et al* 2007, Boscutti *et al* 2018) diminished pasture resource and quality (Klein *et al* 2007), and altered soil chemical composition (Pornon *et al* 1996).

This paper assesses the impacts of global warming on shrub growth for a dominant dwarf shrub species in alpine heathlands, *R. ferrugineum* (L.), with a focus on the possible mediating role of topoclimatic conditions could have on shrub growth responses to climate change. To this end, we (a) assembled annual growth records from a network of eight sites designed to be representative of the contrasts in continentality, elevation and slope aspect across the French Alps. Analyses were performed (b) with SAFRAN-Crocus (Durand *et al* 2009a, 2009b, Vionnet *et al* 2012, Vernay *et al* 2019), a meteorological and snow cover reanalysis providing an estimation of meteorological and snow cover variables for different slope, aspects and per 300 m altitude steps within mountainous regions called 'massifs'. In a last analytical step, we (c) combined bootstrap correlation functions with mixed effects models applied to single *R. ferrugineum* shrubs to quantify threshold effects and shifts in shrub-climate relations resulting from ongoing global warming in the French Alps.

2. Material and methods

2.1. Shrub-ring chronology development

R. ferrugineum is an evergreen dwarf shrub species with highly branched trailing that can reach up to 0.8 m in height. It has a wide geographic range of occurrence across the European Alps (Ozenda 1985) and is in expansion in the treeline ecotone (Pornon *et al* 1996). Complementary sexual and vegetative reproductive strategies (Doche *et al* 2005). This strategy also allows *R. ferrugineum* to outcompete other plants in subalpine heaths (Theurillat and Schlüssel 2000), to accumulate large amounts of biomass per unit area and to form large heathlands that reach up to 90%–100% cover after 150–250 years (Pornon *et al* 1996, Pornon and Doche 1996)—explain its abundance in the subalpine belt. Given its (a) wide distribution from *c.* 1600–2500 m asl across the European Alps, (b) its longevity, as well as (c) the formation of clearly identifiable annual growth rings, *R. ferrugineum* is a reliable model to study shrub response to long-term climate variability (Francon *et al* 2017). We thus sampled *R. ferrugineum*

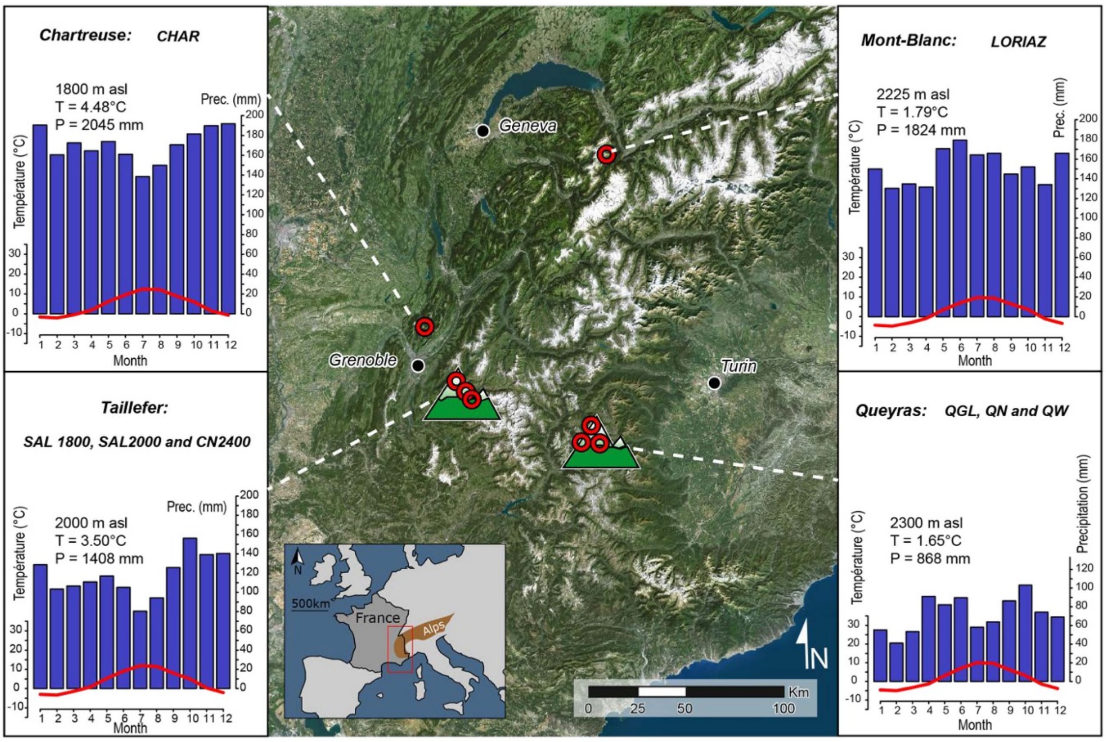

Figure 1. Location of the eight study sites of the *R. ferrugineum* network used in this study: CHAR refers to the site sampled in the Chartreuse massif; CN2400, SAL2000, SAL1800 to three sites with different slope aspects in the Taillefer massif at 2400, 2000 and 1800 m asl; LORIAZ to the site sampled in the Mont-Blanc massif; QGL, QN, QW refer to three sites with different slope aspects sampled at elevations ranging from 2350 to 2550 m asl in the Queyras massif. Details on site characteristics are given in table 1. Umbro-thermal diagrams (Chartreuse, Oisans, Mont-Blanc and Queyras) were obtained from the Safran-CROCUS (S2M) reanalysis (Météo France, 1981–2010).

Table 1. Characteristics of the eight study sites with the name of the mountain massif (Massif), elevation of plots above sea level (Elev.), index of continentality (α), and aspect (Asp.) as well as growth ring chronology characteristics and period covered (Length), number of individuals used (Nb.), signal strength (expressed population signal or EPS), mean intercorrelation between individual series inter-series correlation (rbar) and autocorrelation of order 1 (AC) included in the dendroecological network. The EPS, rbar and AC values have been computed for detrended chronologies.

Massif	Site	Elev.	α	Asp.	Length	Nb.	$\text{Year}_{\text{EPS} > 0.8}$	rbar	AC
Mont-Blanc	LORIAZ	2225	50.70	135°	1905–2017	14	1960	0.42	0.07
Chartreuse	CHAR	1800	41.40	270°	1900–2016	16	1958	0.29	0.21
Taillefer	CN2400	2400	60.00	45°	1896–2016	14	1959	0.31	0.01
	SAL2000	2000	54.8	315°	1821–2015	24	1918	0.41	0.22
	SAL1800	1800	53.20	315°	1862–2016	11	1963	0.32	0.14
Queyras	QGL	2550	71.50	30°	1940–2017	15	1954	0.41	0.24
	QN	2350	69.50	30°	1906–2016	10	1954	0.42	0.22
	QW	2350	68.70	270°	1918–2016	14	1946	0.57	0.13

individuals at eight sites across four mountain massifs of the French Alps. Sites were chosen along a continentality gradient and extend from the Chartreuse (total annual rainfall: 2045 mm) to the Queyras (868 mm) massifs (figure 1), i.e. from the wettest to the driest of the 23 massifs of the French Alps (Durand *et al* 2009b). Topographic and climatic characteristics of all massifs considered are synthesized in figure 1 and table 1. At seven sites, substrate is composed of metamorphic or plutonic (i.e. acid rocks), whereas bedrock consists of fractured limestone favoring rapid water infiltration in the Chartreuse massif (CHAR). At all sites, vegetation height ranged between 30 and 50 cm.

Specimens of *R. ferrugineum* were sampled in heathlands or large patches at all sites except at CN2400 where individuals were growing isolated. When sampling, a minimum distance of 4 m was maintained between each sample selected for analysis so as to avoid replication of samples from the same individual (Escaravage *et al* 1998). For each individual, one to three sections were taken from one or two stems to allow for a serial sectioning and repeat measurements of growth-ring series on the same individual (figure S2 (available online at stacks.iop.org/ERL/16/074026/mmedia)), but also to detect missing rings in growth-ring series as shrubs often produce very narrow, wedging growth rings

(Kolishchuk 1990). From each section, a microsection was obtained with a sliding microtome; each section was then stained, colored with safranin and astra blue dye to enhance ring boundaries and finally mounted on slides (Schweingruber and Poschold 2005).

Cross-dating (i.e. the assignment of exact calendar years to the formation of each ring) was realized on the digitalized images of thin sections with CooRecorder and CDendro (CYBIS Elektonik & Data AB); this included a three-step procedure relying on the visual synchronicity between (a) elementary ring-width (RW) series measured at three radii of the same cross section, (b) mean RW series obtained for each section of the same individual, and finally (c) between individual chronologies at a given site. Visual cross-dating was validated statistically with COFECHA (Holmes 1994). In a subsequent step, we detrended each section chronology using a negative exponential function to eliminate non-climatic biological trends using ARSTAN (Cook 1987). After detrending, ring-width indices (RWIs) were averaged for each cross-dated section and individual with a bi-weighted robust mean; this step aimed at reducing the influence of outliers and at developing mean detrended site chronologies (Cook and Peters 1981). Finally, the eight detrended site chronologies were compared with each other using a correlation matrix to check for radial growth consistency between the sites.

We computed descriptive statistics including standard deviation, first-order AC, mean rbar and the running 35 years EPS for each detrended site chronology with ARSTAN (table 1), whereby EPS quantifies the strength of the common climate signal in growth-ring proxies (Wigley *et al* 1984). We used a quality threshold EPS $\geqslant 0.8$ to evaluate reliability of our chronologies. Sample depth is shown on figure S2.

2.2. Meteorological time series and topoclimatic characteristics of network sites

We extracted series of hourly temperature, hourly precipitation totals and daily snowpack depths at each of the 8 network sites from SAFRAN-Crocus (S2M) reanalyzes for the period 1959–2017 (Durand *et al* 2009a, 2009b, Vionnet *et al* 2012, Vernay *et al* 2019). They provide continuous time series of meteorological variables at hourly resolution, for different elevation bands, slope aspects and angles within massifs, i.e. horizontally climatologically homogeneous regions. Furthermore, they also provide snow height and snow water equivalent values. Note however, that vegetation is represented in a simplified way in the simulations, assuming continuous grass cover to simulate typical snow conditions and underlying ground temperature for open areas (Vionnet *et al* 2012). Based on these reanalyzes, we derived snow melt-out dates at our study sites according to the elevation, slope aspect and angle that had been measured in the field for each plot. Melt-out dates correspond to the date when snow cover depth reaches 10 cm for the last time within a snow cover period of at least 7 d. From the date of melt-out to August 31 (considered here as the last day of growth, based on multiple dendrometric series, unpublished data), we summed all above-zero daily mean temperatures to obtain snow-free growing degree days (SFGDDs). SFGDD summarize thermal conditions experienced during the period during which growth occurs. We also generated monthly and seasonal mean temperature series and precipitation totals. To account for the potential impact of summer drought on radial growth, we computed series of standardized precipitation-evapotranspiration indices (or SPEI, Vicente-Serrano *et al* 2010) for two month periods corresponding to the length of the growing season. Trends in summer precipitation and temperature, SFGDD and melt-out dates are shown in the supplementary materials attached to this manuscript (figure S3). Topographic characteristics (elevation and slope aspect) and the Gams continentality index (α, Gams 1932) were employed as additional variables to characterize each site, whereas the Northness index—ranging from—1 for a southern to 1 for a northern orientation—was given at each site as the cosine of slope aspect (α) and is used here as an indicator of rain-shadow effects while controlling for the effect of elevation. α was calculated following the equation:

$$\operatorname{cotg}(\alpha) = P/A$$

where P and A represent the mean annual precipitation sum (mm) and the elevation (m asl), respectively, at each site (table 1). Elevation and slope aspect are known to affect temperature, light availability, solar incidence angles and soil conditions in mountainous terrain (Scherrer and Körner 2009, Bonet *et al* 2010, Riihimäki *et al* 2017).

2.3. Relationships between shrub radial growth and climate

Climate-growth analyses were performed in two steps: we first calculated bivariate correlation functions (BCFs) between the detrended site chronologies (RWI) and time series of monthly (and summer) temperature, precipitation, SPEI, melt-out dates and SFGDD. This preliminary analysis was intended to detect the main drivers of radial growth at each site. BCFs were computed separately for the periods 1960–1988 and 1989–2017 so as to detect potential shifts in climate-growth relationships related to global warming. The two periods of equal length cover almost 30 years each, in accordance with the definition of a climate normal. The second period also reflects the marked warming observed since the late 1980s (Lo and Hsu 2010, Reid *et al* 2016). This regime shift to warmer temperatures had a particularly significant impact on biophysical environments including the physiology, development, behavior and phenology of living organisms (Oberhuber *et al* 2008, Reid *et al* 2016). Subsequently, relationships between SFGDD and log-transformed scaled raw RW of *R. ferrugineum* were investigated further using linear mixed models. The advantage of these models relies in (a) their ability to manage intra-site variance (Myers-Smith *et al* 2015b); (b) the possibility to compare shrub response between different topoclimatic conditions, thereby allowing to account for potential interactions between variables, for example topography and climate (Myers-Smith *et al* 2015b); (c) the possibility to use raw ring measurements, thus avoiding detrending that could remove meaningful ecological information from growth RW series (Ackerman *et al* 2018); (d) the detection of possible non-linear relationships and threshold effects in climate-growth relations by introducing, for example, quadratic effects; and in (e) the inference of predictions of general trends for sites that have not been sampled by using data of multiple sites.

Linear mixed models computed using the *nlme* package (Pinheiro and Bates 2000) in R (R Core Team 2016) are an extension of simple linear models to allow both fixed and random effects. The inclusion of random effects enables control of pseudo-replication, i.e. of the degree of dependence between observations within the same group. In our case, we chose multiple nested grouping levels for the random intercept structure of models: section nested within individual as well as individual within site as random terms (Harrison *et al* 2018). Fixed effects, equivalent to explanatory variables in standard linear regressions, are variables that we expect to affect RWs. These include cambial age, elevation, Gams continentality index, northness index and mean annual SFGDD (normalized and scaled). Cambial age (i.e. number of years) was introduced in the model to account for age-related trends in growth-ring series. Particular attention was also paid to interactions between SFGDD and other geographical variables (elevation, Gams continentality index and northness index) as they could modulate shrub response to increasing air temperature.

To detect potential threshold effects, we also explored second-order (non-linear) relationships between SFGDD and radial growth in the models. We therefore log-transformed and scaled mean raw RW measurements at the level of individual sections (hereafter referred to as RW) to obtain the required normality of residuals. An AC structure (AR1, first-order autoregressive process) was included as well so as to eliminate temporal biological memory from growth-ring series (Weijers *et al* 2018b). The predictive capacity of a single independent variable was then determined by the absolute value of Student's t statistics for its linear or quadratic effect on RW. We calculated a pseudo-R^2 of the selected models comprising marginal (R^2m) and conditional (R^2c) values (Nakagawa and Schielzeth 2013). R^2m and R^2c account for the proportions of the variance explained by the fixed factors and by the whole model (i.e. fixed plus random factors), respectively. R^2m and R^2c values were calculated with the *MuMIn* package (Barton 2019). Elimination of non-statistically significant terms (at $p \leqslant 0.05$) was then used to select the most parsimonious model. The Akaike Information Criterion (AIC) and the Bayesian Information Criterion—imposing a stronger penalty for increasing model complexity—were then used to compare the resulting models. We considered the overall climate sensitivity to be the comparison in AIC value between the best model and a null model (Myers-Smith *et al* 2015a). Finally, multicollinearity issues where checked based on the variance inflation factor with a threshold set at three (Zuur *et al* 2010) in *car* package available in R. To detect potential impacts of global warming on climate-growth relationships, three models were implemented for the periods 1960–88, 1989–2017 and 1960–2017.

3. Results

Figure 2 provides a synthesis of changes in SFGDDs and RWI values at the eight sites sampled across the French Alps. The SFGDD series do not exhibit any significant trend from 1960 until the late 1980s. By contrast, and starting in the early 1990s, a clear shift of SFGDD is observed at each site along with an increasing trend in all SFGDD series over the period 1989–2017. No comparable trend is observed in the RWI chronologies over the same period (figure 2).

Using the growth RW series obtained from the 225 cross-sections sampled from 119 individuals of *R. ferrugineum*, we constructed eight detrended site chronologies (see table 1 and figures S1 and S2 for their characteristics) that were subsequently used for the analysis of climate-growth relationships. All chronologies exceed the 0.8 EPS threshold over the 1960–2017 period with the exception of SAL1800 (1963–2017) (table 1). Over the period 1960–89, BCFs (see figure S4) computed between meteorological variables and detrended chronologies reveal strong (r values ranging between 0.39 and 0.75, figure 2) and statistically significant correlations ($p < 0.05$) between RWIs and SFGDD at all sites except at CHAR ($r = 0.22$, $p = 0.24$, figures 2 and S4). SFGDD was the main climatic driver of radial growth at SAL1800, CN2400, LORIAZ, QGL and QN. At SAL2000, comparable correlations ($r = 0.46$, $p < 0.05$) were computed between the shrub-ring chronology, SFGDD and summer temperature while at QW, correlation with SFGDD ranks second after the correlation with February precipitation. More generally, RWI correlates negatively with winter precipitation at a vast majority of sites (except for SAL1800 and SAL2000). Finally, mean late summer

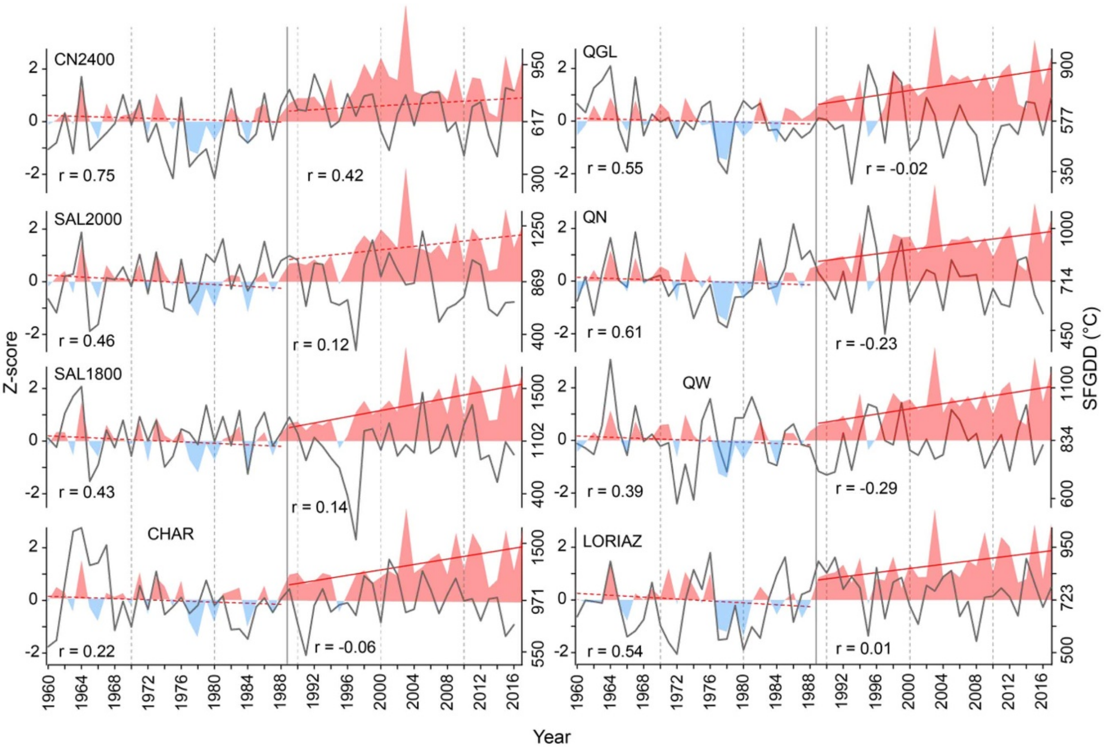

Figure 2. Annual SFGDD series with positive and negative anomalies with respect to the 1960–1988 average indicated by red and blue colors, respectively as well as mean (RWIs, black line) (1960–2017) for each of the eight sites within the French Alps. SFGDD values were transformed into Z-scores with respect to their mean over the 1960–1988 reference period. Dashed and solid red lines represent linear trends (non-significant and significant at $p \leqslant 0.05$) in SFGDD series for the time periods 1960–1988 and 1989–2017. Correlation coefficients between SFGDD and RWI are given for each period.

and early fall temperature in the year preceding growth-ring formation (September–October) correlated positively with RWI at SAL2000, CN2400, LORIAZ and QGL (figure S4).

Over the period 1989–2017, site-to-site climate-growth correlation profiles (figure S4) differ much more than over the period 1960–88. Interestingly, SFGDD remains the single most important driver of radial growth only at CN2400 ($r = 0.42$, $p < 0.05$, figure 2), whereas correlations between SFGDD and radial growth dropped close to zero at CHAR, LORIAZ, QGL, and SAL1800—and even become significantly negative at QW and QN (figure 2). Moreover, we find significant negative correlations between shrub chronologies and August air temperatures at CHAR, QN, QGL, and QW (figure S4). At QW, a negative impact of drought on *R. ferrugineum* radial growth is also evidenced by significant correlations between SFGDD ($r = -0.29$, $p < 0.05$) and summer SPEI ($r = 0.55$, $p < 0.001$). By contrast, detrended RW chronologies from SAL1800, SAL2000 and QGL are positively correlated with summer and early fall (September–October) temperatures. Finally, winter precipitation remains an important driver of radial growth at CN2400, LORIAZ, QGL and QN (figure S4).

The correlation matrices computed between site chronologies confirm the loss of consistency between both time periods (figure 3) and indicates that median intercorrelation decreased from 0.36 to 0.13 from 1960–88 to 1989–2017, respectively. Whereas all chronologies—with exception of LORIAZ—were significantly and positively correlated between sites until 1988, we observe a shift to low and mostly statistically insignificant values for a majority of correlation coefficients over the period 1989–2017.

To further explore potential drivers of shrubs growth, we used a linear mixed modeling approach to associate RW with SFGDD and a suite of geographical variables (i.e. elevation, Gams continentality index and northness index). Prior to computing mixed models, we investigated relationships between RW and SFGDD (figure S5). Conditional R^2 values reveals that, regardless of the period, all models can explain ∼50% of the interannual growth variability (44%, 45%, and 47% for 1960–2017, 1960–88, and 1989–2017, respectively; table 2). Marginal R^2 values (fixed factors) explain approximately half of the conditional R^2 showing that the proportions of variance explained by fixed and random variables remain comparable, regardless of the time period considered. According to the $\Delta\mathrm{AIC}_{\text{null vs model}}$ values, the models explain a greater part of the interannual growth variability than the null model. $\Delta\mathrm{AIC}_{\text{null vs model}}$ values yet are much higher for 1960–88 than for 1989–2017 (with values of 701.8 and 151.8, respectively).

For the period 1960–88, the model yields a positive, highly significant linear relation between

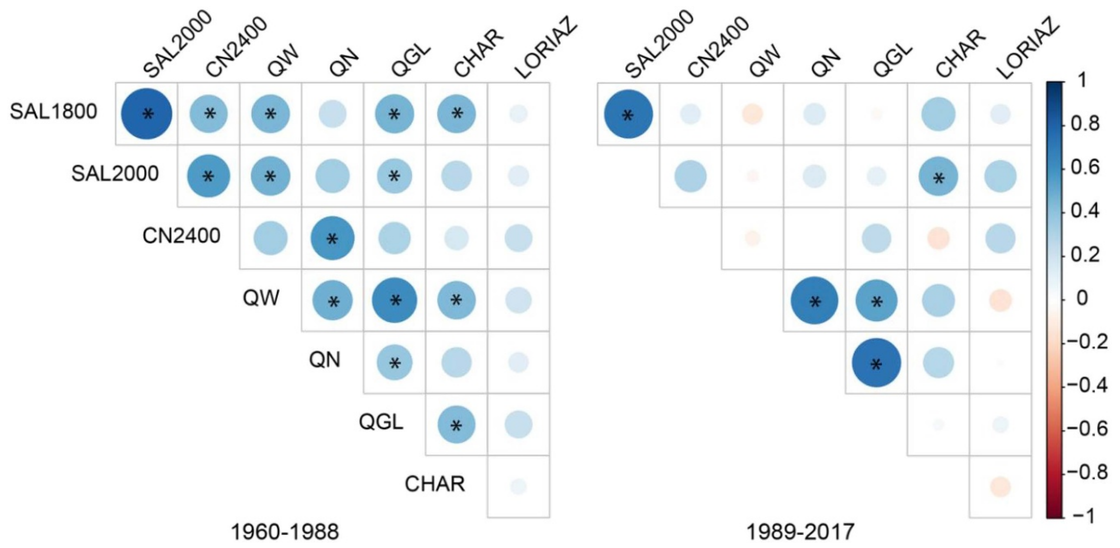

Figure 3. Correlation matrices between detrended *R. ferrugineum* site chronologies for 1960–1988 (left panel) and 1989–2017 (right panel). Color intensity and circle size are proportional to the correlation coefficients (see color scale). * ($p < 0.05$) indicates the level of significance.

Table 2. Fixed effect coefficients and Student's *t* values of the most parsimonious mixed models predicting *R. ferrugineum* RWs (mm, log-transformed) over the French Alps for the periods 1960–2017, 1960–88 and 1989–2017. Conditional R^2 (R^2c), marginal R^2 (R^2m) and AIC differences between each model and a null model ($\Delta\text{AIC}_{\text{null vs model}}$) are given for each model. All variables are scaled, with the exception of stem age. *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$) indicate the level of significance.

	1960–2017		1960–1988		1989–2017	
	R^2c = 0.44: R^2m = 0.23		R^2c = 0.45; R^2m = 0.19		R^2c = 0.47; R^2m = 0.19	
	$\Delta\text{AIC}_{\text{null vs model}} = 705.2$		$\Delta\text{AIC}_{\text{null vs model}} = 701.8$		$\Delta\text{AIC}_{\text{null vs model}} = 151.8$	
Parameter	Value	*t*-value	Value	*t*-value	Value	*t*-value
Intercept	0.584^{***}	10.35	0.304^{***}	4.05	0.494^{***}	6.37
SFGDD	0.276^{***}	21.78	0.404^{***}	28.60	0.175^{***}	8.63
$(\text{SFGDD})^2$	-0.114^{***}	−16.74	—	—	-0.065^{***}	−5.75
Continentality	-0.141^{*}	−2.69	—	—	-0.244^{**}	−4.08
Cos(aspect)	−0.060	−1.24	—	—	−0.021	−0.38
SFGDD*continentality	-0.190^{***}	−11.70	—	—	-0.208^{***}	−7.94
SFGDD*cos(aspect)	0.108^{***}	8.23	—	—	0.135^{***}	7.39
$(\text{SFGDD})^{2*}$continentality	—	—	—	—	0.066^{***}	7.54
$(\text{SFGDD})^{2*}$cos(aspect)	0.056^{***}	8.92	—	—	—	—
Age	-0.016^{***}	−17.55	-0.011^{***}	−6.06	-0.012^{***}	−9.72

SFGDD and RW, which is consistent with the fact that temperature during the snow-free period is the main driver of *R. ferrugineum* radial growth across the French Alps. By contrast, the independent variables slope aspect, elevation and continentality or the interaction with SFGDD were not significant predictors of RW and were removed from the final model for the period 1960–88. Comparison of the 1960–88 model with that obtained for 1989–2017 shows that, since 1989, *R. ferrugineum* radial growth is less constrained by SFGDD and that its response to temperature is increasingly modulated by continentality and slope aspect (table 2). The model computed over the entire period (1960–2017) indicates that the response of radial growth to SFGDD is non-linear and that it depends on slope aspect and continentality (table 2 and figure 4). The negative, statistically significant quadratic term computed between SFGDD and RW further points to a decline of *R. ferrugineum* radial growth above a certain SFGDD threshold. The interactions between SFGDD, slope aspect and continentality—included as significant in the model—points to some modulation of threshold values by these geographic variables. Accordingly, maximum radial growth can be expected if SFGDD reaches 1600 °C in the humid massifs characterized by a Gams angle of ~41°. The same threshold drops to 900 °C in the drier areas where the Gams angles are >68° (figure 4(A)). Similar differences are observed depending on slope aspect: That is, maximum RW values are modeled at 900 °C and 1700 °C on south- and north-facing slopes, respectively (figure 4(B)). By contrast, elevation does not seem to be a significant predictor in any model and therefore was eliminated as independent variable. This last result is probably due to the fact that snow

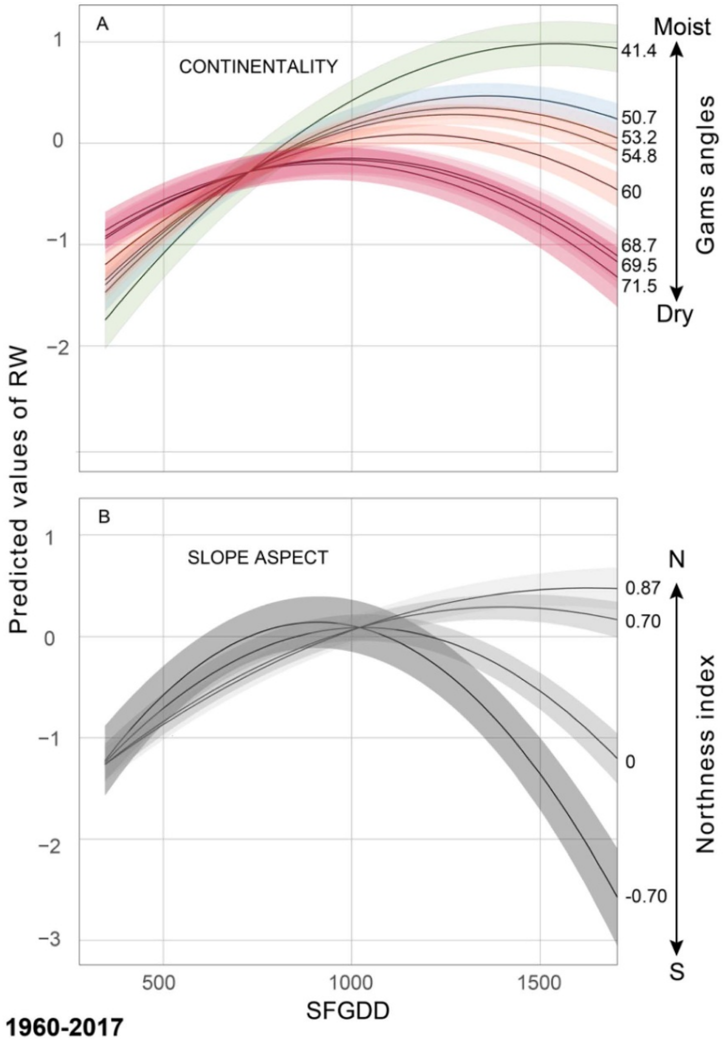

Figure 4. Linear mixed models of *R. ferrugineum* RWs (log-transformed and scaled RW values) as a function of SFGDDs and their interaction with continentality (A) and slope aspect (B) for the period 1960–2017. Ranges for northness and Gams continentality index are indicated to the right side of each panel.

and meteorological variables already encapsulate a great dependence on elevation.

4. Discussion

4.1. SFGDDs as the main driver of *R. ferrugineum* radial growth before 1989

Our results reveal strong, highly significant and consistent relationships between SFGDD and shrub radial growth until 1988 for all eight sites considered in the network. Our findings are consistent with the widely accepted concept that temperature—and more particularly growing degree days (Jochner *et al* 2018)—indeed are the single-most important drivers of plant growth in cold environments by driving cell division and phenological transitions (Körner 2003, Kudo and Suzuki 2003, Wipf 2010, Hoch 2015). Our findings are also in line with dendroecological studies realized in the Alps (Pellizzari *et al* 2014, Francon *et al* 2017, Carrer *et al* 2019). These studies demonstrated the positive effect of summer temperatures and the negative effect of snowpack duration on shrub radial growth at their upper elevational limit. In the Arctic, the vast majority of dendroecological studies found summer temperatures to be the main driver of shrub growth (Blok *et al* 2011, Jørgensen *et al* 2015, Myers-Smith *et al* 2015a, Andreu-Hayles *et al* 2020). Furthermore, previous studies considered sensitivity to temperature was considered to be consistent over contrasted topographic contexts in most studies (Bär *et al* 2008, Ackerman *et al* 2018, Carrer *et al* 2019).

4.2. Temperatures and RWs diverge since 1989

Interestingly, the increasing number of growing degree days observed in our meteorological series after 1989 did not result in a release of radial growth rates from thermal limitations. On the contrary, our results suggest a divergence between increasing SFGDD and shrub radial growth and thus, point to non-linear relationships between the two variables. In other words, and in agreement with smaller scale studies carried out in the Taillefer and Queyras massifs (Francon *et al* 2020a, 2020b), our data suggest a loss of sensitivity of shrub growth to SFGDD beyond a certain threshold, and that this threshold is indeed modulated by continentality and slope aspect. We hypothesize that the observed non-linear response of shrub growth is affected by a combination of two effects. On the one hand, the strong increase in growing season length makes shrubs less constrained by the availability of energy to complete their life cycle (Francon *et al* 2020a). On the other hand, however, this beneficial effect of rising temperatures on growth also seems to be compromised by the negative effects of drought, with the latter depending strongly on the position of the shrub along moisture gradients (Francon *et al* 2020b). Such non-linearity was not observed by Carrer *et al* (2019) who reported a consistent and negative role of winter precipitation on *J. communis nana* growth in the Italian Alps, despite the fact that a persistent and significant warming trend could be observed at their site as well. By contrast, warming climate negatively impacted alpine juniper shrub growth and shrub recruitment in the central Himalayas and Tibetan Plateau due to increasing drought stress (Lu *et al* 2019, Pandey *et al* 2020). Moreover, a loss of sensitivity to temperature has been observed since the 1990s in *Betula nana* and *Salix glauca* shrubs from Western Greenland (Gamm *et al* 2018), *Betula nana* and *Empetrum hermaphroditum* shrubs in the central Norwegian Scandes (Weijers *et al* 2018a) and in *Rumex alpinus* herbs in the Low Tatras of Slovakia (Dolezal *et al* 2020) which was attributed to global warming and its effects on increasing soil moisture limitation or more frequent late frost events. Similar negative effects of increasingly higher summer temperatures have been highlighted in terms of productivity of alpine meadows in the European Alps (de Boeck *et al* 2016, Cremonese *et al* 2017, Corona-Lozada *et al* 2019), underlining that, if combined with water deficit, heat waves will lead to vegetation browning. The loss of sensitivity to temperature that we highlight in this study echoes the 'divergence problem' that has been reported for trees growing in certain regions of circumpolar northern latitudes (Briffa *et al* 1998, Driscoll 2005, D'Arrigo *et al* 2008) and high-elevation sites (Büntgen *et al* 2008). This body of literature suggests—although with a focus on trees—complex and non-linear growth responses of trees to climate changes, thereby leading to a decrease of year-to-year sensitivity of tree growth in previously temperature-limited environments since the mid to late 20th century (D'Arrigo *et al* 2004, 2008, Wilmking 2005, Büntgen *et al* 2008, Oberhuber *et al* 2008, Leonelli *et al* 2009). Potential causes for this divergence include warming-induced thresholds of tree growth (D'Arrigo *et al* 2004) or increasing drought stress (Büntgen *et al* 2006). Assessment of divergence phenomena for shrubs has been only mentioned once at the Arctic tundra biome in response to warming and drying climate (Buchwal *et al* 2020). In the same manner as for *R. ferrugineum*, Arctic shrubs display a pronounced growth response heterogeneity starting in the mid-1990s. However, a careful assessment of a divergence problem for alpine shrubs would require shrub ring chronologies covering longer periods, but also broader regions and accounting for other species.

4.3. Topographically driven moisture limitation as a possible driver of divergence

The fact that lower correlations are observed between the chronologies at all eight sites after 1989 and that greater heterogeneity emerges in the BCF profiles points to strong site effects that have become the key modulators of shrub growth responses to climate over the last few decades. Thus, we hypothesize that the recent loss of sensitivity and the non-linearity in the response of shrub growth to SFGDD, also referred to the 'divergence problem' in forestry and tree-ring research, could be explained by moisture limitations driven by topoclimate and microsite (Wilmking *et al* 2004, Wilmking 2005). The influence of topoclimate is confirmed by our mixed modeling approach which includes continentality and slope aspect variables in interaction with SFGDD as significant terms. Indeed, both variables directly control soil moisture both at the mesoscale (slope aspect) and at regional (continentality) scales. Therefore, shrubs growing on drier sites (characterized by higher Gams angles and lower northness indices) are more affected by the ongoing increase of air temperatures. Based on dendroecological studies realized in the Arctic, Myers-Smith *et al* (2015a) likewise postulated that topography, soil properties and snow-related moisture availability would modulate the positive effect of rising temperature on shrub growth. In other words, the sensitivity of shrubs to moisture stress has increased clearly over the last few decades, but this evolution still greatly depends on site characteristics. We are not aware of other studies reporting on topographical effects of moisture stress on shrub growth. In the Italian Alps, the absence of topographic effects on shrub growth reported by Carrer *et al* (2019) for *J. communis nana* can be explained by the its lesser sensitivity to drought as compared to *R. ferrugineum* (Gracia *et al* 2007) or to less pronounced topographic variability within the Italian site network. Besides moisture limitation, an increasing frequency of late frost events has been shown to cause both short-term (through damage to aerial parts of the shrub, Bokhorst *et al* 2009, Treharne *et al* 2019) and longer-term (through winter droughts, Phoenix and Bjerke 2016, Charrier *et al* 2017) stresses to shrub vegetation and could, thus, further exacerbate the observed divergence in growth responses. However, when comparing the RWI with the freezing degree days index (calculated as the sum of daily minimum temperature below −2 °C estimated from the moment of melt-out to the end of August), we do not detect any significant effects

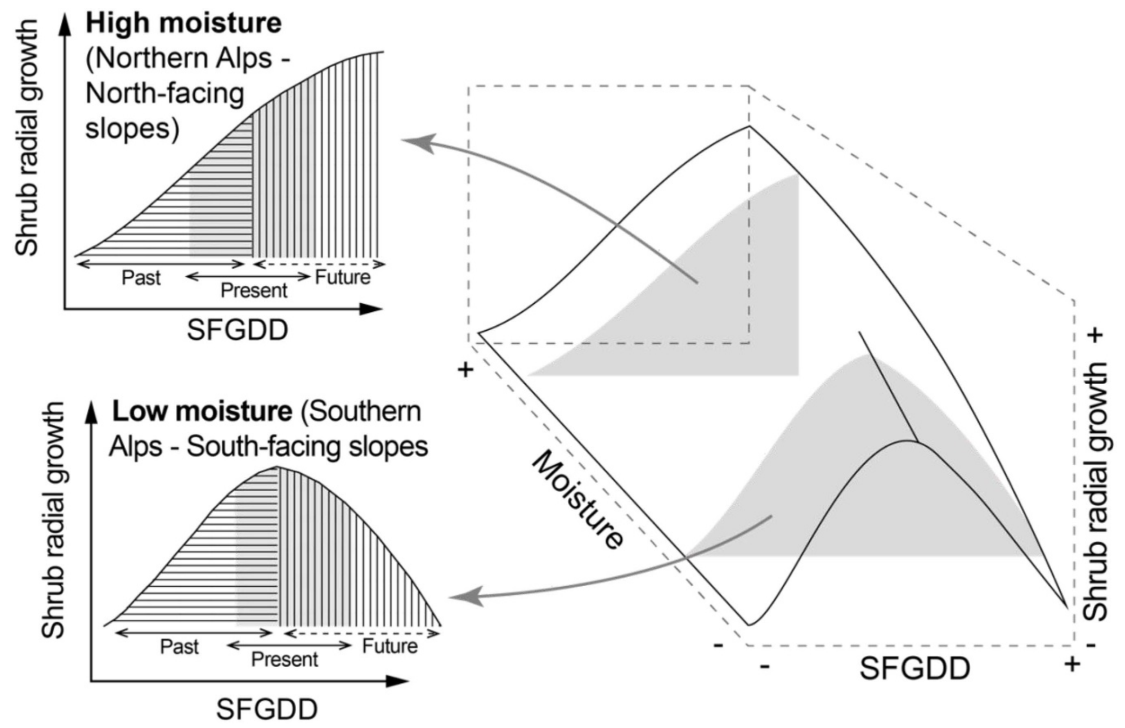

Figure 5. Conceptual model synthesizing potential responses of *R. ferrugineum* radial growth along the moisture gradient to increasing SFGDD in a warmer climate. In wetter sites (top left panel), increasing SFGDD are expected to favor radial growth. By contrast, at drier sites (bottom left panel), a non-linear response is anticipated and will likely limit radial growth above a certain SFGDD threshold.

of late frost on *R. ferrugineum* growth in our dataset. This absence of frost effects should yet be interpreted with caution as frost risk depends strongly on plant exposure and vulnerability, which in turn will be determined by microtopography, plant phenology and hardening (Bréda and Peiffer 2014). On this specific point, studies coupling high-resolution microclimatic and ecophysiological monitoring are yet to be realized to allow for more robust conclusions about effects of frost on shrub growth (Charrier *et al* 2017).

By contrast, the linear mixed model approach allowed determination, for the first time, of thresholds for the occurrence of divergence. Accordingly, values of 900 °C and 1600 °C represent SFGDD thresholds for *R. ferrugineum* radial growth in the dry (or eastern) and moist (or western) mountain massifs of the French Alps. The threshold also varies with changing aspect and could be set to 900 °C and 1700 °C for south-facing and north-facing slopes, respectively. However, one should keep in mind that the linear mixed model only explains 45% of the interannual RW variability with 24% attributed to the fixed effects. In that respect, taking both microsite (microtopography, soil properties) and (inter-)individual characteristics (competition, morphology, genetic/phenotypic variability) into account will facilitate the definition of potential drivers of shrubs growth further (Wipf *et al* 2006, Myers-Smith *et al* 2015a, Boulanger-Lapointe *et al* 2016, Bjorkman *et al* 2018, Berner *et al* 2020) and thereby also enhance the reliability of our approach.

5. Conclusion

The approach developed in this study relies on a network of *R. ferrugineum* RW series from eight contrasted topoclimatic locations across the French Alps. The unprecedented size and spatial coverage of the dataset, along with the temporal resolution of the meteorological and snow cover reanalyzes data used allowed facilitated the disentanglement of variables driving shrub growth at the individual level across sites. We demonstrated that a clear divergence emerged between shrub growth across the French Alps and increasing air temperatures after the early 1990s, a phenomenon that has previously not been demonstrated in the alpine environment (Carrer *et al* 2019), but has been detected in shrub rings in the arctic environment (Buchwal *et al* 2020). Our study also points to a likely modulation of the observed divergence by temperature thresholds, which in turn are controlled by differences in moisture availability resulting from contrasted topographical and geographical parameters. Given the increasing air temperatures and the earlier snow melt-out timing projected by climate model simulations (Gobiet *et al* 2014, Beniston *et al*, 2018, IPCC 2019), these thresholds will likely be exceeded even more frequently during the 21st century. By synthesizing the findings of this study, we offer a conceptual model (figure 5) summarizing the potential response of *R. ferrugineum* radial growth to increasing SFGDD in a warmer climate for wetter and moisture-limited sites. Individuals should benefit from increasing temperatures on north-facing slopes in the north-westernmost regions of the French Alps. By contrast, we expect their productivity to decrease as a result of increasingly severe moisture limitations at the drier sites in the Southern Alps. Collectively, our results underline the high sensitivity of *R. ferrugineum* to climate change. We therefore consider this shrub to be a valuable sentinel species as it integrates the complex and multi-directional effects that climate change will continue to have on alpine ecosystems (Francon *et al* 2020a). Scaling up, we encourage future studies to investigate potential relationships between divergent growth responses demonstrated by dendroecological analyses and the greening or browning trends quantified with remote sensing methods (Cunliffe *et al* 2020). At a more micro-scale, further work is also need to disentangle the underlying eco-physiological processes for the non-linear relationships observed between ring growth and temperature increase (de Swaef *et al* 2015, de Micco *et al* 2019). The latter should necessarily be complemented with high-resolution spatial imagery (Myers-Smith *et al* 2020) to account for the heterogeneity of alpine environments. We encourage future alpine studies to focus on the implications of the bidirectional evolution of shrub growth evidenced here on shrub expansion, carbon transfers, radiative feedbacks, and biodiversity.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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