



Climate response of a glacial relict conifer across its distribution range is invariant in space but not in time

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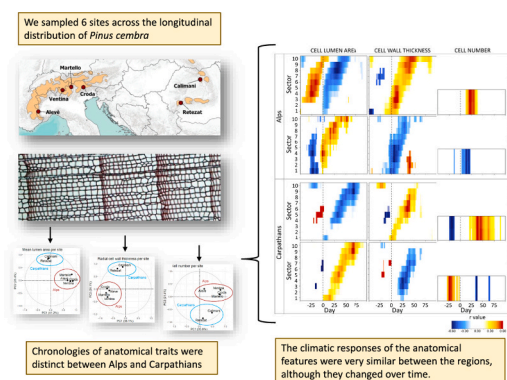
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HIGHLIGHTS

- We investigated *Pinus cembra* xylem anatomy at 6 sites in the Alps and Carpathians.
- Climate responses were consistent across sites, but varied over the study period.
- At all sites, we observed negative effect of high temperature on cell lumen area.
- Climate warming can harm xylem hydraulic system of *P. cembra* in its entire range.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate change impacts on forest trees will be particularly severe for relict species endemic to the subalpine forest, such as *Pinus cembra* in the Alps and Carpathians. Most current knowledge about the response of this species to climate comes from tree-ring width analysis. However, this approach cannot perform in-depth and highly time-resolved analysis on the climate influence on specific growth processes and xylem functions. We analyzed xylem anatomical traits from six sites covering most of the longitudinal range of this species. Associations between climate and cell number, lumen area and cell wall thickness were computed for the 1920–2010 period using climate records aligned to degree-day temperature sum thresholds. The anatomical chronologies were clearly distinct between the Alps and Carpathians. However, climate responses were similar for all sites, suggesting common species-specific response mechanisms. Temperature showed a positive correlation with both cell number and cell wall thickness. Cell lumen size exhibited an early positive association, followed by strong negative association with temperature and a positive one with precipitation. This highlights that the cell enlargement process was negatively related to high temperature at high elevation, where meristematic processes are rather supposed to be constrained by low temperatures. Therefore, long-term climate warming can have

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negative consequences on the xylem potential to transport water at all investigated sites. Moreover, in the last 30 years, we observed a slight anticipation of some responses and a decrease in climate sensitivity of some xylem parameters. Our findings provide evidence of temporally unstable but spatially consistent climate response of *Pinus cembra* from the Alps to the Carpathians. The low diversity in xylem phenotypic responses to climate suggests that future warming could extensively and evenly affect the species throughout its entire distribution.

1. Introduction

Recent global warming is strongly affecting plant performance, growth and distribution, especially in heat-limited environments (Harsch et al., 2009; Hagedorn et al., 2014; Lamprecht et al., 2018; Allan et al., 2021), with direct effects also on ecosystems structural and biodiversity attributes (Holtmeier and Broll, 2007). In Europe the start of the growing season is advancing by 2.5 days/decade, with consequent advance of the phenological phases (Parmesan and Yohe, 2003; Menzel et al., 2006; Vitasse et al., 2021). Within the Alpine region, isotherms moved upward in the last century as result of increasing temperature (Grace et al., 2002; Rubel et al., 2017). Since one of the major global effects of warming at high elevation is to enhance tree radial growth (Camarero et al., 2021), we might expect significant consequences also in the European mountain forests. However, responses of high-elevation tree species to temperature are highly heterogeneous and not always a direct consequence of increasing temperature, since other factors, such as water availability or soil conditions, can play an important role (Harsch et al., 2009; Isaac-Renton et al., 2018; Fajardo et al., 2019). For example, many conifer species growing at the northern treeline showed a negative association between radial growth and warming, likely due to moisture limitation (Lloyd and Fastie, 2002; Girardin et al., 2014; D'Orangeville et al., 2018). Additionally, even precipitation will likely be altered in the near future, though with a more heterogeneous and less clear pattern than temperature (Allan et al., 2021). This leads to future predictions that are far from linear and emphasizes the need for a comprehensive understanding of tree responses to climatic factors.

Pinus cembra L. is a glacial relict conifer, endemic to the Alps and Carpathians and is a typical high-elevation tree species, mostly important for biodiversity conservation, soil and avalanche protection and natural landscape preservation. Its confined distribution range resulted from post-glacial competition with other species, anthropogenic pressure, and seed dispersal issues (Tomback et al., 1993; Casalegno et al., 2010; San-Miguel-Ayanz et al., 2016; Neuschulz et al., 2018). The

current Carpathian and Alpine populations seem to share a common gene pool, indicating a previous spatially continuous distribution (Höhn et al., 2009; Dauphin et al., 2020). In the context of the modern warming scenario, at the lower distribution limits, this species will likely be outcompeted by the coexisting *Picea abies* L. Karst. and *Larix decidua* Mill. while, at high elevation, the expansion of new patches is already documented (Lingua et al., 2008; Casalegno et al., 2010). This upward shift of the upper forest limit (Gehrig-Fasel et al., 2007) might imply a consequent progressive upward confinement of *Pinus cembra*. Therefore, despite the potential gains for growth due to warming conditions, *Pinus cembra* may also be threatened by other side-effects of climate change. Yet, future responses to climatic factors for this species are still uncertain, especially from the spatial and temporal variability point of view. The radial growth of actual treeline species is predicted to decouple from temperature (Camarero et al., 2021). However, the small area of continuous distribution and the high number of isolated populations that characterize this taxon make predicting its future distribution challenging (San-Miguel-Ayanz et al., 2016).

Climate-growth responses of high-elevation tree species have usually been explored through tree-ring width analysis (e.g. Frank and Esper, 2005; Camarero et al., 2021). Recently, retrospective quantitative wood anatomy (dendroanatomy) disclosed its potential in revealing climate-influence on tree species not evident with classical approaches (Arzac et al., 2021; Lange et al., 2020). In fact, different anatomical traits are related to different xylogenetic phases (cell formation, cell enlargement and wall thickening). This may result, within the growing season, in a partial temporal separation between traits during xylogenesis (Rossi et al., 2016), which may stem from different responses to climatic factors (De Micco et al., 2019; Borghetti et al., 2020). Moreover, xylem traits can be investigated at the intra-ring level, allowing intra-seasonal climate responses to be detected with an unprecedented definition not reachable with any classical tree-ring parameters (Castagneri et al., 2017; Pérez-de-Lis et al., 2022). Yet, until now no studies aimed to investigate the spatial pattern of climate-anatomical associations at high

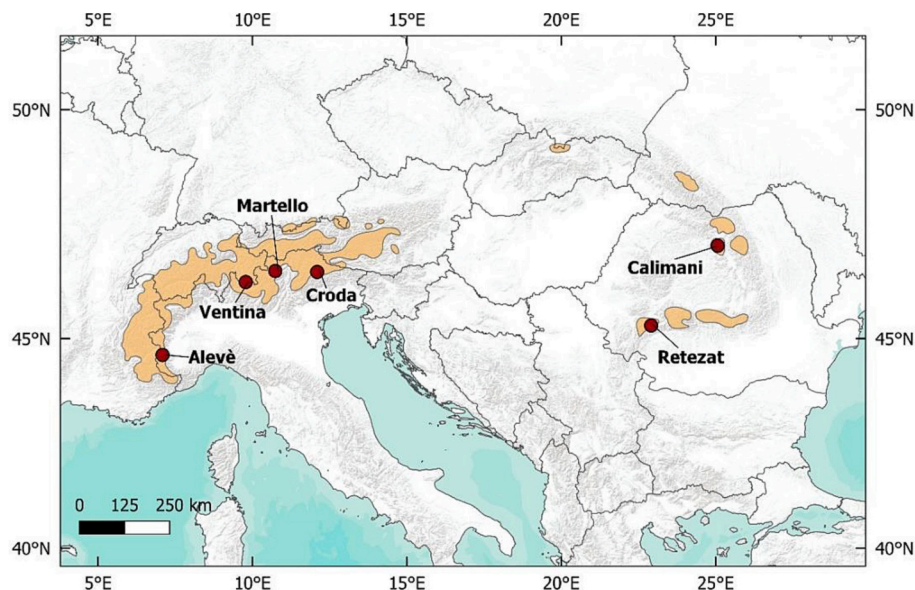


Fig. 1. Sampling sites (red dots) and distribution range of *Pinus cembra* (dark yellow area). Sources ESRI Terrain and www.euforgen.org.

Table 1

Yearly and April-to-September mean maximum temperature (Tmax; °C) and precipitation sum (mm) for all sites for the period 1920–2010.

Site	Tmax (°C)		Precipitation (mm)	
	Year	Apr–Sep	Year	Apr–Sep
Alevè	6.9	11.4	871	482
Ventina	5.8	10.5	1122	674
Martello	4.5	9.5	942	567
Croda	5.7	10.6	1157	725
Calimani	8.6	15.9	715	490
Retezat	8.6	15.7	794	479

elevation dealt with a broad site network of xylem anatomical traits. To this end, we selected *Pinus cembra* as one of the most iconic mountain conifers across Europe known for its narrow and distinctive distribution range, which is confined to the subalpine belt in parts of the Alps and to some high-elevation regions of the Carpathians (Ulber et al., 2004). This allowed us to establish the first network encompassing large part of the distribution range of a species, aiming to investigate xylem anatomical associations with temperature and precipitation records at sub-monthly resolution. We aimed to understand i) if the climate influence on xylem traits of *Pinus cembra* is spatially consistent between disjointed sites and regions and ii) if it is possible to detect any sign of misfitting potentially linked to current climate warming. We hypothesize I) that most xylem

traits, population-wise, are sensitive to summer temperature, heat being the key limiting factor for plant tissue formation at high elevation; (II) the presence of some geographically-related difference in climate-growth response patterns, given the distance between the Alps and Carpathians and (III) given the recent global warming, a relaxation of the temperature constraints on xylem traits in the last decades.

2. Materials and methods

2.1. Study sites and sample collection

We selected six sites at high elevation covering the longitudinal range of *Pinus cembra* (Fig. 1). Four sites in the Alps (Italy): Alevè (44.61 N, 7.04 E; 2100 m a.s.l.), Ventina (46.29 N, 9.79 E; 2200 m a.s.l.), Martello (46.53 N, 10.72 E; 2280 m a.s.l.) and Croda da Lago (46.48 N, 12.10 E; 2100 m a.s.l.); and two in the Carpathians (Romania): Retezat (45.39 N, 22.89 E; 1780 m a.s.l.) and Calimani (47.10 N, 25.24 E; 1700 m a.s.l.). At each site we selected 20 dominant trees growing on similar environmental settings in terms of microclimate, topography and substrate, and collected one 10-mm core at breast height (1.30 m above the ground).

Temperature regimes exhibit a classical bell curve pattern, with a peak occurring between late July and early August at all sites. However, in the Carpathians, temperatures are higher during summertime

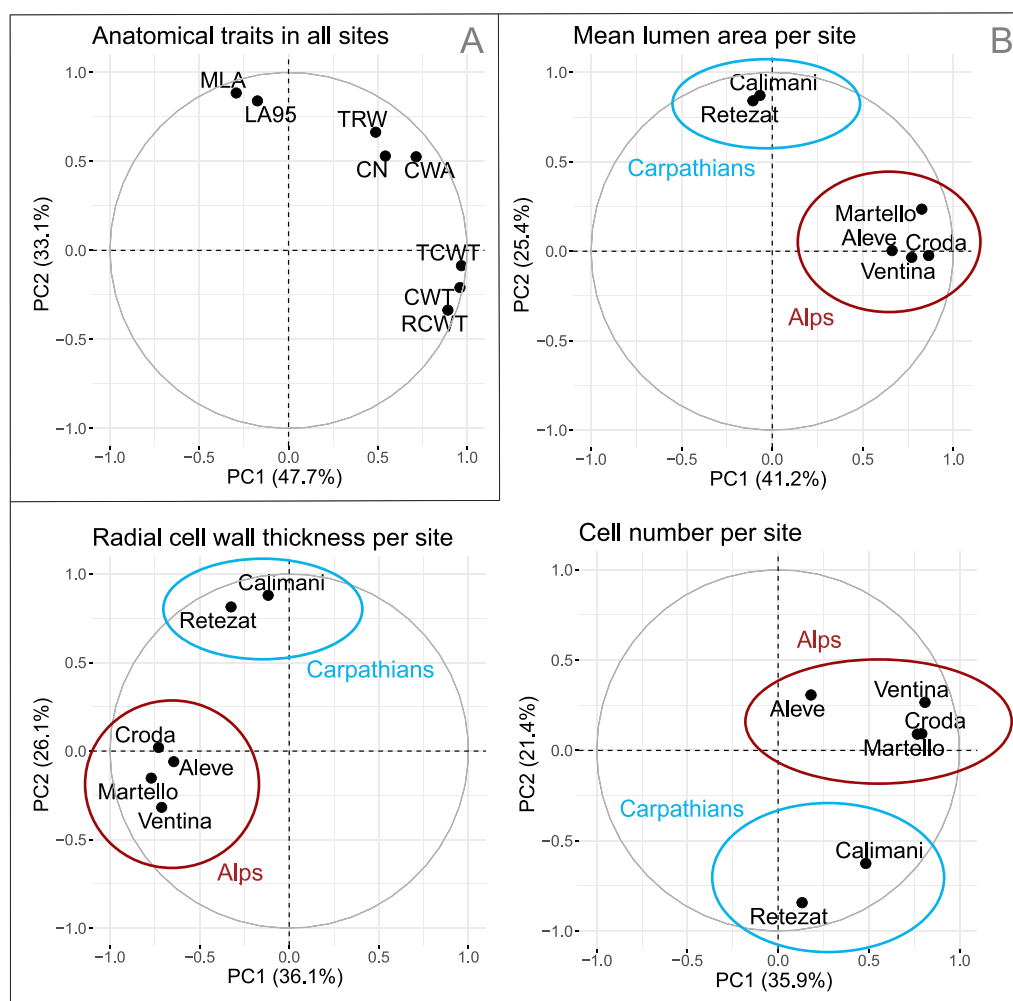


Fig. 2. (A) Loading plot of the principal component analysis (PCA) performed with all measured traits, i.e., mean tree-ring width (TRW), cell number (CN), mean lumen area (MLA), lumen area at 95 % percentile (LA95), radial and tangential cell wall thickness (RCWT, TCWT), total cell wall thickness (CWT) and cell wall area (CWA), in all sites together. (B) Loading plots of the principal component analysis performed with mean lumen area, radial cell wall thickness and cell number chronologies of the six investigated sites separately.

compared to the Alps, and there is a larger temperature range between summer and winter months, indicating more continental conditions. The Alps feature a higher yearly precipitation sum than the Carpathians, while the precipitation regime is highly variable between sites and regions (Table 1; Supplementary Fig. 1; Supplementary Table 1. We used climatic data from the E-OBS gridded dataset (Cornes et al., 2018) for the Carpathians, and from the last homogenized Italian daily-climate dataset as described in Brunetti et al., 2004, 2006 for the Alps.

2.2. Samples processing

In the laboratory, cores were first sanded with progressive grid sandpaper and ring widths measured to the nearest 0.01 mm with TsapWin software (Rinntech, Heidelberg, Germany). Individual series were then crossdated following standard dendrochronological procedures (Stokes and Smiley, 1968; Cook and Kairiukstis, 1990) and finally checked for dating and measuring errors using the COFECHA program (Holmes, 1983). The cores with no visible defects (torsion, cracks, knots, missing or rotten parts, etc.) were selected for anatomical analysis. We applied the standard protocol (von Arx et al., 2016) following these steps: i) cores were split in ca. 5 cm segments, from which 10 μm transverse sections were cut using a rotary microtome (Leica, Heidelberg, Germany); ii) slices were then stained with safranin (1 % in distilled water) and fixed to create permanent slides with Eukitt mounting medium (BiOptica, Milan, Italy) and iii) microscopic digital images were collected at 100 \times magnification (resolution 1.99 pixel/ μm or 0.502 $\mu\text{m}/\text{pixel}$; D-sight by A. Menarini Diagnostic s.r.l. Florence, Italy). Images were later analyzed through the ROXAS v3.0 software that provides measurements of a vast array of anatomical traits (von Arx and Carrer, 2014; Prendin et al., 2017). Besides tree-ring width (TRW), we considered the following anatomical parameters in each ring: cell number (CN) in an area with fixed tangential width of 1 mm and a variable radial length corresponding to the ring width (Castagneri et al., 2015), mean lumen area (MLA), lumen area at 95 % percentile (LA95), radial and tangential cell wall thickness (RCWT, TCWT), total cell wall thickness (CWT) and cell wall area (CWA).

To increase the resolution of the associations between climate and anatomical traits and having the relative position of each cell within each dated ring, every ring was split into 10 tangential sectors of equal width (Castagneri et al., 2017) ranging from the 1st sector at the beginning of the earlywood to the 10th sector that corresponds to the final part of the latewood. For each sector, we assessed the median of cell size parameters (i.e. excluding CN). All the resulting series were then standardized to remove age/size related trends (Cook and Kairiukstis, 1990; Carrer et al., 2015) using a smoothing spline with 50 % frequency cut-off of 30 years. For each sector and anatomical trait, individual detrended series were finally averaged at site level by bi-weight robust mean to build the mean site anatomical chronologies using the R package dplR (Bunn, 2008). Since climate series can have long-term trends that can affect climate correlations, climate data series were detrended using the same spline function used for wood anatomical series (Ols et al., 2023).

2.3. Data analysis

We performed principal component analysis (PCA; Abdi and Williams, 2010) on the correlation matrix at two stages. The first PCA was run with all anatomical traits (MLA, LA95, CN, TRW, CWA, RCWT, TCWT, CWT) considering both single sites and all sites together to explore the relationships among traits (Fig. 2A). Based on these results, to avoid redundancy for the successive analyses we selected three representative traits: MLA (related to the cell enlargement phase and hydraulic transport), CN (related to cambial activity, stem growth and carbon stock), and RCWT (related to cell wall thickening phase, stem mechanical support and carbon stock). We performed the second PCA on the three selected parameters to assess the spatial variability of

anatomical chronologies between sites. According to these results (Fig. 2B), in the following analysis we aggregated the four Alpine and two Carpathians sites, averaging both the standardized anatomical chronologies and the corresponding climatic series.

Climate/anatomical trait associations were assessed by computing the correlation between trait chronologies (MLA, RCWT and CN) and minimum, maximum, and mean daily temperature and precipitation series considering time windows of 15, 20 and 30 days at daily step. Instead of considering climatic records aligned in the conventional way, i.e. to the calendar day of year (DOY), we aligned daily-resolved climate records to the day when a certain degree-day (DD) temperature sum was reached in each year. The temperature sum was calculated as (McMaster and Wilhelm, 1997):

$$\sum_j^m \left(\frac{T_{\max} + T_{\min}}{2} \right) - 5$$

where $j = 1, 2, \dots, m$ are days with an average temperature higher than 5 °C (commonly used as the lower limit for plant growth; Grigorieva et al., 2010), while T_{\max} and T_{\min} are the daily maximum and minimum air temperatures (°C). This approach should improve the identification of the correct period to consider in the climate-anatomical trait associations. In fact, xylem phenology does not only depend on the photoperiod (associated to the DOY), but is highly variable between years and significantly influenced by the peculiar progression of seasonal temperature (Rossi et al., 2014; Gričar et al., 2014). After testing different (1) climate parameters, (2) time windows and (3) temperature sum thresholds, we finally selected (1) precipitation and maximum temperature, (2) the 20-day window and (3) the temperature sum of 74° days, on average reached on June 29th (day of the year 180) for the Alps and the temperature sum of 102° days, on average reached on June 9th (day of the year 160) for the Carpathians. That is, the “day 0” in each year was the day when the temperature sum of 74 (Alps) 102 (Carpathians) degree days was reached. All the analyses were performed for the period 1920–2010, which represents the temporal window covered by all meteorological and anatomical trait time series and were implemented in R v. 3.1.0 (R Core Team, 2021). Given that precipitation and maximum temperature may exhibit negative associations, we also conducted a partial correlation analysis to disentangle their effects on xylem anatomy (Jevšenak, 2020). Specifically, we assessed the connection between xylem anatomical chronology (the response variable) and, alternatively, maximum temperature and precipitation (the predictor), controlling for the effects of, alternatively, precipitation and maximum temperature (the other predictor), using pcor (Kim and Yi, 2007) package in R.

To assess the consistency of the temperature-growth correlations over time we split the 90-year period into two sub-periods defined for each region after performing the piecewise linear regression on the April–September temperature records (Yang et al., 2016). This time window broadly corresponds to the typical xylem growth season for trees in cold environments (Rossi et al., 2016). Climate responses for all the xylem traits were then performed for these sub-periods, maintaining all the settings as for the previous analysis of the whole period.

3. Results

The PCA computed on the standardized site chronologies of MLA, RCWT and CN highlighted a clear separation between the Alps and Carpathians. The first two components explained a rather similar percentage of variance: 66.6 % for MLA, 62.2 % for RCWT and 57.3 % for CN (Fig. 2B). Accordingly, in the following analysis we aggregated the Alpine and Carpathian chronologies.

TRW at Alpine sites were ca. 25 % narrower but less variable with respect to Carpathian ones, while xylem tracheids in the Alps were slightly smaller and thicker than in the Carpathians (Supplementary Table 2).

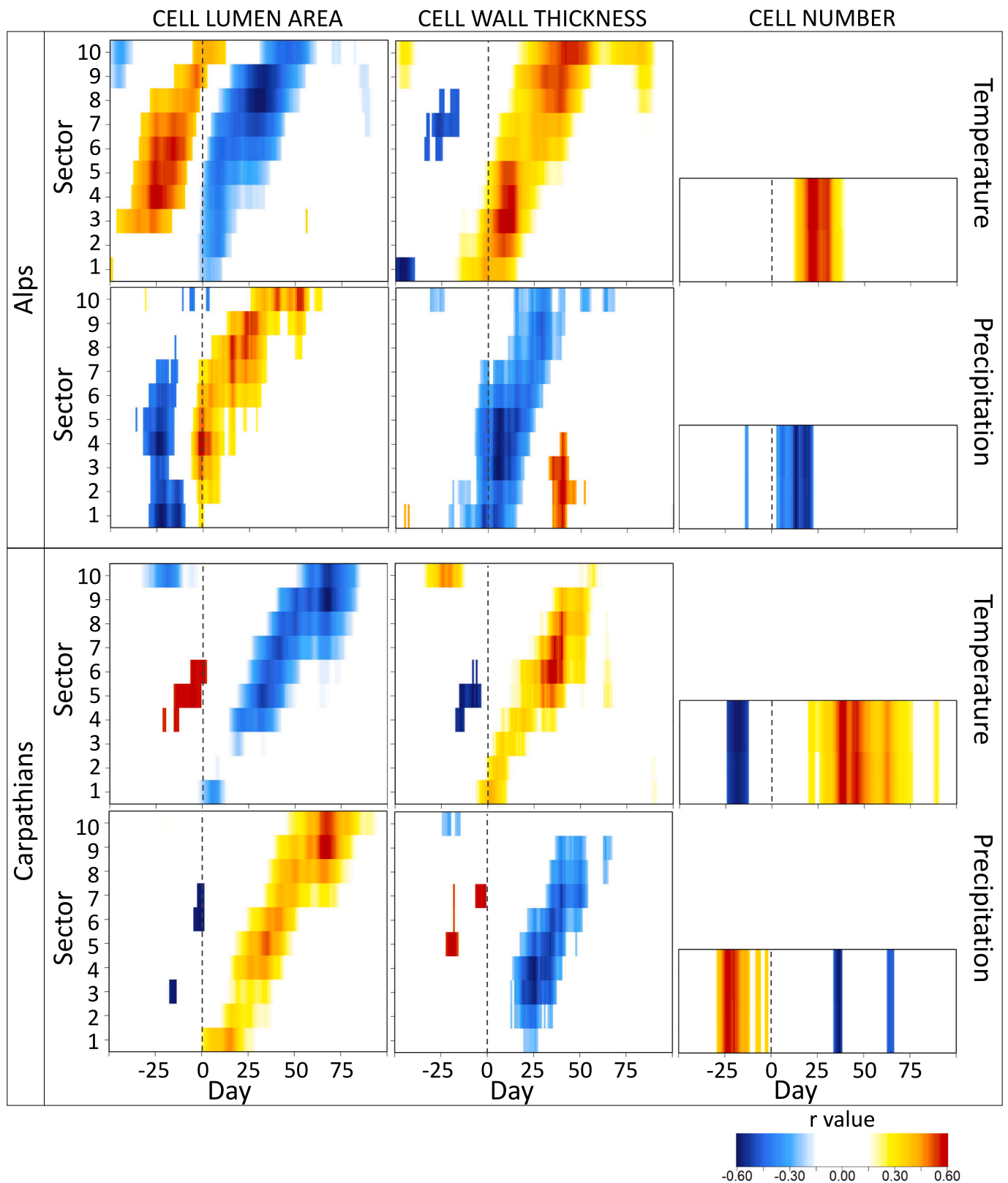


Fig. 3. Correlations between xylem anatomical chronologies and daily climate data over the period 1920–2010 for the Alps and Carpathians. Anatomical parameters are cell lumen area and radial cell wall thickness partitioned in 10 sectors (y-axis), and cell number (entire ring). Climate data are mean maximum temperature and precipitation sum expressed as 20-day moving windows. On x-axis, the 0 corresponds to the day when the degree day sum threshold (74° days for the Alps, 102° days for the Carpathians) is reached. Correlations on 20-day moving windows centred 50 days before to 100 days after the day 0 are shown. Coloured areas indicate significant correlations ($p < 0.05$), ranging from -0.60 (blue) to 0.60 (red).

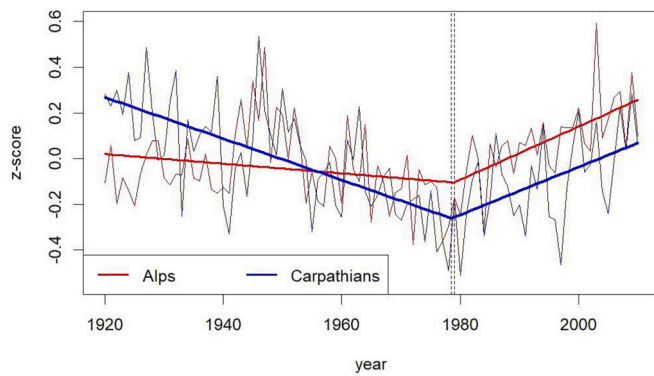


Fig. 4. Thin lines represent the standardized (z-scores) series of April-to-September mean maximum temperature (1920–2010) for the Alps (red) and Carpathians (blue), while thick lines represent the respective piecewise linear regression models. Dashed vertical lines indicate the year corresponding to the detected breakpoints.

The day when the selected degree day sum (74 DD for the Alps and 102 DD for the Carpathians) was reached showed high inter-annual variability in all sites (Supplementary Fig. 2). Correlations computed with the DD approach showed clearer patterns along the sectors and were stronger than those calculated with the DOY approach (e.g. see Supplementary Fig. 3).

Temperature and precipitation responses of MLA, RCWT and CN were mostly similar for all the sites (Supplementary Fig. 4 and 5) and in the two regions (Fig. 3) with all the main significant associations of MLA and RCWT gradually shifted from early- to late-sectors in a few weeks. Maximum temperature showed mostly a positive correlation with CN and RCWT, and with MLA a few days before the day 0, especially in the Alps. A consistent negative correlation between temperature and MLA was observed after the day 0 along all ring sectors. Precipitation generally showed opposite patterns. Partial correlation analysis indicates that negative correlations of precipitation were mostly related to correlations with temperature (Supplementary Fig. 6). However, in the Carpathians CN was positively related to precipitation 25 days before the day-degree sum threshold was reached. Maximum temperature extended its influence for a shorter period in the Alps (ca. 20 days for CN and 60 days for MLA) than in the Carpathians (ca. 60 days for CN and ca. 80 days for MLA).

The piecewise linear regression identified 1978 for the Carpathians and 1979 for the Alps (Fig. 4) as the year from which a change of trend slopes occurred. Accordingly, we tested the stability in climate-trait associations splitting both Alpine and Carpathian climatic and anatomical time series into two periods: 1920–1979 and 1980–2010.

Despite the correlations with temperature and precipitation retaining the same sign in both sub-periods, a few changes occurred from the first to the second period (Figs. 5 and 6). We observed reduction of the positive correlation between maximum temperature and MLA before the day 0, and of the positive correlation between maximum temperature and RCWT, in both the Alps and Carpathians. The maximum temperature signal in the Alps occurred earlier during the second period, whereas it decreased in the Carpathians.

4. Discussion

By investigating xylem anatomical chronologies of high elevation *Pinus cembra* across its whole longitudinal distribution, we found a clear separation between the Alps and the Carpathians. This reflects the different climate modes of the two regions, with the Alps mostly influenced by the central European climate and the nearby Mediterranean, and the Carpathians mostly affected by the inner continental eastern European mode (Supplementary Figs. 7 and 8). Nonetheless, for all the investigated xylem traits, response to climate was remarkably consistent

between the regions, despite the different sites environmental settings, soils, rock types, stand and disturbance histories. Within a species, distinct genetic groups (provenances) are expected to show different responses to environmental constraints (Montwé et al., 2018; Matison et al., 2019). Common climate response mechanisms observed in this study probably reflect the low genetic differentiation between the Alpine and Carpathian *Pinus cembra* populations. Indeed, this glacial relict species shares a common ancient genetic pool, even featuring a geographical separation in two distinct sub-regions and in many disjointed areas (Höhn et al., 2009; Gugerli et al., 2023).

Identified temperature sum thresholds were in line with a study on high-elevation *Pinus cembra* xylogenesis in Austria (Gruber et al., 2009). By aligning the climatic series to the degree day temperature sums, we tuned the climate-growth associations according to the idiosyncratic behavior of year-to-year temperature variability. This permitted the climate response of the species to be better highlighted in relation to site peculiarities. Additionally, the intra-ring approach revealed a temporal shift of climate responses from the first to last cells in the ring, underlying the persisting and significant climate influence on xylem cell formation over time within the growing season in both regions. Climate association of xylem traits in the Carpathians seemed to start earlier (early June) than in the Alps (late June) and last longer. This can be framed considering: i) the more continental climate of the Carpathians, with stronger temperature difference between winters and summers with respect to the Alps, and ii) the elevation differences between the sampling sites (ca. 1700 for the Carpathians and 2150 m a.s.l. for the Alps), though in both regions these altitudes reflected the current elevational margin of *Pinus cembra* populations (Casalegno et al., 2010).

Heat limitation usually affects growth of high-elevation species, including *Pinus cembra* (Carrer et al., 2007; Normand et al., 2009; Körner, 2012; Lopez-Saez et al., 2023; Izvorska et al., 2023) and accordingly we observed cell number and cell wall thickness to be positively affected by air temperature. Partial correlation analysis showed that the negative relationships of anatomical chronologies with precipitation were mostly due to the negative correlation between summer temperature and precipitation. Since cell number is strictly linked to ring width in conifers (Castagneri et al., 2015) and warming in temperature-limited environments promote cambial cells division, i.e. the cell number in the ring (Rossi et al., 2014), with future climate conditions we could expect an increase in tree radial growth (Gao et al., 2022), even if this beneficial effect may be transient (D'Orangeville et al., 2018). Cell wall thickening is known to be positively affected by summer temperature in cold environments (Björklund et al., 2017). In both the Alps and Carpathians this trait is likely favoured by high temperature along the whole season, i.e. from the first to last ring sector. Differently, this positive effect of temperature on wall thickness was documented just in the latewood in other conifers (*Larix decidua* and *Picea abies*) at the upper tree limit in the Alps (Carrer et al., 2016; Castagneri et al., 2020). A positive influence of temperatures on the lumen area was observed, as for other high-elevation species (Carrer et al., 2016; Castagneri et al., 2017), mostly for the Alpine sites and over a rather short period, a few weeks before the temperature sum threshold was reached. However, later on in the season, we detected a prolonged negative influence of temperature on lumen area, and a positive effect of precipitation. Similar associations to water stress (due to low water availability or evapotranspirative stress associated to high temperatures) are typical for drought-prone areas (Pellizzari et al., 2016; Belokopytova et al., 2019). Despite the cell lumen size being strictly linked to water availability and detracted by water deficit during the xylogenesis phase (Hsiao, 1973), the negative effect of temperature seems rather counterintuitive at these high elevation sites, where woody tissue formation is expected to be heat limited (Körner, 2012; but see Cabon et al., 2020). These signals confirm the high sensitivity of xylem anatomical traits in recording latent signals of potential stressful conditions due to water deficit even in temperature-limited regions, as recently detected in boreal stands of North America (Lange et al., 2020; Puchi et al., 2020).

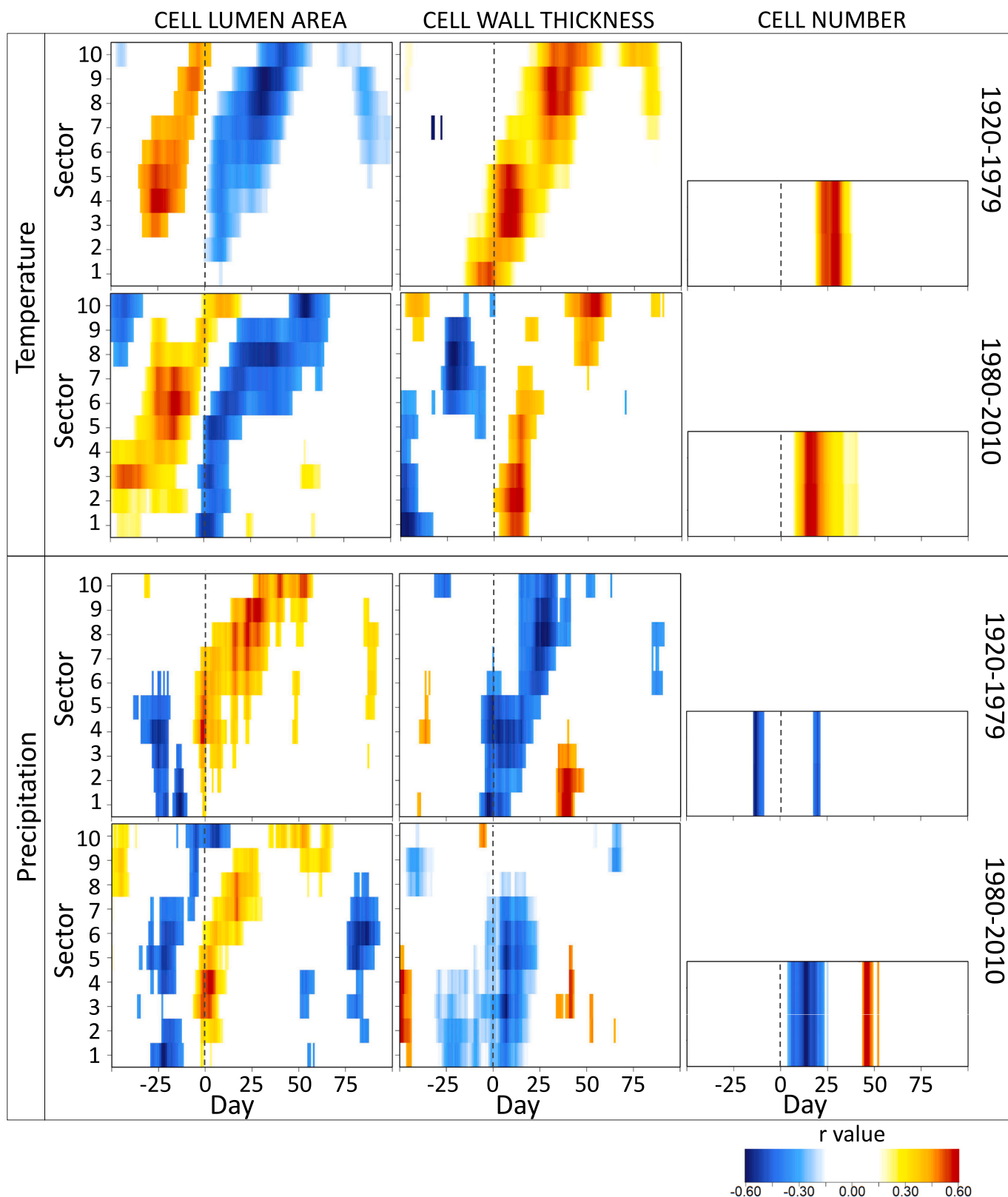


Fig. 5. Correlations between xylem anatomical chronologies and daily climate data over the periods 1920–1979 and 1980–2010 for the Alps. Anatomical parameters are cell lumen area and radial cell wall thickness partitioned in 10 sectors (y-axis), and cell number (entire ring). Climate data are mean maximum temperature (upper panels) and precipitation sum (lower panels) expressed as 20-day moving windows. On x-axis, the 0 corresponds to the day when the threshold of 74° days is reached. Correlations on 20-day moving windows centred 50 days before to 100 days after the day 0 are shown. Coloured areas indicate significant correlations ($p < 0.05$), ranging from -0.60 (blue) to 0.60 (red).

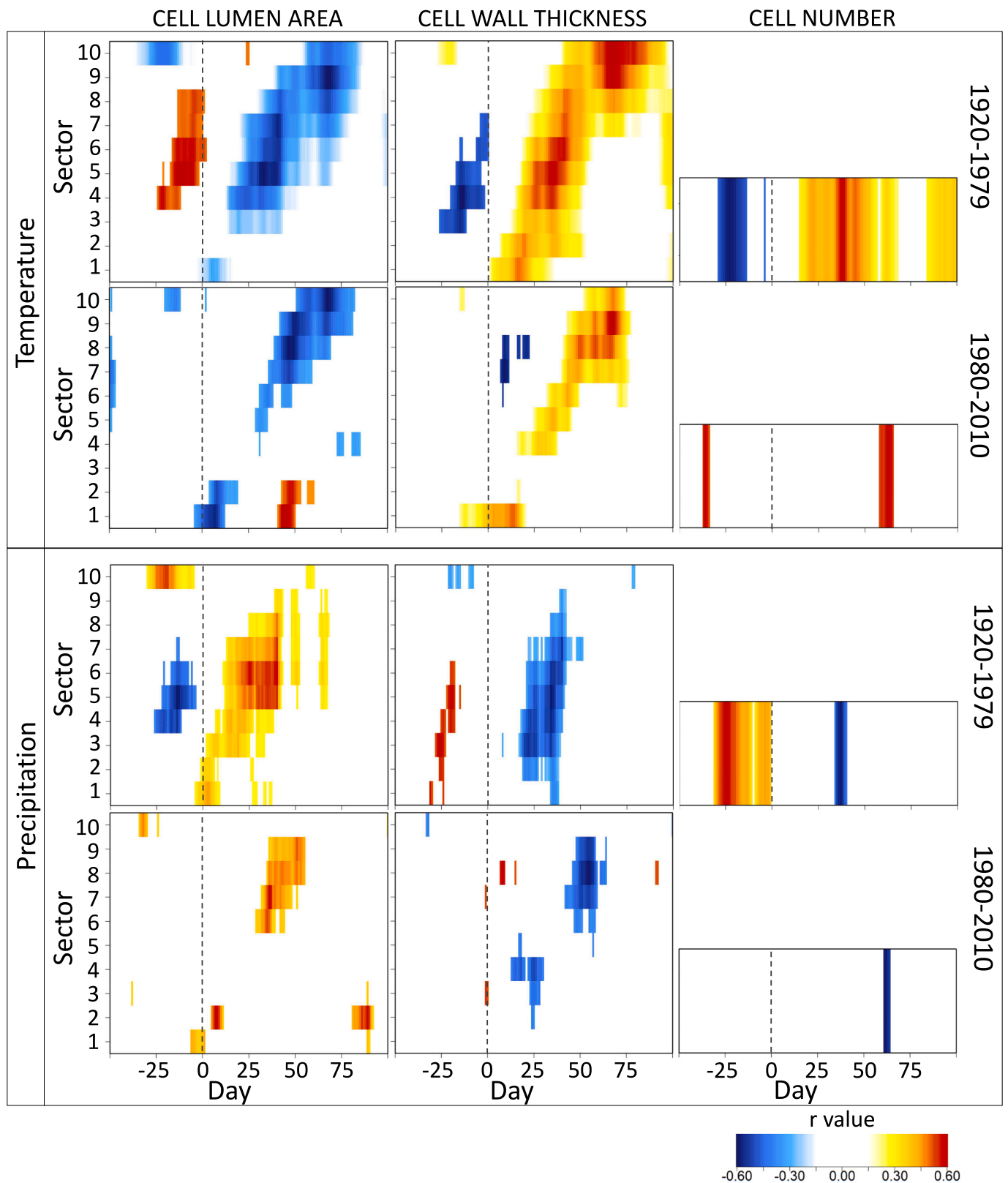


Fig. 6. Correlations between xylem anatomical chronologies and daily climate data over the periods 1920–1979 and 1980–2010 for the Carpathians. Anatomical parameters are cell lumen area and radial cell wall thickness partitioned in 10 sectors (y-axis), and cell number (entire ring). Climate data are mean maximum temperature (upper panels) and precipitation sum (lower panels) expressed as 20-day moving windows. On x-axis, the 0 corresponds to the day when the threshold of 102° days is reached. Correlations on 20-day moving windows centred 50 days before to 100 days after the day 0 are shown. Coloured areas indicate significant correlations ($p < 0.05$), ranging from -0.60 (blue) to 0.60 (red).

Our results represent the first of this type for a high-elevation conifer across a species geographical range. Nonetheless, we should report the possible indirect effect of high temperature on lumen area. Indeed, favourable temperature conditions enhance the kinetics and deposition of cell wall material, with the direct effect of increasing cell wall thickness in latewood, reducing lumen area. However, the small size and small variability of cell wall thickness in the early part of the ring suggests negligible effect of cell wall thickening on the final lumen size in the earlywood.

Non-stationary relationships between tree-growth proxies and environment variability have been extensively observed (Wilmking et al., 2020), and a general temperature-radial growth decoupling at high-elevation stands has recently been highlighted at global level (Camarero et al., 2021). In the investigated regions, the 1978–1980 years represent a turning point in the temperature records with a significant warming in the following decades. After this turning point, the climate associations remained consistent in sign but we observed a site-wise weakening of the positive effects of temperature on xylem traits. A similar signal weakening was observed in *Pinus cembra* tree-ring chronologies (Leonelli et al., 2009) and, to a lesser extent, in maximum latewood density chronologies (Cerrato et al., 2019), at high elevation in the Central Italian Alps. Increasing temperature at high elevation is likely causing a relaxation of thermal constraint, not only on radial growth (i.e. cell formation in the cambium) but also on the processes (cell enlargement and cell wall thickening) that determine the xylem structure. In the second period we also observed that the significant associations occurred a few days before the first one for cell number in the Alps, suggesting an advance of the phenological phases related to xylem formation. This indirect evidence agrees with the widely reported advance of phenological phases of different growth processes observed at high elevation (Menzel et al., 2006; Vitasse et al., 2018). Anticipated onset of the cambial activity can be associated to a higher risk of early-frost events in this species (Kern and Popa, 2008; Gruber et al., 2009). However, if snowmelt and frost date retreat at a similar rate, the risk of plant damage would not vary significantly (Klein et al., 2018). Moreover, we observed very few frost rings in the investigated period, and in general *Pinus cembra* is considered less prone to frost damage than other coexisting species, such as *Larix decidua*, due to delayed sprouting (Neuner, 2014).

5. Conclusions

Exploring both spatial and temporal variability in the climate response of tree species is crucial for predicting future scenarios and making informed management decisions, particularly in vulnerable environments such as treeline areas and relict species with fragmented distribution, like *Pinus cembra* in Europe (Dirnböck et al., 2011). Previous tree-ring width analyses in the Alps and Carpathians have generally indicated that the radial growth of high-elevation *Pinus cembra* benefits from high summer temperatures (Carrer et al., 2007; Izvorska et al., 2023). Our analysis enabled us to assess the past influence of climate on the processes that determine xylem structure. While results on cell number (which mostly determines ring width) confirmed previous findings, observed association between climate and cell lumen area suggested that the process of cell enlargement can be negatively affected by high temperatures. In the long term, this can have a negative impact on xylem water transport capacity. Notably, despite the distance between the Alpine and Carpathian populations, the climate response of xylem traits was almost invariant. The common genetic pool of *Pinus cembra*, indicative of a pre-glacial larger and continuous distribution range (Höhn et al., 2009; Gugerli et al., 2023), could provide the reason for this convergence. We therefore expect that warming will extensively and evenly influence xylem formation processes and the resulting xylem structure across the entire species distribution, including the isolated populations in the Carpathians. The absence of any populations with different sensitivity to climate variability can question the future species

resistance to climatic change: the potential long-term structural deterioration of the xylem hydraulic system caused by warmer and/or drier conditions (a major cause of tree dieback, Hereş et al., 2014, Pellizzari et al., 2016) in one region will likely echo on all the others. This knowledge can help to improve state-of-the-art climate models to accurately represent this challenging component of the biosphere lying at the interface between subalpine forests and high-elevation grasslands. Understanding the dynamics of this area remains crucial for biodiversity conservation and landscape preservation efforts.

CRedit authorship contribution statement

Lucrezia Unterholzner, Marco Carrer and Cătălin-Constantin Roibu contributed to the study conception and sampling design. Data acquisition and analysis were conducted by Lucrezia Unterholzner, Marian-Ionuț Știrbu, Riccardo Cerrato and Daniele Castagneri. Lucrezia Unterholzner wrote the draft of the manuscript with inputs from Marco Carrer and Daniele Castagneri. All authors discussed and agreed to the final version of the manuscript.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.167512>.

References

- Abdi, H., Williams, L.J., 2010. Principal component analysis. Wiley Interdiscip. Rev. Comput. Stat. 2, 433–459. <https://doi.org/10.1002/wics.101>.
- Allan, R.P., Hawkins, E., Bellouin, N., Collins, B., 2021. IPCC, 2021: Summary for Policymakers. Cambridge University Press.
- von Arx, G., Carrer, M., 2014. ROXAS — a new tool to build centuries-long tracheid-lumen chronologies in conifers. Dendrochronologia 32, 290–293. <https://doi.org/10.1016/j.dendro.2013.12.001>.
- von Arx, G., Crivellaro, A., Prendin, A.L., Čufar, K., Carrer, M., 2016. Quantitative wood anatomy—practical guidelines. Front. Plant Sci. 7, 1–13. <https://doi.org/10.3389/fpls.2016.00781/abstract>.
- Arzac, A., Fonti, M.V., Vaganov, E.A., 2021. An Overview on Dendrochronology and Quantitative Wood Anatomy Studies of Conifers in Southern Siberia (Russia), pp. 1–22. https://doi.org/10.1007/124_2021_52.
- Belokopytova, L.V., Babushkina, E.A., Zhirmova, D.F., Panyushkina, I.P., Vaganov, E.A., 2019. Pine and larch tracheids capture seasonal variations of climatic signal at moisture-limited sites. Trees 33, 227–242. <https://doi.org/10.1007/s00468-018-1772-2>.
- Björklund, J., Seftigen, K., Schweingruber, F., Fonti, P., von Arx, G., Bryukhanova, M.V., Cuny, H.E., Carrer, M., Castagneri, D., Frank, D.C., 2017. Cell size and wall

- dimensions drive distinct variability of earlywood and latewood density in Northern Hemisphere conifers. *New Phytol.* 216, 728–740. <https://doi.org/10.1111/nph.14639>.
- Borghetti, M., Gentilesca, T., Colangelo, M., Ripullone, F., Rita, A., 2020. Xylem functional traits as indicators of health in Mediterranean forests. *Curr. For. Rep.* 6, 220–236.
- Brunetti, M., Buffoni, L., Mangianti, F., Maugeri, M., Nanni, T., 2004. Temperature, precipitation and extreme events during the last century in Italy. *Glob. Planet Change* 40, 141–149. <https://linkinghub.elsevier.com/retrieve/pii/S0921818103001048>.
- Brunetti, M., Maugeri, M., Nanni, T., Auer, I., Böhm, R., Schöner, W., 2006. Precipitation variability and changes in the greater Alpine region over the 1800–2003 period. *J. Geophys. Res.* 111, D11107. <https://doi.org/10.1029/2005JD006674>.
- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26, 115–124. <https://linkinghub.elsevier.com/retrieve/pii/S1125786508000350>.
- Cabon, A., Peters, R.L., Fonti, P., Martínez-Vilalta, J., De Cáceres, M., 2020. Temperature and water potential co-limit stem cambial activity along a steep elevational gradient. *New Phytol.* 226, 1325–1340. <https://doi.org/10.1111/nph.16456>.
- Camarero, J.J., Gazol, A., Sánchez-Salguero, R., Fajardo, A., McIntire, E.J.B., Gutiérrez, E., Battlori, E., Boudreau, S., Carrer, M., Diez, J., Dufour-Tremblay, G., Gaire, N.P., Hofgaard, A., Jomelli, V., Kirilyanov, A.V., Lévesque, E., Liang, E., Linares, J.C., Mathisen, I.E., Moiseev, P.A., Sangüesa-Barreda, G., Shrestha, K.B., Toivonen, J.M., Tutubalina, O.V., Wilmking, M., 2021. Global fading of the temperature-growth coupling at alpine and polar treelines. *Glob. Chang. Biol.* 27, 1879–1889. <https://doi.org/10.1111/gcb.15530>.
- Carrer, M., Nola, P., Eduard, J.L., Motta, R., Urbini, C., 2007. Regional variability of climate–growth relationships in *Pinus cembra* high elevation forests in the Alps. *J. Ecol.* 95, 1072–1083. <https://doi.org/10.1111/j.1365-2745.2007.01281.x>.
- Carrer, M., von Arx, G., Castagneri, D., Petit, G., 2015. Distilling allometric and environmental information from time series of conduit size: the standardization issue and its relationship to tree hydraulic architecture. *Tree Physiol.* 35, 27–33. <https://doi.org/10.1093/treephys/tpu108>.
- Carrer, M., Brunetti, M., Castagneri, D., 2016. The imprint of extreme climate events in century-long time series of wood anatomical traits in high-elevation conifers. *Front. Plant Sci.* 7, 1–12. <https://doi.org/10.3389/fpls.2016.00683/abstract>.
- Casalegno, S., Amatulli, G., Camia, A., Nelson, A., Pekkarinen, A., 2010. Vulnerability of *Pinus cembra* L. in the Alps and the Carpathian mountains under present and future climates. *For. Ecol. Manage.* 259, 750–761. <https://linkinghub.elsevier.com/retrieve/pii/S0378112709007257>.
- Castagneri, D., Petit, G., Carrer, M., 2015. Divergent climate response on hydraulic-related xylem anatomical traits of *Picea abies* along a 900-m altitudinal gradient. *Tree Physiol.* 35, 1378–1387. <https://academic.oup.com/treephys/article/35/12/1378/2364649>.
- Castagneri, D., Fonti, P., von Arx, G., Carrer, M., 2017. How does climate influence xylem morphogenesis over the growing season? Insights from long-term intra-ring anatomy in *Picea abies*. *Ann. Bot.* 119, mcw274. <https://doi.org/10.1093/aob/mcw274>.
- Castagneri, D., Prendin, A.L., Peters, R.L., Carrer, M., von Arx, G., Fonti, P., 2020. Long-term impacts of defoliator outbreaks on larch xylem structure and tree-ring biomass. *Front. Plant Sci.* 11. <https://doi.org/10.3389/fpls.2020.01078/full>.
- Cerrato, R., Salvatore, M.C., Gunnarson, B.E., Linderholm, H.W., Carturan, L., Brunetti, M., De Blasi, F., Baroni, C., 2019. A *Pinus cembra* L. tree-ring record for late spring to late summer temperature in the Rhaetian Alps, Italy. *Dendrochronologia* 53, 22–31. <https://doi.org/10.1016/j.dendro.2018.10.010>.
- Cook, E.R., Kairiukstis, L.A., 1990. *Methods of Dendrochronology: Applications in the Environmental Sciences*. Springer Science & Business Media.
- Cornes, R.C., van der Schrier, G., van den Besselaar, E.J.M., Jones, P.D., 2018. An ensemble version of the E-OBS temperature and precipitation data sets. *J. Geophys. Res. Atmos.* 123, 9391–9409. <https://doi.org/10.1029/2017JD028200>.
- Dauphin, B., Wüest, R.O., Brodbeck, S., Zoller, S., Fischer, M.C., Holderegger, R., Gugerli, F., Reilstab, C., 2020. Disentangling the effects of geographic peripherality and habitat suitability on neutral and adaptive genetic variation in Swiss stone pine. *Mol. Ecol.* 29, 1972–1989.
- De Micco, V., Carrer, M., Rathgeber, C.B.K., Julio Camarero, J., Voltas, J., Cherubini, P., Battipaglia, G., 2019. From xylogenesis to tree rings: wood traits to investigate tree response to environmental changes. *IAWA J.* 40, 155–182. https://brill.com/view/journals/iawa/40/2/article-p155_3.xml.
- Dirnböck, T., Essel, F., Rabitsch, W., 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Glob. Chang. Biol.* 17, 990–996. <https://doi.org/10.1111/j.1365-2486.2010.02266.x>.
- D'Orangeville, L., Houle, D., Duchesne, L., Phillips, R.P., Bergeron, Y., Kneeshaw, D., 2018. Beneficial effects of climate warming on boreal tree growth may be transitory. *Nat. Commun.* 9, 1–10. <https://www.nature.com/articles/s41467-018-05705-4>.
- Fajardo, A., Gazol, A., Mayr, C., Camarero, J.J., 2019. Recent decadal drought reverts warming-triggered growth enhancement in contrasting climates in the southern Andes tree line Scheiter S (ed). *J. Biogeogr.* 46, 1367–1379. <https://doi.org/10.1111/jbi.13580>.
- Frank, D., Esper, J., 2005. Characterization and climate response patterns of a high-elevation, multi-species tree-ring network in the European Alps. *Dendrochronologia* 22, 107–121. <https://linkinghub.elsevier.com/retrieve/pii/S1125786505000032>.
- Gao, S., Liang, E., Liu, R., Babst, F., Camarero, J.J., Fu, Y.H., Piao, S., Rossi, S., Shen, M., Wang, T., Peñuelas, J., 2022. An earlier start of the thermal growing season enhances tree growth in cold humid areas but not in dry areas. *Nat. Ecol. Evol.* 6, 397–404. <https://www.nature.com/articles/s41559-022-01668-4>.
- Gehrig-Fasel, J., Guisan, A., Zimmermann, N.E., 2007. Tree line shifts in the Swiss Alps: climate change or land abandonment? *J. Veg. Sci.* 18, 571–582. <https://doi.org/10.1111/j.1654-1103.2007.tb02571.x>.
- Girardin, M.P., Guo, X.J., De Jong, R., Kinnard, C., Bernier, P., Raulier, F., 2014. Unusual forest growth decline in boreal North America covaries with the retreat of Arctic sea ice. *Glob. Chang. Biol.* 20, 851–866.
- Grace, J., Berninger, F., Nagy, L., 2002. Impacts of climate change on the tree line. *Ann. Bot.* 90, 537–544. <https://academic.oup.com/aob/article/90/4/537/185822>.
- Gričar, J., Prislán, P., Gryc, V., Vavrčík, H., De Luis, M., Čufar, K., 2014. Plastic and locally adapted phenology in cambial seasonality and production of xylem and phloem cells in *Picea abies* from temperate environments. *Tree Physiol.* 34, 869–881. <https://academic.oup.com/treephys/article/34/8/869/2446701>.
- Grigorieva, E.A., Matzarakis, A., Freitas, C.R., 2010. Analysis of growing degree-days as a climate impact indicator in a region with extreme annual air temperature amplitude. *Climate Res.* 42, 143–154. <https://www.int-res.com/abstracts/cr/v42/n2/p143-154/>.
- Gruber, A., Baumgartner, D., Zimmermann, J., Oberhuber, W., 2009. Temporal dynamic of wood formation in *Pinus cembra* along the alpine treeline ecotone and the effect of climate variables. *Trees* 23, 623–635. <https://doi.org/10.1007/s00468-008-0307-7>.
- Gugerli, F., Brodbeck, S., Lendvay, B., Dauphin, B., Bagnoli, F., van der Knaap, W.O., Tinner, W., Höhn, M., Vendramin, G.G., Morales-Molino, C., Schwörer, C., 2023. A range-wide postglacial history of Swiss stone pine based on molecular markers and palaeoecological evidence. *J. Biogeogr.* 50, 1049–1062. <https://doi.org/10.1111/jbi.14586>.
- Hagedorn, F., Shiyatov, S.G., Mazepa, V.S., Devi, N.M., Grigor'ev, A.A., Bartysh, A.A., Fomin, V.V., Kapralov, D.S., Terent'ev, M., Bugman, H., Rigling, A., Moiseev, P.A., 2014. Treeline advances along the Urals mountain range — driven by improved winter conditions? *Glob. Chang. Biol.* 20, 3530–3543. <https://doi.org/10.1111/gcb.12613>.
- Harsch, M.A., Hulme, P.E., McGlone, M.S., Duncan, R.P., 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecol. Lett.* 12, 1040–1049. <https://doi.org/10.1111/j.1461-0248.2009.01355.x>.
- Hereš, A.-M., Camarero, J.J., López, B.C., Martínez-Vilalta, J., 2014. Declining hydraulic performances and low carbon investments in tree rings predate Scots pine drought-induced mortality. *Trees* 28, 1737–1750. <https://doi.org/10.1007/s00468-014-1081-3>.
- Höhn, M., Gugerli, F., Abran, P., Bisztray, G., Buonamici, A., Cseke, K., Hufnagel, L., Quintela-Sabaris, C., Sebastiani, F., Vendramin, G.G., 2009. Variation in the chloroplast DNA of Swiss stone pine (*Pinus cembra* L.) reflects contrasting post-glacial history of populations from the Carpathians and the Alps. *J. Biogeogr.* 36, 1798–1806. <https://doi.org/10.1111/j.1365-2699.2009.02122.x>.
- Holmes, R., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43, 69–78. <http://hdl.handle.net/10150/261223>.
- Holtmeier, F.K., Broll, G.E., 2007. Treeline advance — driving processes and adverse factors. *Landscape Online* 1, 1–33. <https://www.landscape-online.org/index.php/lo/article/view/LO.200701/82>.
- Hsiao, T.C., 1973. Plant responses to water stress. *Annu. Rev. Plant Physiol.* 24, 519–570. <https://doi.org/10.1146/annurev.pp.24.060173.002511>.
- Isaac-Renton, M., Montwé, D., Hamann, A., Spiecker, H., Cherubini, P., Treydte, K., 2018. Northern forest tree populations are physiologically maladapted to drought. *Nat. Commun.* 9, 1–9. <https://doi.org/10.1038/s41467-018-07701-0>.
- Izworska, K., Muter, E., Matulewski, P., Zielonka, T., 2023. Tree rings as an ecological indicator of the reaction of Swiss stone pine (*Pinus cembra* L.) to climate change and disturbance regime in the extreme environment of cliff forests. *Ecol. Indic.* 148, 110102. <https://linkinghub.elsevier.com/retrieve/pii/S1470160X23002443>.
- Jevšenak, J., 2020. New features in the dendroTools R package: bootstrapped and partial correlation coefficients for monthly and daily climate data. *Dendrochronologia* 63, 125753. <https://linkinghub.elsevier.com/retrieve/pii/S1125786520300928>.
- Kern, Z., Popa, I., 2008. Changes of frost damage and treeline advance for Swiss stone pine in the Calimani Mts. (eastern Carpathians, Romania). *Acta Silv. Lign. Hung.* 4, 39–48.
- Kim, S.-H., Yi, S.V., 2007. Understanding relationship between sequence and functional evolution in yeast proteins. *Genetica* 131, 151–156. <https://doi.org/10.1007/s10709-006-9125-2>.
- Klein, G., Rebetez, M., Rixen, C., Vitasse, Y., 2018. Unchanged risk of frost exposure for subalpine and alpine plants after snowmelt in Switzerland despite climate warming. *Int. J. Biometeorol.* 62, 1755–1762. <https://doi.org/10.1007/s00484-018-1578-3>.
- Körner, C., 2012. *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits*. Springer Science & Business Media.
- Lamprecht, A., Semenchuk, P.R., Steinbauer, K., Winkler, M., Pauli, H., 2018. Climate change leads to accelerated transformation of high-elevation vegetation in the central Alps. *New Phytol.* 220, 447–459.
- Lange, J., Carrer, M., Pisarcic, M.F.J., Porter, T.J., Seo, J.W., Trouillier, M., Wilmking, M., 2020. Moisture-driven shift in the climate sensitivity of white spruce xylem anatomical traits is coupled to large-scale oscillation patterns across northern treeline in northwest North America. *Glob. Chang. Biol.* 26, 1842–1856. <https://doi.org/10.1111/gcb.14947>.
- Leonelli, G., Pelfini, M., Battipaglia, G., Cherubini, P., 2009. Site-aspect influence on climate sensitivity over time of a high-altitude *Pinus cembra* tree-ring network. *Clim. Change* 96, 185–201.
- Lingua, E., Cherubini, P., Motta, R., Nola, P., 2008. Spatial structure along an altitudinal gradient in the Italian central Alps suggests competition and facilitation among coniferous species. *J. Veg. Sci.* 19, 425–436.
- Lloyd, A.H., Fastie, C.L., 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Clim. Change* 52, 481–509. <https://doi.org/10.1023/A:1014278819094>.

- Lopez-Saez, J., Corona, C., von Arx, G., Fonti, P., Slamova, L., Stoffel, M., 2023. Tree-ring anatomy of *Pinus cembra* trees opens new avenues for climate reconstructions in the European Alps. *Sci. Total Environ.* 855, 158605.
- Matisons, R., Krišāns, O., Kärkliņa, A., Adamovičs, A., Jansons, A., Gärtner, H., 2019. Plasticity and climatic sensitivity of wood anatomy contribute to performance of eastern Baltic provenances of Scots pine. *For. Ecol. Manage.* 452, 117568. <https://linkinghub.elsevier.com/retrieve/pii/S037811271930862X>.
- McMaster, G.S., Wilhelm, W.W., 1997. Growing degree-days: one equation, two interpretations. *Agric. For. Meteorol.* 87, 291–300. <https://linkinghub.elsevier.com/retrieve/pii/S0168192397000270>.
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aaasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheffinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.E., Zach, S., Züst, A., 2006. European phenological response to climate change matches the warming pattern. *Glob. Chang. Biol.* 12, 1969–1976. <https://doi.org/10.1111/j.1365-2486.2006.01193.x>.
- Montwé, D., Isaac-Renton, M., Hamann, A., Spiecker, H., 2018. Cold adaptation recorded in tree rings highlights risks associated with climate change and assisted migration. *Nat. Commun.* 9, 1574. <https://www.nature.com/articles/s41467-018-04039-5>.
- Neuner, G., 2014. Frost resistance in alpine woody plants. *Front. Plant Sci.* 5, 654. <https://doi.org/10.3389/fpls.2014.00654/abstract>.
- Neuschulz, E.L., Merges, D., Bollmann, K., Gugerli, F., Böhning-Gaese, K., 2018. Biotic interactions and seed deposition rather than abiotic factors determine recruitment at elevational range limits of an alpine tree. *J. Ecol.* 106, 948–959.
- Normand, S., Treier, U.A., Randin, C., Vittoz, P., Guisan, A., Svenning, J., 2009. Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. *Glob. Ecol. Biogeogr.* 18, 437–449. <https://doi.org/10.1111/j.1466-8238.2009.00451.x>.
- Ols, C., Klesse, S., Girardin, M.P., Evans, M.E.K., DeRose, R.J., Trouet, V., 2023. Detrending climate data prior to climate–growth analyses in dendroecology: a common best practice? *Dendrochronologia* 79, 126094. <http://creativecommons.org/licenses/by/4.0/>.
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42. www.nature.com/nature.
- Pellizzari, E., Camarero, J.J., Gazol, A., Sanguesa-Barreda, G., Carrer, M., 2016. Wood anatomy and carbon-isotope discrimination support long-term hydraulic deterioration as a major cause of drought-induced dieback. *Glob. Chang. Biol.* 22, 2125–2137.
- Pérez-de-Lis, G., Rathgeber, C.B.K., Fernández-de-Uña, L., Ponton, S., 2022. Cutting tree rings into time slices: how intra-annual dynamics of wood formation help decipher the space-for-time conversion. *New Phytol.* 233, 1520–1534. <https://doi.org/10.1111/nph.17869>.
- Prendin, A.L., Petit, G., Carrer, M., Fonti, P., Björklund, J., von Arx, G., 2017. New research perspectives from a novel approach to quantify tracheid wall thickness. *Tree Physiol.* 37, 976–983. <https://academic.oup.com/treephys/article/37/7/976/3100230>.
- Puchi, P.F., Castagneri, D., Rossi, S., Carrer, M., 2020. Wood anatomical traits in black spruce reveal latent water constraints on the boreal forest. *Glob. Chang. Biol.* 26, 1767–1777. <https://doi.org/10.1111/gcb.14906>.
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. <http://www.r-project.org>.
- Rossi, S., Girard, M.-J., Morin, H., 2014. Lengthening of the duration of xylogenesis engenders disproportionate increases in xylem production. *Glob. Chang. Biol.* 20, 2261–2271. <https://doi.org/10.1111/gcb.1247>.
- Rossi, S., Anfodillo, T., Čufar, K., Cuny, H.E., Deslauriers, A., Fonti, P., Frank, D., Gričar, J., Gruber, A., Huang, J., Jyske, T., Kašpar, J., King, G., Krause, C., Liang, E., Mäkinen, H., Morin, H., Nöjd, P., Oberhuber, W., Prislan, P., Rathgeber, C.B.K., Saracino, A., Swidrak, I., Treml, V., 2016. Pattern of xylem phenology in conifers of cold ecosystems at the Northern Hemisphere. *Glob. Chang. Biol.* 22, 3804–3813. <https://doi.org/10.1111/gcb.13317>.
- Rubel, F., Brügger, K., Haslinger, K., Auer, I., 2017. The climate of the European Alps: shift of very high resolution Köppen-Geiger climate zones 1800–2100. *Meteorol. Zeitsch. (Contrib. Atmos. Sci.)* 26, 115–125.
- San-Miguel-Ayanz, J., De Rigo, D., Caudullo, G., 2016. The European Atlas of Forest Tree Species: Modelling, Data and Information on Forest Tree Species. Publications Office of the European Union.
- Stokes, M.A., Smiley, T.L., 1968. An Introduction to Tree-ring Dating. The University of Arizona Press, Tucson.
- Tomback, D.F., Holtmeier, F.-K., Mattes, H., Carsey, K.S., Powell, M.L., 1993. Tree clusters and growth form distribution in *Pinus cembra*, a bird-dispersed pine. *Arct. Alp. Res.* 25, 374–381. <https://www.tandfonline.com/action/journalInformation?journalCode=uaar20>.
- Ulber, M., Gugerli, F., Bozic, G., 2004. Technical guidelines for genetic conservation and use for Swiss stone pine (*Pinus cembra*). In: EUFORGEN. International Plant Genetic Resources Institute, Rome, Italy.
- Vitasse, I., Wurzelbacher, S., Klein, G., Bohnenstengel, T., et al., 2021. Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. *Biol. Rev.* 96, 1816–1835.
- Vitasse, Y., Signarbieux, C., Fu, Y.H., 2018. Global warming leads to more uniform spring phenology across elevations. *Proc. Natl. Acad. Sci. U. S. A.* 115, 1004–1008. <https://doi.org/10.1073/pnas.1717342115>.
- Wilmking, M., van der Maaten-Theunissen, M., van der Maaten, E., Scharnweber, T., Buras, A., Biermann, C., Gurskaya, M., Hallinger, M., Lange, J., Shetti, R., Smiljanic, M., Trouillier, M., 2020. Global assessment of relationships between climate and tree growth. *Glob. Chang. Biol.* 26, 3212–3220. <https://doi.org/10.1111/gcb.15057>.
- Yang, L., Liu, S., Tsoka, S., Papageorgiou, L.G., 2016. Mathematical programming for piecewise linear regression analysis. *Expert Syst. Appl.* 44, 156–167. <https://linkinghub.elsevier.com/retrieve/pii/S0957417415005904>.