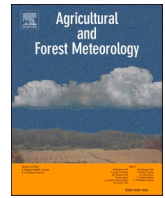




Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

In pursuit of change: Divergent temporal shifts in climate sensitivity of Norway spruce along an elevational and continentality gradient in the Carpathians

Andrei Popa^{a,b}, Jernej Jevšenak^{c,d}, Ionel Popa^{a,e,*}, Ovidiu Badea^{a,b}, Allan Buras^c

^a National Institute for Research and Development in Forestry 'Marin Dracea', Bucharest, Romania

^b Faculty of Silviculture and Forest Engineering, Transilvania University of Brasov, Brasov, Romania

^c TUM School of Life Sciences, Technical University of Munich, Freising, Germany

^d Department for Forest and Landscape Planning and Monitoring, Slovenian Forestry Institute, Ljubljana, Slovenia

^e Center for Mountain Economy (CE-MONT), Vatra Dornei, Romania

ARTICLE INFO

Keywords:

Temperature
Water availability
Climate change
Tree-ring width
Non-stationarity
Picea abies
Daily climate-growth relationships

ABSTRACT

Across much of Europe, climate change has caused a major dieback of Norway spruce (*Picea abies* L.), an economically important tree species. However, the southeasternmost fringe of this tree species – the Eastern Carpathians – has not yet suffered large-scale dieback. Studying temporal shifts of climate sensitivity (TSCS) over time may elucidate the degree to which Norway spruce may be vulnerable to climate-change induced decline in upcoming decades. Under this framework, we analyzed a regional tree-ring network comprising >3000 trees, with the aim of quantifying TSCS since 1950. We mathematically defined TSCS as the slope parameter of the regression of climate sensitivity (the correlation coefficient) over time. Given the often-observed contrasting shift of climate sensitivity at low versus high elevations, we were particularly interested in studying potentially divergent TSCS along elevational and spatial gradients. Our analyses revealed several indications of TSCS for Norway spruce in the Eastern Carpathians. First, at high elevations (>1100 m a.s.l.), we found that the positive link between summer temperature and spruce growth decreased significantly over the study period. In turn, these trees, over time, featured an increasing positive relationship with late winter temperatures. At low elevations (<800 m a.s.l.), the signal of positive summer Standardised Precipitation-Evapotranspiration Index (SPEI) correlation became more frequent among sites towards 2021, while the strength of the positive winter SPEI correlation from the previous growing season weakened. Our results revealed that TSCS was driven significantly by an elevational climate gradient and a longitudinal continentality gradient. Overall, our findings indicate that Norway spruce is increasingly affected by water limitations under climate change at low elevations, highlighting a potentially rising risk of decline of this species in the Eastern Carpathians.

1. Introduction

Forests are one of the most important terrestrial carbon sinks on Earth, storing ~45 % of terrestrial carbon and contributing ~50 % of terrestrial net primary production (Bonan, 2008; Pan et al., 2011). Consequently, forests are critical for achieving carbon neutrality and mitigating climate change effects (Fetting, 2020). As the climate changes, so does the sensitivity of tree-growth to environmental drivers is changing (Camarero et al., 2021), making understanding and predicting forest ecosystem responses to environmental changes challenging (Luo et al., 2015). Yet, assessing tree and forest responses is

imperative to forecast the implications of a changing climate on the biosphere (Peltier and Ogle, 2020).

In regions with clearly defined growing seasons, trees typically form annual growth rings (commonly known as tree rings), whose variability over time is often linked to annual climate conditions that constrain growth, such as low temperature or drought. To date, numerous tree-ring studies have highlighted the consequences of global warming on forest ecosystems, including mortality events (Cailleret et al., 2019, 2017), changes in carbon and water dynamics (Babst et al., 2019, 2014; Buras et al., 2023; Frank et al., 2015), and reconstruction of past climatic variability (Büntgen et al., 2010; Esper et al., 2016; Popa and Kern,

* Corresponding author.

E-mail address: popaicas@gmail.com (I. Popa).

<https://doi.org/10.1016/j.agrformet.2024.110243>

Received 8 February 2024; Received in revised form 31 July 2024; Accepted 20 September 2024

Available online 28 September 2024

0168-1923/© 2024 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC license (<http://creativecommons.org/licenses/by-nc/4.0/>).

2009; Rocha et al., 2021). Tree rings thus represent an invaluable climate change proxy, which integrates climate variability from various parts of the growing season (Babst et al., 2018) and can contribute greatly to Intergovernmental Panel on Climate Change (IPCC) assessment reports (Calvin et al., 2023). However, deciphering the climate information stored in tree-ring parameters is difficult since tree growth is influenced by many factors, such as various climate parameters, silvicultural management practices, or disturbances (Fritts, 1976).

Global environmental change has strongly influenced species distribution, carbon stock, growth dynamics, and mortality rates in forest ecosystems (Mueller et al., 2005; Schuldt et al., 2020; Zhang et al., 2018). At the individual tree level, climate affects tree growth by interacting with carbon assimilation at the leaf level (McDowell et al., 2022) and carbon storage at the stem level (Litton et al., 2007). As a consequence of climate change, the temperature response of trees weakens in temperature-limited environments and becomes more negative in water-limited ones (Charney et al., 2016). Hence, under increasingly dry conditions, the water limitations on wood formation intensify globally (Babst et al., 2019).

In recent decades, non-stationarity of climate-growth relationships (also known as the divergence problem) has been reported in cold-limited ecosystems, respectively at high latitudes (Briffa et al., 1998; D'Arrigo et al., 2008; Hofgaard et al., 2019) and high elevations (Büntgen et al., 2006). Furthermore, changes in tree sensitivity to climate have also been observed in temperate forests (Bošel'a et al., 2014; Carrer and Urbinati, 2006; Leonelli et al., 2011), and this phenomenon has been recognized at a global scale in response to climate change (Babst et al., 2019). Wilmking et al. (2020) found 56 % of studies that tested for non-stationarity to identify clear signs of unstable climate-growth relationships. In the current context of continuous warming (IPCC, 2023), we may expect severe changes in forest sensitivity to climatic factors (Brodribb et al., 2020). Moreover, the sensitivity of secondary growth to climate parameters can change after extreme drought events (Leifsson et al., 2023). Consequently, tree growth sensitivity to climatic conditions is shifting over time, sometimes abruptly (Leifsson et al., 2023), which will impact forest resilience, forest vulnerability, and tree growth patterns in the short term and tree-species composition of forests in the long term (De Marco et al., 2022). Taken together, the rising awareness of the non-stationarity of climate-growth relationships mirrors a temporal shift in trees' climate sensitivity (TSCS) potentially induced by climate change. In mathematic terms, TSCS can be quantified as the temporal change/shift of the coupling between measurements of secondary tree growth (e.g., tree rings) and measurements of climate parameters that govern tree growth (e.g., temperature and precipitation).

While assessments of changes in the climate sensitivity of trees in Europe are common (Castaldi et al., 2020; Kolář et al., 2017; Ponocná et al., 2016; Schurman et al., 2019; Svobodová et al., 2019), most studies rely on monthly climatic data. However, applying climate data with a monthly resolution induces an artificial barrier that lacks a physiological explanation. In particular, Jevšenak (2019) showed that daily climatic data allow for more precise quantification of climate-growth relationships and may thus reveal more detailed insights into TSCS.

Within temperate forests, the climatic factors limiting tree growth typically vary from low summer temperatures at high elevations to scarce water availability at lower elevations (Babst et al., 2013). In forest ecosystems, where temperature and moisture limitations interact, trees can alter their sensitivity from one climatic factor to another (Tumajer et al., 2023, 2017). In boreal forests, the climate sensitivity of trees to summer temperatures changed significantly under different climate regimes (dry versus wet periods) (Lange et al., 2018). In the Carpathian Mountains, the summer temperature sensitivity of various xylem parameters (e.g., cell lumen area, radial cell wall thickness, cell number) has decreased in recent decades (Știrbu et al., 2022; Unterholzner et al., 2024). These studies indicate that quantifying TSCS for a given tree species in a given region may provide insights into how well

that species may cope with ongoing climate change.

In Europe, the increased intensity and frequency of droughts under climate change has affected large areas of forests (Hlásny et al., 2021a; Senf et al., 2020). Norway spruce (*Picea abies* L.), hereafter referred to as spruce, is one of the most vulnerable tree-species (Hlásny et al., 2021b; Obladen et al., 2021; Synek et al., 2020), and is highly important from both economic and ecological perspectives (Klimo et al., 2000). In Europe, spruce is distributed from sea level to the timberline at elevations of 2400 m (Caudullo et al., 2016). The Eastern Carpathians represent the southeasternmost edge of the natural distribution of spruce (Caudullo et al., 2017, 2016). Thus, at the easternmost limits spruce may face growth constraints in terms of water availability due to an increased continentality effect (Sidor et al., 2015). In managed forests - which constitute the majority of European forests - spruce is typically cultivated in even-aged monocultures, both inside and outside its natural range (Spiecker, 2004). Recently, large spruce diebacks in Central Europe (Hlásny et al., 2021b) have focused the attention of forest managers and researchers on this species, which is projected to vastly decline across Central and Eastern Europe, including the Eastern Carpathians, under various future climate scenarios (Buras and Menzel, 2019). Spruce mortality is, however, less pronounced in Eastern Europe than Central Europe (Synek et al., 2020), yet knowledge on the decline of spruce in the Eastern Carpathians is sparse (Popa et al., 2024b).

Climate-growth relationships of spruce have been extensively investigated across Europe (Begović et al., 2020; Bošel'a et al., 2014; Jevšenak et al., 2021; Schurman et al., 2019; Sidor et al., 2015; Svobodová et al., 2019; van der Maaten-Theunissen et al., 2013). This species was reported to be drought-limited, particularly at low elevations (Sidor et al., 2015; van der Maaten-Theunissen et al., 2013), which is further modulated by prevailing soil conditions (Rehseh et al., 2017). Recently, studies conducted in primary spruce forests in the Carpathians revealed an increased sensitivity of this species to drought at high elevations as well (Björklund et al., 2019; Schurman et al., 2019). While Sidor et al. (2015) found that tree growth at high-elevation sites in the Eastern Carpathians was mostly determined by summer temperature, a recent study in the same region highlighted the pronounced impact of winter temperatures on tree growth (Popa et al., 2022). These contrasting findings may hint TSCS of spruce in the Eastern Carpathians, which has already been reported for the Western Carpathians (Bošel'a et al., 2014). Yet, to the best of our knowledge, no large-scale studies on TSCS of spruce using daily climatic data in Eastern Europe have been conducted. While previous studies focused mostly on non-stationarity of primary climatic signals, this paper introduces a much more thorough assessment of climate-growth non-stationarity. It extends the focus to include shifting responses related to secondary climate effects and influences from the previous growing season.

The absence of large-scale studies addressing TSCS of spruce using daily climate data in Eastern Europe highlights a significant knowledge gap that warrants further investigation. To address this, we developed a novel method for assessing temporal shifts in climate sensitivity (TSCS) for spruce in the Eastern Carpathians. Our study utilizes a large tree-ring network that encompasses >3000 trees from 158 stands, covering a wide range of elevation from 475 to 1675 m. This network is combined with gridded climate data at a daily temporal resolution to more precisely identify the climate-parameter specific season of interest. A central aim of our study is to develop a comprehensive understanding of TSCS of spruce in the Carpathians, with the goal of identifying the dominant underlying mechanisms. To address this aim, we hypothesize that:

- (H1) with the progression of global warming, summer temperature is becoming less constraining factor for spruce growth at high elevations;
- (H2) however, the importance of water availability for tree growth at low elevations is increasing due to the intensification of drought events;

(H3) due to the pronounced east-west continentality gradient in the Carpathians, we expect differences in temporal shifts in climate sensitivity (TSCS) between the eastern and western regions.

2. Material and methods

2.1. Study area

The Carpathians constitute the largest continuous area of natural spruce distribution in Southeastern Europe (Caudullo et al., 2016; Stanescu et al., 1997). The study area consisted of managed, monospecific spruce stands located along latitudinal, ($46^{\circ} 36'$ to $47^{\circ} 53'$ N), longitudinal ($24^{\circ} 55'$ to $26^{\circ} 00'$ E), and elevational gradients (from 475 m to the upper forest limit, up to 1675 m) (Fig. 1). To evaluate the effect of elevation on the response of spruce to climate (H1 and H2), sites were sampled in four elevational belts: <800 m (30 plots), 800 to 1100 m (40 plots), 1100 to 1400 m (46 plots), and >1400 m (42 plots). This extensive coverage provided a unique opportunity to capture the diversity of climatic conditions faced by spruce in Southeastern Europe. To assess the response of spruce to climate change, 158 even-aged, managed forest stands were sampled for increment cores. Most of the sampled stands were pure spruce, whereas some were admixed stands with >80 % spruce represented in the growing stock. The admixed stands featured other species in combination with spruce, including

European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) at low and intermediate elevations, and rowan (*Sorbus aucuparia* L.) and birch (*Betula pendula* L.) at high elevations. The climate of the study area is characterized by a mountainous, temperate, and continental climate. The hottest month is July, the coldest month is January, and the largest amount of precipitation usually occurs in June. The mean annual temperature ranges from 7.4 °C at low elevations to 3.2 °C at high elevations, while the annual precipitation varies from 620 to 820 mm (Fig. 1C).

2.2. Tree-ring data collection and sample preparation

In each of the studied stands, 20 to 22 dominant trees without visible injuries were sampled from 2021 to 2022. For plots sampled in early summer of 2021 radial growth was not accomplished, thus, this year was not included in the analyses for 11 % of the plots. From each tree, one increment core was extracted using a 5 mm Pressler increment borer. The cores were prepared according to standard dendrochronological procedures (Speer, 2010), meaning they were air-dried, mounted on wood supports, and sanded with progressive grit-level sanding paper until the ring borders were clearly visible. Increment cores were scanned at a high resolution (2400 dpi true resolution) with an Epson Expression 12,000 XL scanner. Tree ring-width measurements were performed on scanned images using the software Coorecorder/CDendro (Version 9.6,

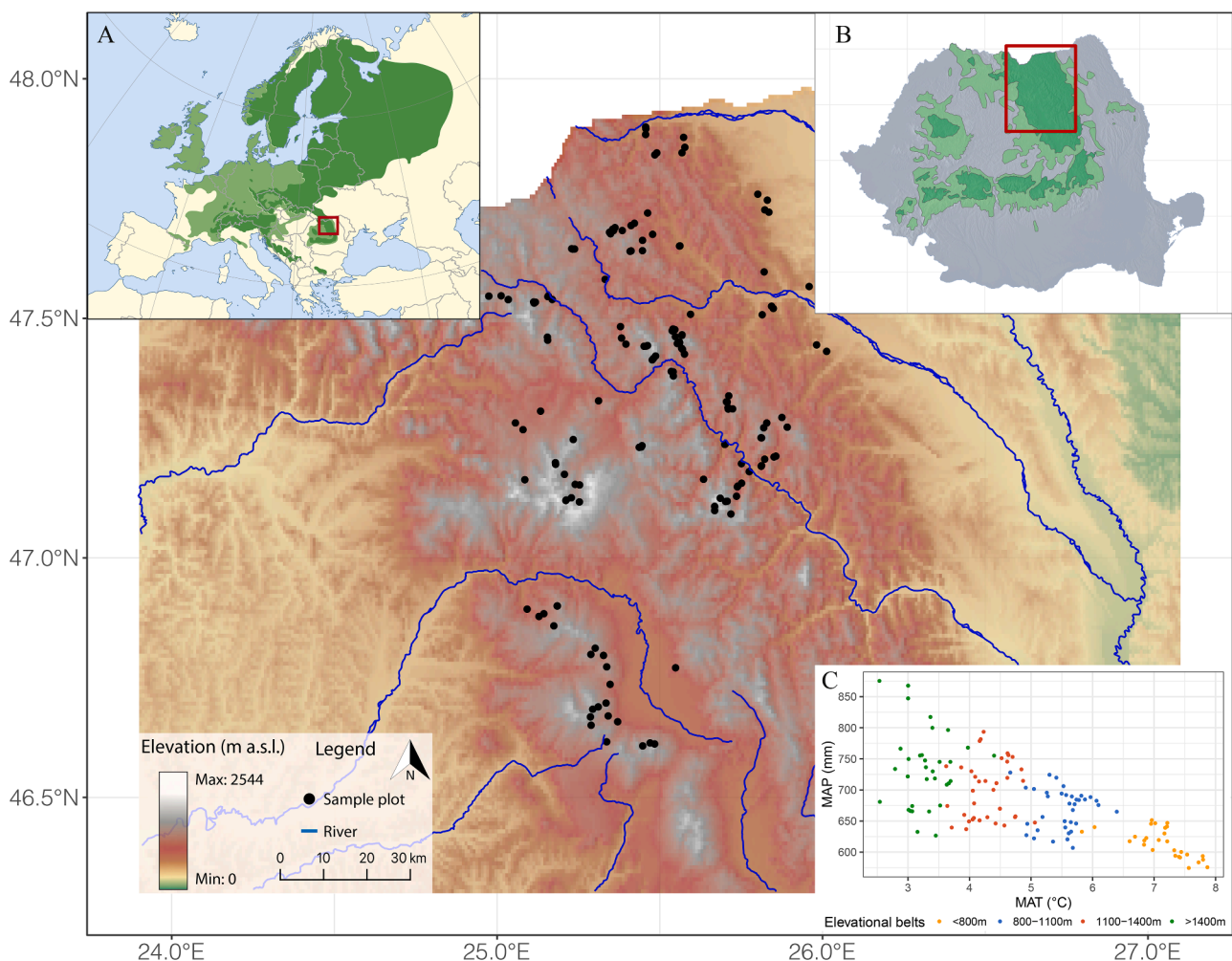


Fig. 1. The location of the study is in the Eastern Carpathians. The map insets show: spruce distribution (A) across Europe (map after www.euforgen.org) and (B) in Romania (Stanescu et al., 1997) (dark green – natural distribution, light green – artificial distribution, red border – study area); and (C) mean annual temperature (MAT) and mean annual precipitation (MAP) in studied sites color coded by elevational belt (yellow – <800 m, blue – 800 to 1100 m, red – 1100 to 1400 m, and green >1400 m).

Cybis Elektronik & Data AB, Sweden) with a precision of 0.01 mm. Individual series were cross-dated visually using TSAPWin software (Rinn, 2012) and statistically checked using the COFECHA software (Grissino-Mayer, 2001). Trees with an age difference higher than 30 years from the mean stand age were excluded from the analyses to assess age homogeneity within the analyzed forest stands. The final database consisted of 3032 trees from 158 stands.

2.3. Tree-growth and climate database

Individual tree ring-width measurements were detrended by applying a cubic-smoothing spline of 32 years with a 50 % frequency cut-off. The aim of detrending was to reduce the non-climatic signals captured in tree rings (e.g., age trends, competition, past silvicultural treatments, and disturbances) (Cook and Kairiukstis, 1990). A cubic

smoothing spline detrending was selected to emphasize high-frequency growth variability, which ideally mirrors the growth variability associated with climate variability. The tree ring-width index series (TRI) was calculated as the ratio between the measured series and the values modeled by the fitted spline function. At the plot level, chronologies were computed by averaging the individual series using a biweight robust mean which effectively minimizes the impact of outliers (Cook and Kairiukstis, 1990). During the site chronology building, an autoregressive model was applied to eliminate the influence of autocorrelation, also known as pre-whitening (Cook, 1985). These site-specific pre-whitened chronologies were used for further analysis. Detrending individual series and chronology development was done in the R environment (R Core Team, 2023) using the ‘dplR’ package (Bunn, 2008).

We deployed a Principal Component Gradient Analysis (PCGA; Buras et al., 2016) based on site chronologies to justify our elevational belt

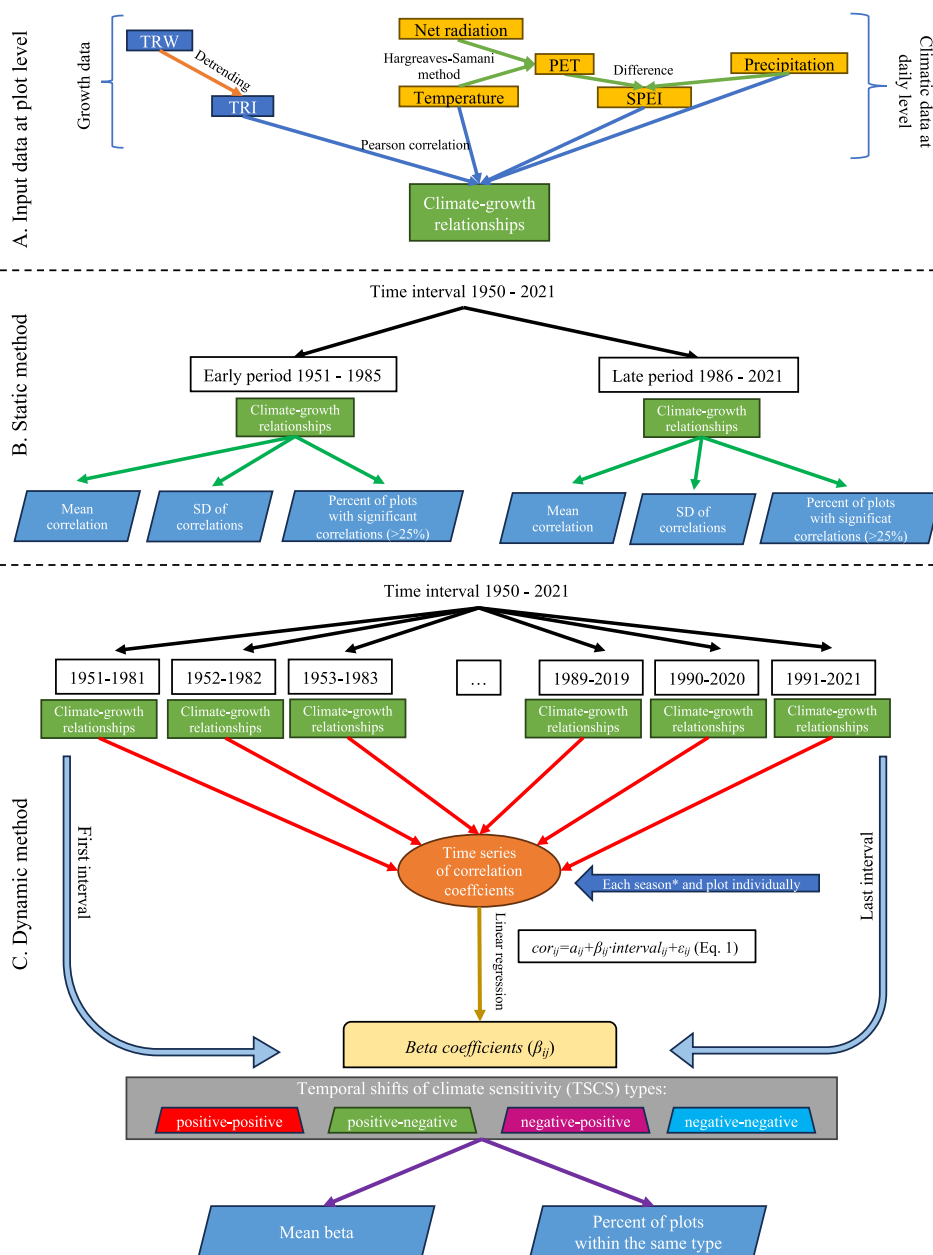


Fig. 2. Flowchart of the statistical analysis: (A) the input data used to assess the climate-growth relationships at the plot level; (B) the static method; and (C) the dynamic method. Climate-growth relationships represents the outputs of the dendroTools analyses which are matrices with correlation coefficients for all considered seasons. One season* represents one pixel in the heatmaps presented later and consists of the ending day of the year (DOY, x-axis) and the season length (y-axis) and refers to all combinations of window length (from 21 to 180 days) and an ending day from May 1st in the previous year until September 30th in the current year.

sampling design. PCGA allows for quantifying the influence of environmental gradients on variations of the population signal in tree-ring data (Buras et al., 2016). PCGA is similar to Principal Component Analysis, but with distinction that it emphasizes on the loadings of the first two principal components only which were shown to mirror patterns of growth synchronicity related to existing sub populations (e.g., Rehschuh et al., 2017, Buras et al., 2023). Consequently, we assessed the influence of elevation on the population inherent gradient as determined using PCGA. The influence was quantified by computing Spearman's rank correlation for site-specific elevations ordered according to the identified PCGA gradient (Rehschuh et al., 2017). Here, a strong and significant positive correlation would indicate that elevation significantly alters the growth signal, thus justifying the separation of our data into elevational belts. PCGA was computed using the 'dendRoLAB' R package (Buras, 2022).

The climatic data (daily maximum and minimum temperatures and precipitation) used in this study were downloaded for the period 1950 to 2021, at the plot level from the *easyclimate* database (Cruz-Alonso et al., 2023), which represents a downscaled version of the E-OBS climatic database (Cornes et al., 2018) at a spatial resolution of (0.0083°, ~1 km). The mean daily temperature was calculated as the average of the minimum and maximum temperatures. The Standardized Precipitation-Evapotranspiration Index (SPEI) was used to characterize water availability in the study area (Begueria et al., 2013). The potential evapotranspiration data were calculated according to the Hargreaves-Samani method based on temperature (mean, maximum, and minimum) and plot latitude, which was used to estimate the net solar radiation at the surface (Hargreaves and Samani, 1985). To calculate SPEI, the climatic water balance values, defined as the difference between precipitation and potential evapotranspiration, were aggregated, at different cumulative daily windows, into a log-logistic probability distribution (Jevšenak, 2019).

2.4. Statistical analysis

The complex workflow of our statistical analysis is presented in Fig. 2. The climate-growth relationships of spruce were assessed for mean temperature, precipitation, and SPEI. Since SPEI is a more precise proxy for actual plant water availability than precipitation, the results for temperature (H1) and SPEI (H2) are shown in the main text, while figures related to precipitation are placed in the supplementary material. To quantify TSCS, we applied two methods. First, the common overlap period of tree-ring and climate data was split into two periods (referred to as static method in the following – Fig. 2B): 1951 to 1985 (early) and 1986 to 2021 (late). For each period, we independently applied the day-wise aggregated climate-growth correlations from the dendroTools R package (Jevšenak, 2020; Jevšenak and Levanič, 2018). In particular, we calculated the Pearson correlation coefficient across 520 seasonal aggregates of climate. This analysis spanned from May 1st of the previous growing season to September 30th of the current growing season, correlating these aggregates with the plot-level mean TRI chronologies. We considered all window sizes (season lengths) between 21 and 180 days. The aim of this static approach was to quantify the change in climate response between the two periods.

For the static method, we first calculated the percentage of plots with significant correlation coefficients independently for each of the two split periods ($p < 0.05$). Next, for each elevational belt, we calculated the mean correlation coefficients and the standard deviations for each season and climate parameter, highlighting the differences in climate sensitivity between the elevational belts (see Fig. 2B for more details).

To further investigate TSCS over time, we applied a dynamic method (Fig. 2C) consisting of a moving-window approach to assess the temporal change of climate-growth relationships. To do this, we applied a window-size of 31 years, starting with the period 1951 to 1981, while shifting the analyzed period by 1 year at a time and ending with the period 1991 to 2021. At each step, we calculated the climate-growth

correlations for the subset period for the three climate parameters and the same seasonal windows and season length used in the static method.

The output matrices of the dynamic approach were used to investigate TSCS in more detail. For each site, we first derived trends in climate sensitivity for all seasons analyzed. To do so, we regressed the correlation coefficients versus time independently for each season-length combination and extracted the beta coefficients from ordinary linear regressions as a mathematical representation of TSCS (Eq. (1)), where cor represents the correlation coefficients in a subset period, a the intercept, β the beta coefficient, $interval$ the subset period, ε the error associated with the model, i the season, and j the plot.

$$cor_{ij} = a_{ij} + \beta_{ij} \cdot interval_{ij} + \varepsilon_{ij} \quad (1)$$

Finally, the beta coefficients, representing TSCS, were averaged within each elevational belt to obtain trends related to different elevations. To define an increase or decrease in correlations within the period from 1950 to 2021, four possible TSCS types were defined. If both correlations had the same sign in the first and last intervals, it was defined as a positive-positive type or a negative-negative type (see Fig. 2C for more details). In the negative-negative type, the sign of the beta coefficient was changed to keep the coherence with the positive-positive type for easier interpretation. If the sign of the correlation coefficients between the first and last intervals was different, it was defined as a positive-negative or negative-positive type.

In our study, we conducted an extensive series of correlation tests and are aware of the issue of multiple comparisons (Gelman and Loken, 2013), wherein the likelihood of erroneously identifying results as significant escalates substantially. To mitigate this risk, we emphasize findings where multiple seasons showed significant values. We did not count on the significance, but rather we used it as an objective threshold for distinguishing meaningful signals from the background noise. Furthermore, we observed significant outcomes for seasons that are closely related, a pattern that strongly suggests these results are not mere products of stochastic processes.

To address the third hypothesis, we regressed TSCS (beta coefficients) against elevation, latitude, and longitude. In this analysis, we selected the four seasonal windows that revealed the strongest TSCS. This selection resulted in two seasons each for temperature (one from the current growing season and one from winter) as well as SPEI (one from the end of the current growing season and one from winter). Here, significant regressions would support H3 since a significant change of TSCS along elevation, longitude, or latitude would indicate TSCS divergence which was the assumption underlying H3 and the central aim of our investigation. To investigate the importance of each of the environmental parameters on TSCS, we fitted multiple linear regression models (Uyanik and Güler, 2013) with Eq. (2), where β is the dependent variable (beta coefficients), β_0 is the intercept, β_1 is the coefficient for the independent variable elevation, β_2 is the coefficient for the independent variable longitude, and β_3 is the coefficient for the independent variable latitude, ε the error associated with the model.

$$\beta = \beta_0 + \beta_1 \cdot Elevation + \beta_2 \cdot Longitude + \beta_3 \cdot Latitude + \varepsilon \quad (2)$$

Based on the fitted models, we calculated the variable importance for elevation, longitude, and latitude, respectively (Grömping, 2015). Independent multiple linear regression models were fitted for each highlighted season. Computation of the model and extraction of the variable importance was done in the R environment using the 'relaimpo' R package (Groemping and Matthias, 2018).

3. Results

3.1. Radial tree growth among elevational belts

Differences in the radial tree growth of spruce were largely explained by the elevational gradient (Fig. 3A). The second principal component

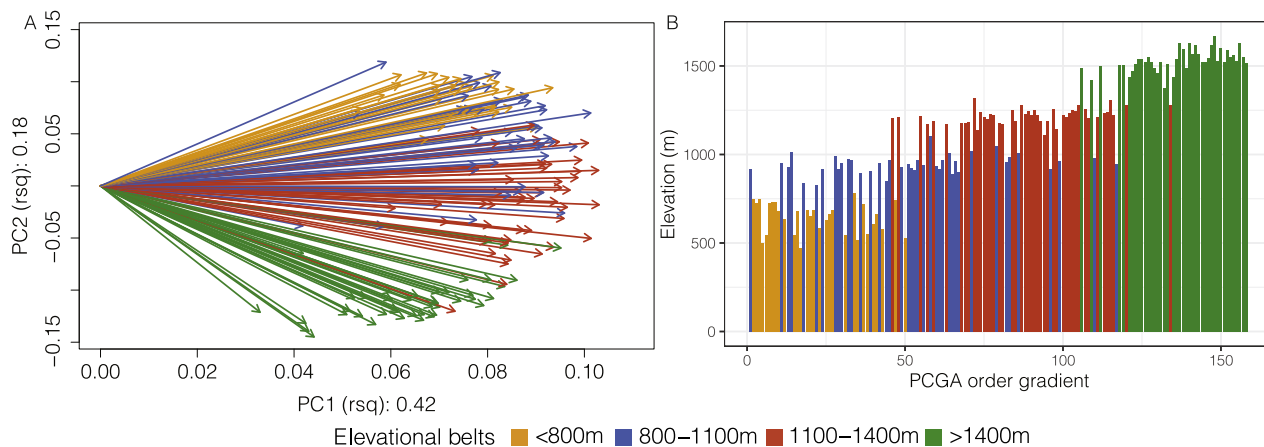


Fig. 3. (A) Principal Component Gradient Analysis (PCGA) computed at the plot level; and (B) distribution of the plots in relation to elevation and order of PCGA gradient, color coded by elevational belt (yellow – <800 m, blue – 800 to 1100 m, red – 1100 to 1400 m, and green >1400 m).

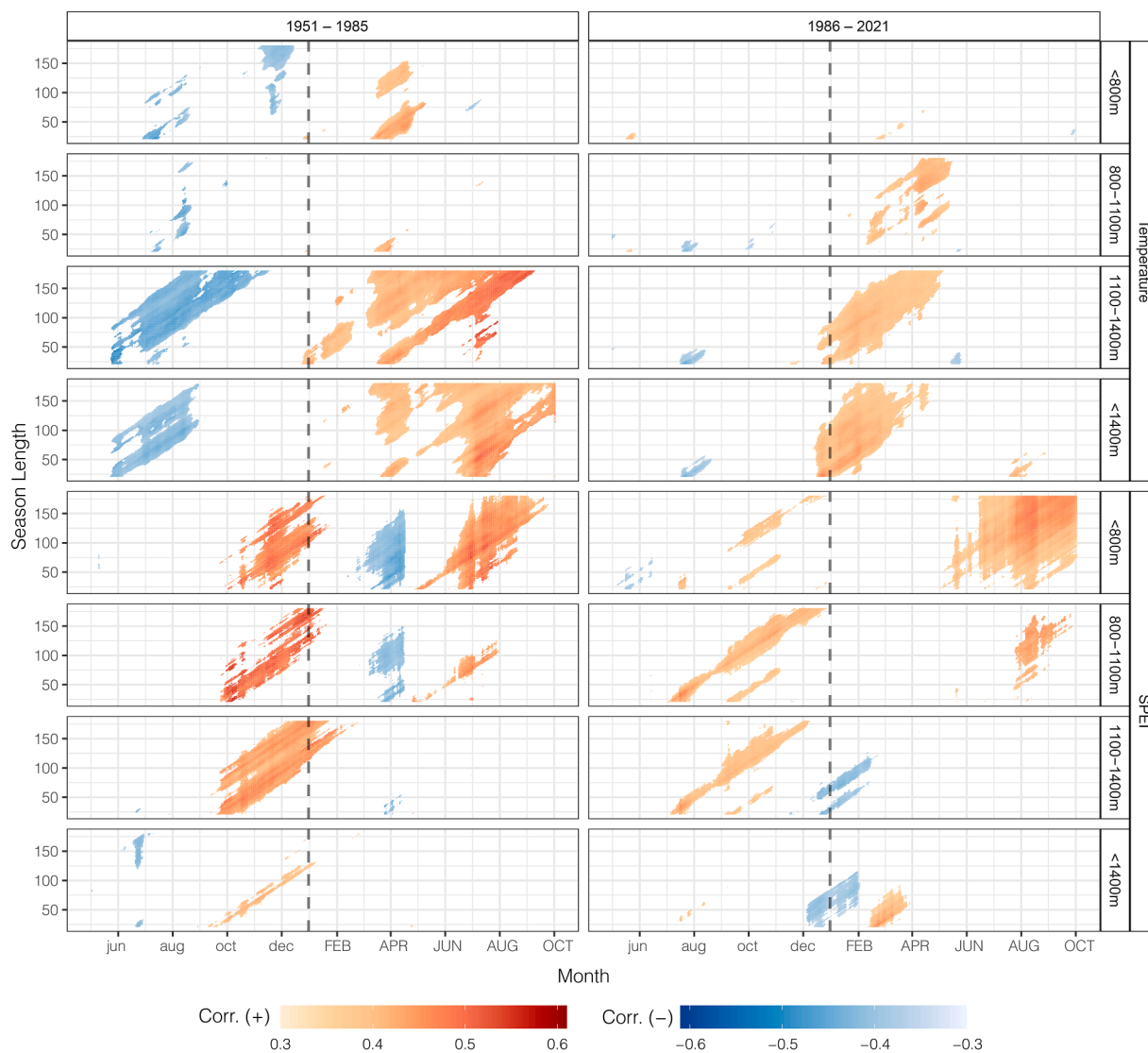


Fig. 4. Mean temperature and Standardized Precipitation-Evapotranspiration Index (SPEI) correlation coefficients with residual tree ring-width index (TRI) values for different elevational belts in the early (1951 to 1985) and late (1986 to 2021) periods. Only the seasons in which at least 25 % of the chronologies had a significant correlation coefficient ($p < 0.05$) are shown. The vertical dotted gray line represents the limit between the previous (lowercase letters) and current (uppercase letters) year. The reference position of each correlation coefficient is the end of the considered time window. Similar results for precipitation and current (uppercase letters) year are shown in Figure S4.

(PC2), which explained 18 % of the variance in radial tree growth, was assumed to be related to the influence of elevation. However, the first principal component (PC1) explained 42 % of variance and was assumed to reflect the common climatic signal. The Spearman's rank correlation for site-specific elevations, ordered according to the identified PCGA gradient (Fig. 3B), was 0.90 ($p < 0.001$), confirming a significant effect of elevation on growth variability and thus supporting the categoric division into four elevational belts. Yet, at elevations below 1100 m i.e. within the optimal distribution range of spruce in the Carpathians, the effect of elevation appeared to be less influential (Fig. 3B). TRI generally showed a similar variability among elevational belts in recent decades (Fig. S1). However, the greatest variability occurred at elevations below 800 m, where extremely low TRI values (< 0.75) were observed in 1968, 2003, 2015, and 2020. In each of these drought years, TRI decreased at all elevational belts.

3.2. Shifting climate sensitivity using the static method

The climate-growth relationships assessed by the static approach indicated shifting responses to climate between the early (1951 to 1985) and late (1986 to 2021) periods. We observed a significant summer temperature signal in the two upper elevational belts in the early period which largely disappeared in the late period (Fig. 4 Temperature panel). In the early period, late spring to early summer (the season between 28 Apr. to 30 Jul.) showed the highest correlation ($r = 0.559$), indicating a strong growth constraint due to low temperatures. Meanwhile, the correlations between temperatures from the end of summer and TRI were associated with the highest standard deviation, indicating diverse growth responses across the network (Fig. S2 Temperature panel). At elevations above 1400 m, current summer temperatures and TRI were significantly correlated in > 75 % of the plots (Fig. S3 Temperature panel), highlighting a common signal within this elevation belt. In the late period, the positive effect of temperature largely disappeared in the summer, while a more widespread temperature sensitivity of TRI was observed in the spring, indicating a significant temperature effect from the beginning of the growing season. Furthermore, winter temperatures and TRI were positively correlated for elevations above 1100 m in the late period. The highest correlations were identified for short seasons, in the first part of winter ($r = 0.491$ for the 21-day season from 3 to 23 Dec.). Selecting larger cumulative seasons, we observed the entire winter (Jan. and Feb.) to be positively, significantly correlated with TRI.

Positive correlations with previous late autumn/early winter SPEI at elevations below 1100 m in the early period indicated a growth limitation due to low water availability, a pattern which strongly decreased in the late period (Fig. 4 SPEI panel). Intense autumn rains or early first snow thus became less constraining for spruce growth at low and intermediate elevations, while water availability from the previous summer remained positively correlated with TRI. In the early period, the highest correlations between previous autumn SPEI and TRI corresponded to short cumulative seasons ($r = 0.581$ for a 23-day season from 15 Sep. to 8 Oct.; these correlations are associated with high standard deviation – Fig. S2 SPEI panel), while, in the later period, they corresponded to month-long seasons ($r = 0.491$ for a 32-day season from 15 Jul. to 13 Jun.). Negative correlations between the current year's spring SPEI values and TRI were observed at elevations below 1100 m in the early period (the highest correlation of $r = -0.489$ for a season length of 52 cumulative days from 16 Feb. to 9 Apr.), potentially reflecting thermal constraints on TRI, but were no longer statistically significant ($p > 0.05$) in the late period. A typical correlation pattern was found at the lowest elevational belt, regarding the positive correlation between the late summer SPEI. However, from the period 1951–1985 to the period 1986–2021, the number of seasons with a significant correlation with water availability increased, indicating an increase in the constraints of water availability over time and supporting H2. Furthermore, < 50 % of plots recorded a significant correlation with water availability in the early period, while > 90 % of the plots were significantly influenced by

water availability in the late period (Fig. S3 SPEI panel). The correlation patterns between precipitation and TRI were similar to those of SPEI for both periods (Fig. S4).

3.3. Temporal shifts of climate sensitivity (TSCS) using the dynamic method

TSCS over time were highlighted by increases or decreases in correlation intensity which sometimes led to a change in correlation sign (from positive to negative or vice versa) (Fig. 5). For elevations above 1100 m, the summer temperature sensitivity declined substantially, namely a decrease in correlation intensity or a shift from positive to negative correlations, thus supporting H1. An interesting fact was the enhancement of the correlation between late winter (Jan. to Feb.) temperatures and TRI only at higher elevations, while an increase of correlation with spring (Mar. to Apr.) temperatures was observed along the entire elevational gradient. Considering the number of plots within the same TSCS type, the strongest common signal (> 80 % plots) (Fig. S5 Temperature panel) was identified for shorter cumulative seasons in the spring (Mar.) at low elevations and in mid-winter (Dec. to Jan.) at high elevations.

The correlation between the late autumn/early winter SPEI and TRI decreased substantially, with a stronger change at low elevations (Fig. 5 SPEI panel). At the same time, correlations shifted from positive to negative at higher elevations (> 1100 m), especially during winter and early spring. Furthermore, most of the sites (over 80 %) recorded this change in correlation sign (Fig. S5 SPEI panel), revealing a strong common pattern within the elevational belts. The correlation intensity between the current summer SPEI and TRI decreased at elevations below 1100 m, but for a smaller percentage of plots (less 60 %) (Fig. S5 SPEI panel). The positive late summer SPEI correlation at sites below 800 m (indicating dry conditions that hamper growth), increased over time, indicating a strongly positive TSCS. In accordance with H2, the positive TSCS was found at most of the low elevation plots (Fig. S5 SPEI panel). Similar to SPEI patterns, we observed a major TSCS for precipitation (Fig. S6). However, for summer precipitation (Jun. to Aug.), we observed a stronger negative TSCS at intermediate elevations, suggesting that water availability is becoming a limiting factor, especially at low elevations.

3.4. Spatial trends in temporal shifts of climate sensitivity (TSCS)

In the context of addressing H3, analyses along the elevational gradient revealed significant trends ($p < 0.001$) in TSCS for all seasons and climatic parameters (Fig. 6, orange lines). Diverging TSCS were present across elevations, with sometimes increasing versus decreasing sensitivity at the edges of the elevational gradient. Considering the late winter temperature signal, positive TSCS were observed at high elevations with a trend toward lower and partly negative TSCS at low elevations. For summer temperatures, the opposite relationship was observed. That is, while the sensitivity to summer temperatures decreased at high elevations, it remained stable (TSCS = 0) at low elevations. Considering sensitivity to winter and summer water availability (SPEI), TSCS also diverged. While sensitivity to SPEI increased over time at low elevations, sensitivity to SPEI in both summer and winter slightly decreased at high elevations.

Regarding the longitudinal gradient, we again observed diverging TSCS from west to east for all four highlighted seasons (Fig. 6, green lines). Interestingly, the regression lines quantifying TSCS divergence of the longitudinal gradient were negatively correlated throughout with those from the elevational gradient (Fig. 6, green versus orange lines). Consequently, for winter SPEI and summer SPEI we found positive TSCS in the eastern part of the Eastern Carpathians, compared to western Carpathians, which featured a slightly negative TSCS and no TSCS for summer SPEI. TSCS of summer temperatures was negative across the whole continentality gradient but represented more negative trends in

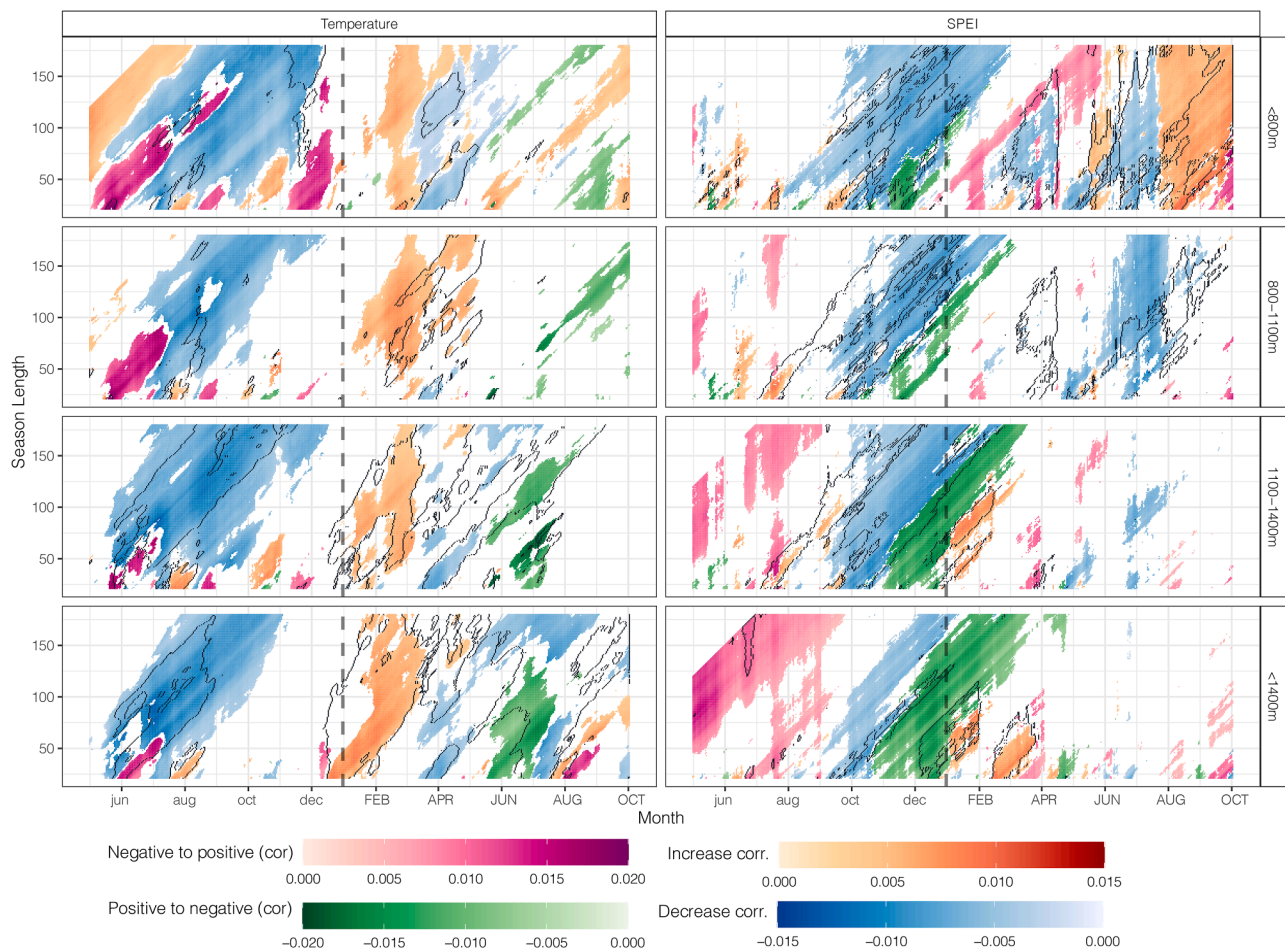


Fig. 5. Seasons with increasing or decreasing correlations (the positive–positive or negative–negative temporal shifts in climate sensitivity (TSCS) types; red and blue), and seasons with a change in correlation sign (the negative–positive or positive–negative TSCS types; pink and green) for temperature and Standardized Precipitation-Evapotranspiration Index (SPEI). The figure shows only the seasons in which at least 50 % of the plots recorded a significant change in correlation. For the negative–negative scenario, signs of beta coefficients were flipped for a consistent interpretation. Polygons indicate seasons with significant correlation coefficients ($p < 0.05$) between tree ring-width index (TRI) and the climate variable, in the early and late periods (for differentiating between the two periods, see Fig. 4). The vertical dotted gray line represents the limit between the previous (lowercase letters) and current (uppercase letters) year.

the western part of the network. In comparison, TSCS of winter temperatures shifted from positive values in the west to negative values in the east. TSCS also diverged along the studied latitudinal gradient, however, to a lesser extent than along the longitudinal gradient (Fig. 6, purple lines). While TSCS did not significantly diverge in the winter for temperature or SPEI, SPEI sensitivity increased in the summer toward the north while remaining stable in the south. Temperature sensitivity decreased in the summer in the south, while remaining stable in the north.

According to the multiple linear regression models, the elevational gradient significantly influenced ($p < 0.001$) TSCS in all seasons, with a variable importance of over 50 % in all models (Table 1). Meanwhile, the elevational gradient described most of the TSCS divergence with explained variances (r^2) of corresponding regressions ranging from 0.22 to 0.27. Longitude, as an expression of the continentality gradient, showed a significant influence ($p < 0.05$) on TSCS only in winter seasons, with a variable importance higher of 30 % in these seasons (Table 1). The explained variances (r^2) of longitude were lower than elevation and varied from 0.09 to 0.22. The longitudinal gradient only significantly influenced ($p < 0.01$) winter temperature TSCS, yet the variable importance was <10 % (Table 1). The latitude explained the least TSCS variance (r^2 of 0.01 to 0.07). In other words, diverging TSCS was mostly related to elevational differences, followed by the longitudinal continentality gradient.

4. Discussion

The results of our analyses supported the initially posed hypotheses. First, the summer-temperature sensitivity of Norway spruce significantly decreased at high elevations (H1). Furthermore, sensitivity to water availability in late summer/early autumn increased widely, indicating that most sites became more sensitive to drought at low elevations (H2). Together, these findings clearly indicate divergent temporal shifts in climate sensitivity along the elevational transect, which was further modified by a continentality gradient along the longitudinal transect (H3). In the following, we conduct an in-depth discussion of each of these findings.

4.1. Continuous warming has changed spruce's growth response to temperature at high elevations

Our results indicate current summer temperatures constrained spruce growth at high elevations in the early period (1951 to 1985) (Fig. 4). This is consistent with previous research in both the study area and other parts of Europe that found temperature and vegetative season length to limit spruce growth at high elevations (Bouriaud and Popa, 2009; Hartl-Meier et al., 2014; Leonelli and Pelfini, 2008; Levanic et al., 2009; Savva et al., 2006; Sidor et al., 2015). Maximal radial growth rates of spruce are likely to occur from June to July in mountainous areas

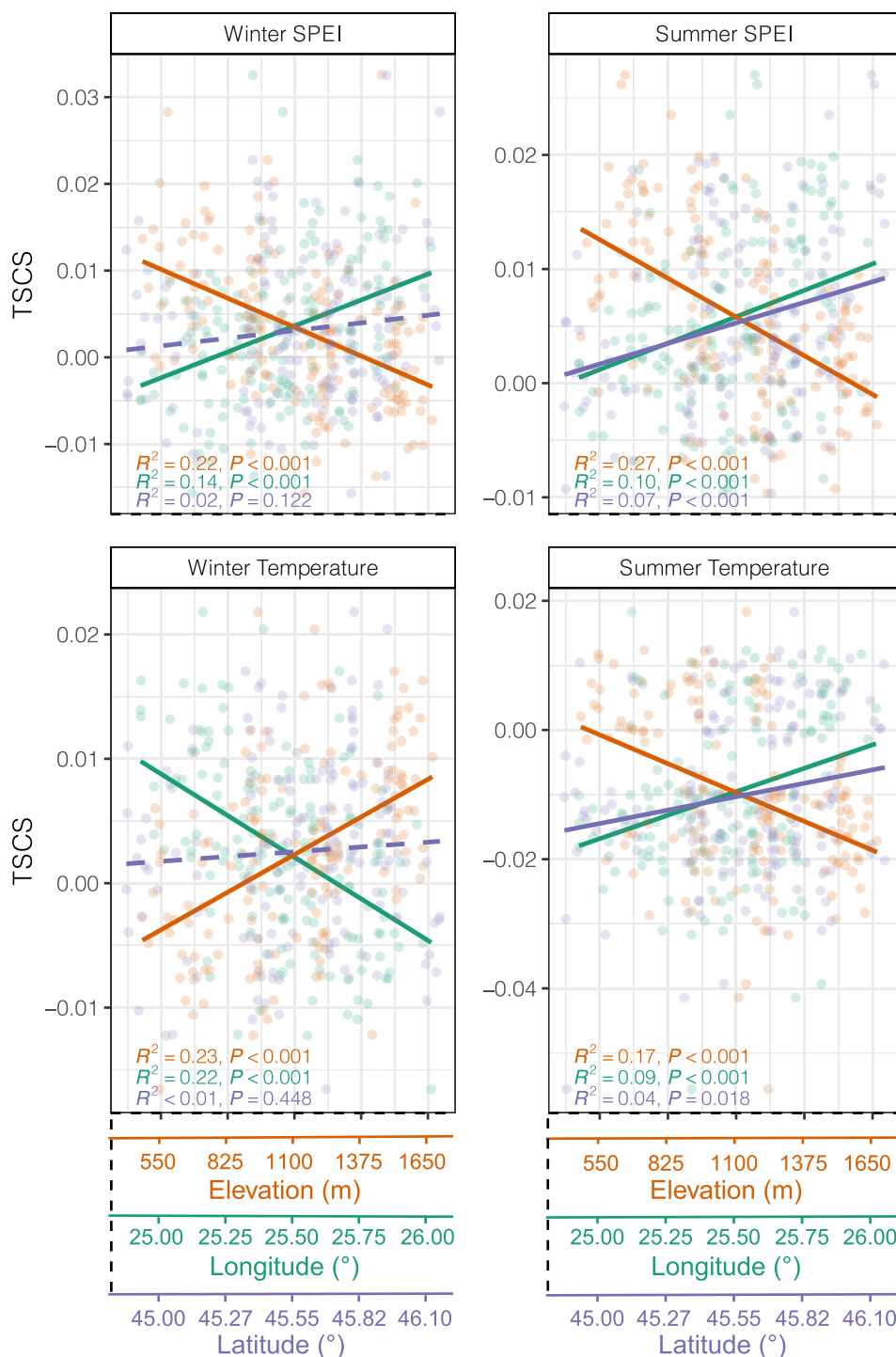


Fig. 6. Trends in temporal shifts of climate sensitivity (TSCS) in relation to elevation (orange), longitude (green), and latitude (purple). Winter Standardized Precipitation-Evapotranspiration Index (SPEI) corresponds to SPEI for a season length of 23 cumulative days ending on 25 Jan.; Summer SPEI corresponds to SPEI for a season length of 78 cumulative days ending on 30 Sep.; Winter Temperature corresponds to temperature for a season length of 56 cumulative days ending on 29 Jan.; and Summer Temperature corresponds to temperature for a season length of 21 cumulative days ending on 2 Aug. Solid lines represent significant trends ($p > 0.05$), while dotted lines indicate insignificant ones.

(Rossi et al., 2007; Trembl et al., 2015), indicating that low temperatures in these months may limit growth and consequently result in narrower tree-ring widths. While the current summer temperature correlation with TRI in the early period is consistent with this physiological pattern, spruce’s climate response decreased strongly in the late period (1986 to 2021), especially at elevations above 1100 m. These TSCS indicate that temperature-related growth constraints have disappeared over time,

which is likely attributed to the continuous warming trend observed at a global scale in recent decades (Babst et al., 2019). Global temperature has increased by approximately 1.1 °C compared with the pre-industrial period (Calvin et al., 2023), with an increase of 0.54 °C in temperature anomalies recorded in the last decades (Valipour et al., 2021). Furthermore, climate warming in mountainous regions has occurred at a rate above the global mean (Wang et al., 2014). The Carpathians have

Table 1

Summary of multiple linear regression models explaining the influence of elevation, longitude, and latitude on temporal shifts of climate sensitivity (TSCS) related to temperature and Standardized Precipitation-Evapotranspiration Index (SPEI) across the Eastern Carpathians. Independent multiple linear regression models were fitted for each of the highlighted seasons (see Fig. 6), with adjusted explained variance ($\text{adj } r^2$) given in brackets. Var. imp. represents variable importance presented in relative terms.

Season ($\text{adj } r^2$)	Predictor Variable	Estimate	Std. Error	t value	P-value	Sig.	Var. imp.
Winter SPEI (0.232)	Intercept	-0.12370	0.116	-1.063	0.289		
	Elevation	-0.00001	0.000	-4.590	<0.001	***	65 %
	Longitude	0.00603	0.003	2.335	0.021	*	32 %
	Latitude	-0.00033	0.002	-0.172	0.864	ns	3 %
Summer SPEI (0.274)	Intercept	-0.19740	0.104	-1.890	0.061		
	Elevation	-0.00001	0.000	-5.364	<0.001	***	69 %
	Longitude	0.00261	0.002	1.124	0.263	ns	17 %
Winter Temperature (0.335)	Latitude	0.00313	0.002	1.820	0.071	ns	14 %
	Intercept	-0.02816	0.096	-0.295	0.769		
	Elevation	0.00001	0.000	5.242	<0.001	***	51 %
Summer Temperature (0.168)	Longitude	-0.00839	0.002	-3.951	<0.001	***	42 %
	Latitude	0.00494	0.002	3.139	0.002	**	7 %
	Intercept	-0.30350	0.186	-1.628	0.106		
	Elevation	-0.00001	0.000	-3.721	<0.001	***	64 %
	Longitude	0.00640	0.004	1.546	0.124	ns	26 %
	Latitude	0.00306	0.003	0.998	0.320	ns	10 %

Significance level *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

similarly experienced a significant warming trend in recent decades (Micu et al., 2021). Continuous warming has changed sensitivity to climate across Europe for spruce (Bošela et al., 2014; Popa et al., 2024a; Schurman et al., 2019; Svobodová et al., 2019) and other tree species as well (Castaldi et al., 2020; Dobrovolný et al., 2016; Hofgaard et al., 2019; Unterholzner et al., 2024).

At the same, with the continuous warming trend, TRI displayed an increasing positive relationship with winter temperatures. During winter, low temperatures may cause xylem embolism (Lens et al., 2013; Mayr et al., 2020) or increase soil freeze depths, delaying the onset of xylogenesis (Lupi et al., 2012). Trees are more responsive to warmer winter or early spring temperatures at high elevations (Primicia et al., 2015), which accelerate spring snow melt and initiate cambium reactivation (Jochner et al., 2018; Rossi et al., 2008). The significant correlations between winter temperature and TRI in the late period, especially at elevations above 1100 m (Fig. 4, Temperature panel), are likely due to high temperatures accelerating snow melt and increasing soil temperature. Earlier snowmelt is likely to result in a longer growing season (Hu et al., 2010) with a positive impact on tree growth (Hinzman et al., 2005). In the last half of the 20th century, the onset of the growing season occurred with an estimated 2.2 days earlier per decade across Europe (Schwartz et al., 2006). The sensitivity of spruce growth to late autumn/early winter SPEI decreased in both the early and late periods at elevations below 1400 m (Fig. 5), which can also be attributed to shifting snow cover patterns associated with continuous warming. In the past, snow in early winter insulated the soil during later, colder periods of winter. In the Romanian Carpathians, snow depth and the number of days with snowfall and snow cover have been decreasing (Micu et al., 2015) and first snow occurrence has been delayed (Micu, 2009). Other studies conducted on spruce in the Carpathians also reported a significant and positive sensitivity to winter temperatures (Popa et al., 2022; Primicia et al., 2015). Altogether, these findings support H1, that spruce growth at high elevations is now constrained more by winter and early spring temperatures than summer temperatures, suggesting that the onset of vegetation, rather than absolute summer temperature, is more decisive for secondary tree growth.

Concerning TSCS of trees to temperature, a shifted response, in relation to elevation, was found from the previous autumn (more significant changes at low elevations) to winter (more significant changes at higher elevations), which is likely related to temperature's influence on physiological processes. At low elevations, long summers and warm autumn conditions may influence physiological processes at the end of the growing season, improving tree performance the following year by enhancing carbohydrate synthesis or favoring bud maturation (Gričar

et al., 2022; Primicia et al., 2015; Von Felten et al., 2007). At low elevations, the historical scarcity of winter precipitation (snow) suggests that recent environmental changes minimally impact TSCS. Meanwhile, winter conditions have changed considerably in recent decades in mountainous areas (Micu et al., 2015), resulting in more pronounced TSCS of spruce to temperature at high elevations during the winter.

Interestingly, TRI was significantly negatively correlated with previous summer temperature in the early period, and yet significantly positively correlated with previous summer/autumn SPEI in the late period, especially at intermediate elevations (Fig. 4). The correlation between previous growing season temperature and TRI is related to the temporal memory of growth (Klesse et al., 2023) and is potentially linked with non-structural carbohydrate dynamics (Michelot et al., 2012). We may assume that a warm summer may favor flowering and seed production of spruce, which could lead to a growth reduction, and hence, reduced TRI, in the following year (Hackett-Pain et al., 2019, 2015; Seifert and Müller-Starck, 2009; Selås et al., 2002). However, cone reproduction data are not available for our study sites. Consequently, an in-depth analysis based on other databases, such as the ICP Forests (<http://icp-forests.net>), may better reveal insights into these physiological mechanisms.

4.2. Diverging effects of climate change on spruce's water-availability sensitivity

Water availability, expressed as total precipitation or drought index SPEI, is an important regulator of spruce growth across large gradients (Jevšenak et al., 2021; Lévesque et al., 2013; Vitali et al., 2017). As with previous research that indicated climatic constraints shifting from temperature to moisture availability (Babst et al., 2019, 2013), we found that summer temperature is no longer the main driving factor at high elevations, where spring water availability has gained importance for tree growth over time (Fig. 4 SPEI panel, Figure S4). We interpret this signal as an increasing importance of snowmelt contributing to soil water content at high elevations early in the season. Similar findings were reported in the Calimani Mountains natural forests, the northern part of the Eastern Carpathians, where winter precipitation in the form of snow represented an important water resource for Carpathian spruce forests (Björklund et al. 2019; Schurman et al., 2019). Snow may play a more important role in maintaining moisture for mountainous soils, which tend to be shallow (Beniston et al., 2003). Importantly, these results highlight the potential for a climate-change-induced drought vulnerability at high elevations in the Eastern Carpathians. The reason why we did not find this phenomenon at intermediate elevations

however remains unclear but might be related to different soil properties, and thus, a lower effect of snowmelt at intermediate elevations.

While the positive summer SPEI sensitivity at low elevations – indicating dry conditions constraining spruce growth – slightly decreased over time, late summer/early autumn SPEI sensitivity became significantly positive (Figs. 4 and 5), signaling a shift in the seasonal impact of water availability on tree-ring width. However, in the last decades, water availability limitations were confirmed by intensification of the shared response of significant correlation among plots. The majority of sites exhibited similar trends (Fig. S3 SPEI panel), suggesting a synchronous response among trees, thus an early warning signal of forest decline (Shestakova et al., 2018). Spruce is known as a drought-intolerant species (Lévesque et al., 2013; Schuster and Oberhuber, 2013; van der Maaten-Theunissen et al., 2013), usually featuring a shallow root system (Caudullo et al., 2016) that limits its ability to access water in deeper soil layers. In strong drought years, usually associated with narrower rings, spruce was found to be more vulnerable than other coniferous species (Bouriaud and Popa, 2009; Vitali et al., 2017). Popa et al. (2024b) found a strong growth reduction of spruce at low elevations, indicating possible negative effects of increasing drought limitations. Thus, our results indicate a high drought vulnerability of spruce at low elevations, which may increase with more frequent and prolonged drought and heatwave events.

4.3. Elevation and continentality modulate temporal shifts of climate sensitivity (TSCS) in the Eastern Carpathians

Our results indicated differences in climate-growth relationships with elevation (Fig. 4), as found in previous studies of trees' response to climate (Kolář et al., 2017; Ponocná et al., 2016; Sidor et al., 2015). However, our findings also indicated significant trends in TSCS with elevation, highlighting that elevation modulates both tree response to climate and TSCS (Fig. 6). The elevational gradient had the highest importance (69 %) in modulating the TSCS of summer SPEI, with most changes occurring at low elevations. The increase of TSCS to winter temperature at high elevations may be related, as previously noted, to a lack of snow and possible changes in the onset of vegetative seasons. These shifts emphasize the need to quantify spruce's adaptability and resilience capacity to new climatic conditions for future management in the Carpathians (Popa et al., 2024).

In addition to elevation, our results indicated differences across the longitudinal gradient (from the east to the west side of the Carpathians), while the latitudinal gradient (from the northern to the southeastern sites) did not differ significantly. The opposite trend between the elevational gradient and the longitudinal gradient were partially related with a smaller correlation ($r = -0.481$), supporting the assumption that these variables influenced TSCS independently. Similarly, low values of correlation coefficients ($r < 0.1$) between latitude and longitude confirmed that these variables independently influenced TSCS, but with different importance (Table 1), thus confirming different findings along the elevational and spatial gradients. The Carpathians are considered one of the major landforms in Southeastern Europe (UNEP, 2008) and form a natural barrier between cold continental Eastern Europe and temperate Central Europe (Spinoni et al., 2015). Hence, this mountain chain with various and fragmented reliefs induces differences in climate along the east-to-west transect, especially inducing a continentality effect to the east. Most TSCS for water availability occurred in the eastern part of the Carpathians, at a longitude greater than 25.5°E , which has previously been identified as a climate change "hot spot" within Eastern Europe (Hlásny et al., 2016). Our results confirmed that a rapid change of climate, coupled with a delayed tree response, is likely to increase the vulnerability of spruce in the region.

The varying changes in winter temperature sensitivity of spruce from west to east can be attributed, in part, to the natural barrier effect exerted by the Carpathian Mountains against westerly winds (Hlásny et al., 2016). During winter, cold winds from the eastern part of the

continent influence the eastern parts of the Carpathian Arch more than the western and inner parts (Micu et al., 2015). At the same time, a more pronounced trend in changing spruce sensitivity to winter and summer SPEI was also observed on the eastern side of the Carpathians. In extremely dry years, water availability differed between the north-eastern part of the Carpathians and the western and southern parts (Spinoni et al., 2013). Altogether, these results confirmed H3 and, with increasing trends and changing drought conditions (Ionita and Nagavciuc, 2021; Spinoni et al., 2018), we may expect different responses of spruce along the Carpathians.

4.4. Methodological consideration and future perspectives

The primary focus of this study was on the principal climatic factors affecting tree growth, namely temperature, precipitation, and plant water availability (Fritts, 1976). However, it's crucial to note that cloud cover and relative sun duration, both of which influence net downwelling shortwave radiation and serve as primary drivers of photosynthesis, bear significant implications for secondary tree growth (D'Arrigo et al., 2008; Nagavciuc et al., 2019). For example, global solar dimming was observed from the 1960s to the 1980s, followed by an increase in brightening from the 1990s to the 2000s (Wild et al., 2007). These changes overlap with our early and late periods and may induce different responses in tree growth. Using this parameter to investigate TSCS is of interest for future investigations. Further uncertainties may be induced by air pollution, which may affect tree growth or climate-growth relationships (Buras et al., 2018; Sidor et al., 2022; Cuciurean et al., 2024). Nevertheless, we are confident that the observed TSCS were mainly driven by a warming and drying climate in the region, due to TSCS indicating meaningful physiological reactions to these climatic changes (see previous sections of the discussion).

The dendrochronological network used in this study was distributed across a wide range of various environmental conditions (e.g., bedrock, soil, and forest management), which likely influence climate-growth relationships as well. Because of the wide area covered by the sampling network, spanning from 475 m to the timberline at 1675 m, the soil characteristics of the studied stands vary. Usually, deeper soils are present at low elevations, while, soils are shallow with bedrock close to the surface at the timberline. Soil characteristics are known to be important drivers of tree growth (Maes et al., 2019) and may result in a differentiation of climate-growth relationships due to significant effects on plant-water availability, as reported previously for spruce (Rehsechub et al., 2017). Although soil conditions may explain part of the local variations of climate sensitivity in our network, they are unlikely to explain the observed TSCS since soil characteristics typically do not change on such a short timescale. Furthermore, the extensive replication in our network aimed to minimize local effects, with each elevational belt represented by at least 30 sites.

Forest management practices have strongly influence tree growth and ability to recover from drought events (Pretzsch, 2021; Schmied et al., 2022). In the current study, forest management practices were not considered, due to the high number of plots and scarcity of management data to address this question adequately. Thus, management activities may represent another source of uncertainty. However, it is worth noting that forestry regulations in Romania since World War II have aimed to standardize and regulate the implementation of forest management plans (Albulescu et al., 2022), likely resulting in similar forest management along our network of managed forest stands. We tested the effect of age on our results by splitting the dataset into three age classes (young stands <70 yrs., mature 71 to 100 yrs. and old >100 yrs.) and found no significant changes to our results.

Despite these potential additional influencing factors, our study strongly suggests that climate change is affecting spruce in the Eastern Carpathians at high rates. Consequently, forest managers need to be alert to improve spruce management in the context of drought-induced forest decline and resulting bark beetle calamities (Schmied et al.,

2022). In our study area, no large-scale bark beetle calamities have been reported so far (Synek et al., 2020) and thus, have not affected TSCS. However, our divergent TSCS findings indicate an increased vulnerability of spruce forests which, under extreme climatic change, may be prone to large-scale diebacks. Additional investigations of how spruce reacts in extreme drought years may reveal more detailed perspective on this species in Eastern Europe. Also, applying a similar methodology to other abundant species (e.g., silver fir, European beech) may provide important insights into the future of Carpathian forests, such as temporarily altered climate-growth relationships as shown recently for a global tree-ring network (Leifsson et al., 2023). Meanwhile, linking TSCS to other tree-ring parameters (stable isotopes, wood-anatomical features, basal area increment trends, or statistical early-warning signals) may reveal important relationships between changes in the climate response of trees, ecophysiology, and biomass accumulation. Ideally, pursuing any of these avenues of investigation will increase understanding of the response of Eastern Carpathian forest biomes to climate change to better project their future performance.

5. Conclusion

The Carpathians host the largest forested area in Eastern Europe, with a major importance in providing ecosystem services to a wider region (Mráz and Ronikier, 2016). Assessing and understanding Carpathian forests' condition and reactions to climate change is an imperative step for sustainable forest management and the continued provision of ecosystem services. In the context of global change, our results provide novel insights as to how temporarily changing climatic factors alter spruce growth in the Eastern Carpathians. By employing a mathematical quantification to assess temporal shifts in climate sensitivity along both an elevational and continentality gradient, our study reveals three key findings. First, summer temperature became less constraining to spruce growth at high elevations. Second, it highlights an expansion in the season of growth sensitivity to water availability, extending into late summer/autumn and becoming a shared characteristic for most sites, at low elevations. Third, the temporal shifts in climate sensitivity of spruce were divergent along the examined gradients in the Eastern Carpathians. Overall, these observed temporal shifts in the climate sensitivity patterns over the past decades suggest potentially significant ongoing shifts in spruce's climate sensitivity and, consequently, a changing performance under continued climate change in the Eastern Carpathians.

CRedit authorship contribution statement

Andrei Popa: Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Jernej Jevšenak:** Writing – review & editing, Visualization, Software, Methodology, Conceptualization. **Ionel Popa:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Ovidiu Badea:** Writing – review & editing. **Allan Buras:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

Acknowledgments

This study was supported by a grant from the Ministry of Research, Innovation and Digitization, CNCS-UEFISCDI, project number PN-III-P4-PCE-2021–1002, within PNCDI III and from project CresPerfInst (contract 34PFE/30.12.2021). JJ was supported by the Alexander von Humboldt postdoctoral fellowship and Slovenian Research and Innovation Agency (P4-017). We would like to thank M. Balabaşciuc for assistance in the field and laboratory with sampling and tree-ring measurements and S. Rauter for proofreading our manuscript.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.agrformet.2024.110243](https://doi.org/10.1016/j.agrformet.2024.110243).

References

- Albulescu, A.-C., Manton, M., Larion, D., Angelstam, P., 2022. The winding road towards sustainable forest management in Romania, 1989–2022: a case study of post-communist social–ecological transition. *Land* (Basel) 11, 1198. <https://doi.org/10.3390/land11081198>.
- Babst, F., Alexander, M.R., Szejner, P., Bouriaud, O., Klesse, S., Roden, J., Ciais, P., Poulter, B., Frank, D., Moore, D.J.P., Trouet, V., 2014. A tree-ring perspective on the terrestrial carbon cycle. *Oecologia* 176, 307–322. <https://doi.org/10.1007/s00442-014-3031-6>.
- Babst, F., Bodesheim, P., Charney, N., Friend, A.D., Girardin, M.P., Klesse, S., Moore, D.J.P., Seftigen, K., Björklund, J., Bouriaud, O., Dawson, A., DeRose, R.J., Dietze, M.C., Eckes, A.H., Enquist, B., Frank, D.C., Mahecha, M.D., Poulter, B., Record, S., Trouet, V., Turton, R.H., Zhang, Z., Evans, M.E.K., 2018. When tree rings go global: challenges and opportunities for retro- and prospective insight. *Quat. Sci. Rev.* 197, 1–20. <https://doi.org/10.1016/j.quascirev.2018.07.009>.
- Babst, F., Bouriaud, O., Poulter, B., Trouet, V., Girardin, M.P., Frank, D.C., 2019. Twentieth century redistribution in climatic drivers of global tree growth. *Sci. Adv.* 5, eaat4313. <https://doi.org/10.1126/sciadv.aat4313>.
- Babst, F., Poulter, B., Trouet, V., Tan, K., Neuwirth, B., Wilson, R., Carrer, M., Grabner, M., Tegel, W., Levanić, T., Panayotov, M., Urbinati, C., Bouriaud, O., Ciais, P., Frank, D., 2013. Site- and species-specific responses of forest growth to climate across the European continent. *Glob. Ecol. Biogeogr.* 22, 706–717. <https://doi.org/10.1111/geb.12023>.
- Begović, K., Rydval, M., Mikac, S., Čupić, S., Svoboda, K., Mikoláš, M., Kozák, D., Kameniar, O., Franković, M., Pavlin, J., Langbehn, T., Svoboda, M., 2020. Climate-growth relationships of Norway spruce and silver fir in primary forests of the Croatian Dinaric mountains. *Agric. For. Meteorol.*, 108000 <https://doi.org/10.1016/j.agrformet.2020.108000>.
- Beguieria, S., Vicente-Serrano, S.M., Reig, F., Latorre, B., 2013. Standardized precipitation evapotranspiration index (SPEI) revisited: parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. *Int. J. Climatol.*
- Beniston, M., Keller, F., Koffi, B., Goyette, S., 2003. Estimates of snow accumulation and volume in the Swiss Alps under changing climatic conditions. *Theor. Appl. Climatol.* 76, 125–140. <https://doi.org/10.1007/s00704-003-0016-5>.
- Björklund, J., Rydval, M., Schurman, J.S., Seftigen, K., Trotsiuk, V., Janda, P., Mikoláš, M., Dušátko, M., Čada, V., Bače, R., Svoboda, M., 2019. Disentangling the multi-faceted growth patterns of primary *Picea abies* forests in the Carpathian arc. *Agric. For. Meteorol.* 271, 214–224. <https://doi.org/10.1016/j.agrformet.2019.03.002>.
- Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320, 1444–1449. <https://doi.org/10.1126/science.1155121>.
- Bošel' a, M., Sedmák, R., Sedmáková, D., Marušák, R., Kulla, L., 2014. Temporal shifts of climate-growth relationships of Norway spruce as an indicator of health decline in the Beskids, Slovakia. *For. Ecol. Manage.* 325, 108–117. <https://doi.org/10.1016/j.foreco.2014.03.055>.
- Bouriaud, O., Popa, I., 2009. Comparative dendroclimatic study of Scots pine, Norway spruce, and silver fir in the Vrancea Range, Eastern Carpathian Mountains. *Trees* 23, 95–106. <https://doi.org/10.1007/s00468-008-0258-z>.
- Briffa, K.R., Schweingruber, F.H., Jones, P.D., Osborn, T.J., Shiyatov, S.G., Vaganov, E. A., 1998. Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature* 391, 678–682. <https://doi.org/10.1038/35596>.
- Brodribb, T.J., Powers, J., Cochard, H., Choat, B., 2020. Hanging by a thread? Forests and drought. *Science* 368, 261–266. <https://doi.org/10.1126/science.aat7631>.
- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26, 115–124. <https://doi.org/10.1016/j.dendro.2008.01.002>.
- Büntgen, U., Frank, D.C., Schmidhalter, M., Neuwirth, B., Seifert, M., Esper, J., 2006. Growth/climate response shift in a long subalpine spruce chronology. *Trees* 20, 99–110. <https://doi.org/10.1007/s00468-005-0017-3>.
- Büntgen, U., Trouet, V., Frank, D., Leuschner, H.H., Friedrichs, D., Luterbacher, J., Esper, J., 2010. Tree-ring indicators of German summer drought over the last millennium. *Quat. Sci. Rev.* 29, 1005–1016. <https://doi.org/10.1016/j.quascirev.2010.01.003>.
- Buras, A., 2022. dendRolAB: analytical tools for tree-ring data.

- Buras, A., Menzel, A., 2019. Projecting tree species composition changes of European forests for 2061–2090 under RCP 4.5 and RCP 8.5 scenarios. *Front. Plant Sci.* 9, 1986. <https://doi.org/10.3389/fpls.2018.01986>.
- Buras, A., Rehsechuh, R., Fonti, M., Lange, J., Fonti, P., Menzel, A., Gessler, A., Rigling, A., Treydte, K., Von Arx, G., 2023. Quantitative wood anatomy and stable carbon isotopes indicate pronounced drought exposure of Scots pine when growing at the forest edge. *Front. For. Glob. Change* 6, 1233052. <https://doi.org/10.3389/fgc.2023.1233052>.
- Buras, A., Spyt, B., Janecka, K., Kaczka, R., 2018. Divergent growth of Norway spruce on Babia Góra Mountain in the Western Carpathians. *Dendrochronologia* 50, 33–43. <https://doi.org/10.1016/j.dendro.2018.04.005>.
- Buras, A., van der Maaten-Theunissen, M., van der Maaten, E., Ahlgrimm, S., Hermann, P., Simard, S., Heinrich, I., Helle, G., Unterseher, M., Schnittler, M., Eusemann, P., Wilmking, M., 2016. Tuning the voices of a choir: detecting ecological gradients in time-series populations. *PLoS ONE* 11, e0158346. <https://doi.org/10.1371/journal.pone.0158346>.
- Caillieret, M., Dakos, V., Jansen, S., Robert, E.M.R., Aakala, T., Amoroso, M.M., Antos, J.A., Bigler, C., Bugmann, H., Caccianaga, M., Camarero, J.-J., Cherubini, P., Coyea, M.R., Cufar, K., Das, A.J., Davi, H., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hartmann, H., Hereš, A.-M., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Levanic, T., Linares, J.-C., Lombardi, F., Mäkinen, H., Mészáros, I., Metsaranta, J.M., Oberhuber, W., Papadopoulos, A., Petritan, A.M., Rohner, B., Sangüesa-Barreda, G., Smith, J.M., Stan, A.B., Stojanovic, D.B., Suarez, M.-L., Svoboda, M., Trotsiuk, V., Villalba, R., Westwood, A.R., Wyckoff, P.H., Martínez-Vilalta, J., 2019. Early-warning signals of individual tree mortality based on. *Annual Rad. Growth. Front. Plant Sci.* 9, 1964. <https://doi.org/10.3389/fpls.2018.01964>.
- Caillieret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianaga, M., Cada, V., Camarero, J.J., Cherubini, P., Cochard, H., Coyea, M.R., Cufar, K., Das, A.J., Davi, H., Delzon, S., Dorman, M., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hartmann, H., Hereš, A., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Kramer, K., Lens, F., Levanic, T., Linares Calderon, J.C., Lloret, F., Lobo-Do-Vale, R., Lombardi, F., López Rodríguez, R., Mäkinen, H., Mayr, S., Mészáros, I., Metsaranta, J.M., Minunno, F., Oberhuber, W., Papadopoulos, A., Peltoniemi, M., Petritan, A.M., Rohner, B., Sangüesa-Barreda, G., Sarris, D., Smith, J.M., Stan, A.B., Sterck, F., Stojanović, D.B., Suarez, M.L., Svoboda, M., Tognetti, R., Torres-Ruiz, J.M., Trotsiuk, V., Villalba, R., Vodde, F., Westwood, A.R., Wyckoff, P.H., Zafirov, N., Martínez-Vilalta, J., 2017. A synthesis of radial growth patterns preceding tree mortality. *Glob. Change Biol.* 23, 1675–1690. <https://doi.org/10.1111/gcb.13535>.
- Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P.W., Trisos, C., Romero, J., Aldunce, P., Barrett, K., Blanco, G., Cheung, W.W.L., Connors, S., Denton, F., Diongue-Niang, A., Dodman, D., Garschagen, M., Geden, O., Hayward, B., Jones, C., Jotzo, F., Krug, T., Lasco, R., Lee, Y.-Y., Masson-Delmotte, V., Meinshausen, M., Mintenbeck, K., Mokssit, A., Otto, F.E.L., Pathak, M., Pirani, A., Poloczanska, E., Pörtner, H.-O., Revi, A., Roberts, D.C., Roy, J., Ruane, A.C., Skea, J., Shukla, P.R., Slade, R., Slangen, A., Sokona, Y., Sörensson, A.A., Tignor, M., Van Vuuren, D., Wei, Y.-M., Winkler, H., Zhai, P., Zommers, Z., Hourcade, J.-C., Johnson, F.X., Pachauri, S., Simpson, N.P., Singh, C., Thomas, A., Totin, E., Arias, P., Bustamante, M., Elgizouli, I., Flato, G., Howden, M., Méndez-Vallejo, C., Pereira, J. J., Pichs-Madruga, R., Rose, S.K., Saheb, Y., Sánchez Rodríguez, R., Ürgü-Vorsatz, D., Xiao, C., Yassaa, N., 2023. *Alegría*. In: *Armour, K., Bednar-Friedl, B., Blok, K., Cissé, G., Dentener, F., Eriksen, S., Fischer, E., Garner, G., Guivarch, C., Haasnoot, M., Hansen, G., Hauser, M., Hawkins, E., Hermans, T., Kopp, R., Leprince-Ringuet, N., Lewis, J., Ley, D., Ludden, C., Niamir, L., Nicholls, Z., Some, S., Szopa, S., Trewin, B., Van Der Wijst, K.-I., Winter, G., Witting, M., Birt, A., Ha, M., Romero, J., Kim, J., Haites, E.F., Jung, Y., Stavins, R., Birt, A., Ha, M., Orendain, D.J.A., Ignon, L., Park, S., Park, Y., Reisinger, A., Cammaramo, D., Fischlin, A., Fuglestedt, J.S., Hansen, G., Ludden, C., Masson-Delmotte, V., Matthews, J.B.R., Mintenbeck, K., Pirani, A., Poloczanska, E., Leprince-Ringuet, N., Péan, C. (Eds.), IPCC, 2023: Climate Change 2023: synthesis report. Contribution of working groups I, II and III to the sixth assessment report of the intergovernmental panel on climate change [Core writing team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland. <https://doi.org/10.59327/IPCC/AR6-9789291691647>.*
- Camarero, J.J., Gazol, A., Sánchez-Salguero, R., Fajardo, A., McIntire, E.J.B., Gutiérrez, E., Battlori, E., Boudreau, S., Carrer, M., Diez, J., Duffour-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. Change Biol.* 27, 1879–1889. <https://doi.org/10.1111/gcb.15530>.
- Carrer, M., Urbinati, C., 2006. Long-term change in the sensitivity of tree-ring growth to climate forcing in *Larix decidua*. *New Phytol.* 170, 861–872. <https://doi.org/10.1111/j.1469-8137.2006.01703.x>.
- Castaldi, C., Marchi, M., Vacchiano, G., Corona, P., 2020. Douglas-fir climate sensitivity at two contrasting sites along the southern limit of the European planting range. *J. For. Res.* 31, 2193–2204. <https://doi.org/10.1007/s11676-019-01041-5>.
- Caudullo, G., Tinner, W., de Rigo, D., 2016. *Picea abies* in Europe: distribution, habitat, usage and threats. *Eur. Atlas For. Tree Species* 3.
- Caudullo, G., Welk, E., San-Miguel-Ayanz, J., 2017. Chorological maps for the main European woody species. *Data Brief* 12, 662–666. <https://doi.org/10.1016/j.dib.2017.05.007>.
- Charney, N.D., Babst, F., Poulter, B., Record, S., Trouet, V.M., Frank, D., Enquist, B.J., Evans, M.E.K., 2016. Observed forest sensitivity to climate implies large changes in 21st century North American forest growth. *Ecol. Lett.* 19, 1119–1128. <https://doi.org/10.1111/ele.12650>.
- Cook, E.R., 1985. A time series analysis approach to tree ring standardization. <https://doi.org/10.1002/9781118134461.ch1>.
- 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>.
- Cruz-Alonso, V., Pucher, C., Ratcliffe, S., Ruiz-Benito, P., Astigarraga, J., Neumann, M., Hasenauer, H., Rodríguez-Sánchez, F., 2023. The easyclimate R package: easy access to high-resolution daily climate data for Europe. *Environ. Model. Softw.* 161, 105627. <https://doi.org/10.1016/j.envsoft.2023.105627>.
- Cuciurean, C.I., Sidor, C.G., Camarero, J.J., Buculei, A., Badea, O., 2024. Detecting changes in industrial pollution by analyzing heavy metal concentrations in tree-ring wood from Romanian conifer forests. *Environ. Res.* 252, 118884. <https://doi.org/10.1016/j.envres.2024.118884>.
- D'Arrigo, R., Wilson, R., Liepert, B., Cherubini, P., 2008. On the 'Divergence Problem' in Northern Forests: a review of the tree-ring evidence and possible causes. *Glob. Planet. Change* 60, 289–305. <https://doi.org/10.1016/j.gloplacha.2007.03.004>.
- De Marco, A., Sicard, P., Feng, Z., Agathokleous, E., Alonso, R., Araminiene, V., Augustatis, A., Badea, O., Beasley, J.C., Branquinho, C., Bruckman, V.J., Collalti, A., David-Schwartz, R., Domingos, M., Du, E., Garcia Gomez, H., Hashimoto, S., Hoshika, Y., Jakovljevic, T., McNulty, S., Oksanen, E., Omid Khaniabadi, Y., Prescher, A., Saitanis, C.J., Sase, H., Schmitz, A., Voigt, G., Watanabe, M., Wood, M. D., Kozlov, M.V., Paoletti, E., 2022. Strategic roadmap to assess forest vulnerability under air pollution and climate change. *Glob. Change Biol.* 28, 5062–5085. <https://doi.org/10.1111/gcb.16278>.
- Dobrovolný, P., Rybníček, M., Büntgen, U., Trnka, M., Brázdil, R., Stachoň, Z., Prokop, O., Kolář, T., 2016. Recent growth coherence in long-term oak (*Quercus* spp.) ring width chronologies in the Czech Republic. *Clim. Res.* 70, 133–141. <https://doi.org/10.3354/cr01402>.
- Esper, J., Krusic, P.J., Ljungqvist, F.C., Luterbacher, J., Carrer, M., Cook, E., Davi, N.K., Hartl-Meier, C., Kirilyanov, A., Konter, O., Myglan, V., Timonen, M., Treydte, K., Trouet, V., Villalba, R., Yang, B., Büntgen, U., 2016. Ranking of tree-ring based temperature reconstructions of the past millennium. *Quat. Sci. Rev.* 145, 134–151. <https://doi.org/10.1016/j.quascirev.2016.05.009>.
- Fetting, C., 2020. *The European Green Deal*. ESDN Office, Vienna, Austria.
- Frank, D.C., Poulter, B., Saurer, M., Esper, J., Huntingford, C., Helle, G., Treydte, K., Zimmermann, N.E., Schleser, G.H., Ahlström, A., Ciais, P., Friedlingstein, P., Levis, S., Lomas, M., Sitch, S., Viovy, N., Andreu-Hayles, L., Bednarz, Z., Berninger, F., Boettger, T., D'Alessandro, C.M., Daux, V., Filot, M., Grabner, M., Gutierrez, E., Haupt, M., Hilasvuori, E., Jungner, H., Kalela-Brundin, M., Krapiec, M., Leuenberger, M., Loader, N.J., Marah, H., Masson-Delmotte, V., Paudyal, P., Pawelczyk, S., Pierre, M., Planells, O., Pukiene, R., Reynolds-Henne, C.E., Rinne, K. T., Saracino, A., Sonninen, E., Stievenard, M., Switsur, V.R., Szczepanek, M., Szychowska-Krapiec, E., Todaro, L., Waterhouse, J.S., Weigl, M., 2015. Water-use efficiency and transpiration across European forests during the Anthropocene. *Nat. Clim. Change* 5, 579–583. <https://doi.org/10.1038/nclimate2614>.
- Fritts, H., 1976. *Tree Rings and Climate*. Elsevier.
- Gelman, A., Loken, E., 2013. *The Garden of Forking Paths: Why Multiple Comparisons Can Be a Problem, Even When There is No "Fishing Expedition" Or "p-hacking" and the Research Hypothesis Was Posited Ahead of Time*. Department of Statistics, Columbia University, pp. 1–17.
- Gričar, J., Jevšenak, J., Hafner, P., Prisljan, P., Ferlan, M., Lavrič, M., Vodnik, D., Eler, K., 2022. Climatic regulation of leaf and cambial phenology in *Quercus pubescens*: their interlinkage and impact on xylem and phloem conduits. *Sci. Total Environ.* 802, 149968. <https://doi.org/10.1016/j.scitotenv.2021.149968>.
- Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA.
- Groemping, U., Matthias, L., 2018. Package 'relaimpo.' Relative importance of regressors in linear models (R package version).
- Grömping, U., 2015. Variable importance in regression models. *WIREs Comput. Stat.* 7, 137–152. <https://doi.org/10.1002/wics.1346>.
- Hackett-Pain, A., Ascoli, D., Berretti, R., Mencuccini, M., Motta, R., Nola, P., Piussi, P., Ruffinatto, F., Vacchiano, G., 2019. Temperature and masting control Norway spruce growth, but with high individual tree variability. *For. Ecol. Manage.* 438, 142–150. <https://doi.org/10.1016/j.foreco.2019.02.014>.
- Hackett-Pain, A.J., Friend, A.D., Lagueard, J.G.A., Thomas, P.A., 2015. The influence of masting phenomenon on growth-climate relationships in trees: explaining the influence of previous summers' climate on ring width. *Tree Physiol.* 35, 319–330. <https://doi.org/10.1093/treephys/tpv007>.
- Hargreaves, G.H., Samani, Z.A., 1985. Reference crop evapotranspiration from temperature. *Appl. Eng. Agric.* 1, 96–99.
- Hartl-Meier, C., Dittmar, C., Zang, C., Rothe, A., 2014. Mountain forest growth response to climate change in the Northern Limestone Alps. *Trees* 28, 819–829. <https://doi.org/10.1007/s00468-014-0994-1>.
- Hinzman, L.D., Bettez, N.D., Bolton, W.R., Chapin, F.S., Dyrgerov, M.B., Fastie, C.L., Griffith, B., Hollister, R.D., Hope, A., Huntington, H.P., Jensen, A.M., Jia, G.J., Jorgenson, T., Kane, D.L., Klein, D.R., Kofinas, G., Lynch, A.H., Lloyd, A.H., McGuire, A.D., Nelson, F.E., Oechel, W.C., Osterkamp, T.E., Racine, C.H., Romanovsky, V.E., Stone, R.S., Stow, D.A., Sturm, M., Tweedie, C.E., Vourlitis, G.L., Walker, M.D., Walker, D.A., Webber, P.J., Welker, J.M., Winker, K.S., Yoshikawa, K., 2005. Evidence and implications of recent climate change in Northern Alaska and other arctic regions. *Clim. Change* 72, 251–298. <https://doi.org/10.1007/s10584-005-5352-2>.
- Hlásny, Tomáš, König, L., Krokene, P., Lindner, M., Montagné-Huck, C., Müller, J., Qin, H., Raffa, K.F., Schelhaas, M.-J., Svoboda, M., Viiri, H., Seidl, R., 2021a. Bark

- beetle outbreaks in Europe: state of knowledge and ways forward for management. *Curr. For. Rep.* 7, 138–165. <https://doi.org/10.1007/s40725-021-00142-x>.
- Hlásny, T., Trombik, J., Dobor, L., Barcza, Z., Barka, L., 2016. Future climate of the Carpathians: climate change hot-spots and implications for ecosystems. *Reg. Environ. Change* 16, 1495–1506. <https://doi.org/10.1007/s10113-015-0890-2>.
- Hlásny, T., Zimová, S., Merganičová, K., Štěpánek, P., Modlinger, R., Turčáni, M., 2021b. Devastating outbreak of bark beetles in the Czech Republic: drivers, impacts, and management implications. *For. Ecol. Manage.* 490, 119075. <https://doi.org/10.1016/j.foreco.2021.119075>.
- Hofgaard, A., Ols, C., Drobyshev, I., Kirchner, A.J., Sandberg, S., Söderström, L., 2019. Non-stationary response of tree growth to climate trends along the arctic margin. *Ecosystems* 22, 434–451. <https://doi.org/10.1007/s10021-018-0279-4>.
- Hu, J., Moore, D.J.P., Burns, S.P., Monson, R.K., 2010. Longer growing seasons lead to less carbon sequestration by a subalpine forest. *Glob. Chang. Biol.* 16, 771–783. <https://doi.org/10.1111/j.1365-2486.2009.01967.x>.
- Ionita, M., Nagavciuc, V., 2021. Changes in drought features at the European level over the last 120 years. *Nat. Hazards Earth Syst. Sci.* 21, 1685–1701. <https://doi.org/10.5194/nhess-21-1685-2021>.
- IPCC, 2023. *Climate Change 2022 – Impacts, Adaptation and Vulnerability: working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, 1st ed. Cambridge University Press. <https://doi.org/10.1017/9781009325844>.
- 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://doi.org/10.1016/j.dendro.2020.125753>.
- Jevšenak, J., 2019. Daily climate data reveal stronger climate-growth relationships for an extended European tree-ring network. *Quat. Sci. Rev.* 221, 105868. <https://doi.org/10.1016/j.quascirev.2019.105868>.
- Jevšenak, J., Levanič, T., 2018. dendroTools: R package for studying linear and nonlinear responses between tree-rings and daily environmental data. *Dendrochronologia* 48, 32–39. <https://doi.org/10.1016/j.dendro.2018.01.005>.
- Jevšenak, J., Tychkov, I., Gričar, J., Levanič, T., Tumajer, J., Prislán, P., Arnič, D., Popkova, M., Shishov, V.V., 2021. Growth-limiting factors and climate response variability in Norway spruce (*Picea abies* L.) along an elevation and precipitation gradients in Slovenia. *Int. J. Biometeorol.* 65, 311–324. <https://doi.org/10.1007/s00484-020-02033-5>.
- Jochner, M., Bugmann, H., Nötzli, M., Bigler, C., 2018. Tree growth responses to changing temperatures across space and time: a fine-scale analysis at the treeline in the Swiss Alps. *Trees* 32, 645–660. <https://doi.org/10.1007/s00468-017-1648-x>.
- Klesse, S., Babst, F., Evans, M.E.K., Hurley, A., Pappas, C., Peters, R.L., 2023. Legacy effects in radial tree growth are rarely significant after accounting for biological memory. *J. Ecol.* 111, 1188–1202. <https://doi.org/10.1111/1365-2745.14045>.
- Klimo, E., Hager, H., Kulhavý, J., 2000. *Spruce Monocultures in Central Europe: Problems and Prospects*. European Forest Institute Joensuu, Finland.
- Kolář, T., Čermák, P., Trnka, M., Žid, T., Rybníček, M., 2017. Temporal changes in the climate sensitivity of Norway spruce and European beech along an elevation gradient in Central Europe. *Agric. For. Meteorol.* 239, 24–33. <https://doi.org/10.1016/j.agrformet.2017.02.028>.
- Lange, J., Buras, A., Cruz-García, R., Ruskaya, M., Jalkanen, R., Kukarskih, V., Seo, J.-W., Wilmking, M., 2018. Climate regimes override micro-site effects on the summer temperature signal of scots pine at its northern distribution limits. *Front. Plant Sci.* 9, 1597. <https://doi.org/10.3389/fpls.2018.01597>.
- Leifsson, C., Buras, A., Rammig, A., Zang, C., 2023. Changing climate sensitivity of secondary growth following extreme drought events in forest ecosystems: a global analysis. *Environ. Res. Lett.* 18, 014021. <https://doi.org/10.1088/1748-9326/aca9e5>.
- Lens, F., Tixier, A., Cochard, H., Sperry, J.S., Jansen, S., Herbette, S., 2013. Embolism resistance as a key mechanism to understand adaptive plant strategies. *Curr. Opin. Plant Biol.* 16, 287–292. <https://doi.org/10.1016/j.copbi.2013.02.005>.
- Leonelli, G., Pelfini, M., 2008. Influence of climate and climate anomalies on norway spruce tree-ring growth at different altitudes and on glacier responses: examples from the central Italian alps. *Geografiska Annaler: Ser. A, Phys. Geogr.* 90, 75–86. <https://doi.org/10.1111/j.1468-0459.2008.00335.x>.
- Leonelli, G., Pelfini, M., D'Arrigo, R., Haeberli, W., Cherubini, P., 2011. Non-stationary responses of tree-ring chronologies and glacier mass balance to climate in the European Alps. *Arct. Antarct. Alp. Res.* 43, 56–65. <https://doi.org/10.1657/1938-4246-43.1.56>.
- Levanič, T., Gričar, J., Gagen, M., Jalkanen, R., Loader, N.J., McCarroll, D., Oven, P., Robertson, I., 2009. The climate sensitivity of Norway spruce [*Picea abies* (L.) Karst.] in the southeastern European Alps. *Trees* 23, 169–180. <https://doi.org/10.1007/s00468-008-0265-0>.
- Lévesque, M., Saurer, M., Siegwolf, R., Eilmann, B., Brang, P., Bugmann, H., Rigling, A., 2013. Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. *Glob. Change Biol.* 19, 3184–3199. <https://doi.org/10.1111/gcb.12268>.
- Litton, C.M., Raich, J.W., Ryan, M.G., 2007. Carbon allocation in forest ecosystems. *Glob. Change Biol.* 13, 2089–2109. <https://doi.org/10.1111/j.1365-2486.2007.01420.x>.
- Luo, Y., Keenan, T.F., Smith, M., 2015. Predictability of the terrestrial carbon cycle. *Glob. Change Biol.* 21, 1737–1751. <https://doi.org/10.1111/gcb.12766>.
- Lupi, C., Morin, H., Deslauriers, A., Rossi, S., Houle, D., 2012. Increasing nitrogen availability and soil temperature: effects on xylem phenology and anatomy of mature black spruce. *Can. J. For. Res.* 42, 1277–1288. <https://doi.org/10.1139/x2012-055>.
- Maes, S.L., Perring, M.P., Vanhellemont, M., Depauw, L., Van Den Bulcke, J., Brümelis, G., Brunet, J., Decocq, G., Den Ouden, J., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kopecký, M., Mális, F., Wulf, M., Verheyen, K., 2019. Environmental drivers interactively affect individual tree growth across temperate European forests. *Glob. Chang. Biol.* 25, 201–217. <https://doi.org/10.1111/gcb.14493>.
- Mayr, S., Schmid, P., Beikircher, B., Feng, F., Badel, E., 2020. Die hard: timberline conifers survive annual winter embolism. *New Phytol.* 226, 13–20. <https://doi.org/10.1111/nph.16304>.
- McDowell, N.G., Sapes, G., Pivovarov, A., Adams, H.D., Allen, C.D., Anderegg, W.R.L., Arend, M., Breshears, D.D., Brodrigg, T., Choat, B., Cochard, H., De Cáceres, M., De Kauwe, M.G., Grossiord, C., Hammond, W.M., Hartmann, H., Hoch, G., Kahmen, A., Klein, T., Mackay, D.S., Mantova, M., Martínez-Vilalta, J., Medlyn, B.E., Mencuccini, M., Nardini, A., Oliveira, R.S., Sala, A., Tissue, D.T., Torres-Ruiz, J.M., Trowbridge, A.M., Trugman, A.T., Wiley, E., Xu, C., 2022. Mechanisms of woody-plant mortality under rising drought, CO2 and vapour pressure deficit. *Nat. Rev. Earth Environ.* 3, 294–308. <https://doi.org/10.1038/s43017-022-00272-1>.
- Michelot, A., Simard, S., Rathgeber, C., Dufrene, E., Damesin, C., 2012. Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. *Tree Physiol.* 32, 1033–1045. <https://doi.org/10.1093/treephys/tps052>.
- Micu, D., 2009. Snow pack in the Romanian Carpathians under changing climatic conditions. *Meteorol. Atmos. Phys.* 105, 1–16. <https://doi.org/10.1007/s00703-009-0035-6>.
- Micu, D.M., Amihaesei, V.A., Milian, N., Cheval, S., 2021. Recent changes in temperature and precipitation indices in the Southern Carpathians, 1961–2018. *Theor. Appl. Climatol.* 144, 691–710. <https://doi.org/10.1007/s00704-021-03560-w>.
- Micu, D.M., Dumitrescu, A., Cheval, S., Birsan, M.-V., 2015. Observed Variability and Trends from Instrumental Records. In: Micu, D.M., Dumitrescu, A., Cheval, S., Birsan, M.-V. (Eds.), *Climate of the Romanian Carpathians: Variability and Trends*. Springer International Publishing, Cham, pp. 149–185. https://doi.org/10.1007/978-3-319-02886-6_8.
- Mráz, P., Ronikier, M., 2016. Biogeography of the Carpathians: evolutionary and spatial facets of biodiversity. *Biol. J. Linn. Soc.* 119, 528–559. <https://doi.org/10.1111/bij.12918>.
- Mueller, R.C., Scudder, C.M., Porter, M.E., Talbot Trotter, R., Gehring, C.A., Whitham, T. G., 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts: *drought-induced differential tree mortality*. *J. Ecol.* 93, 1085–1093. <https://doi.org/10.1111/j.1365-2745.2005.01042.x>.
- Nagavciuc, V., Roibu, C.-C., Ionita, M., Mursa, A., Cotos, M.-G., Popa, I., 2019. Different climate response of three tree ring proxies of *Pinus sylvestris* from the Eastern Carpathians, Romania. *Dendrochronologia* 54, 56–63. <https://doi.org/10.1016/j.dendro.2019.02.007>.
- Obladen, N., Decherig, P., Skiadaresis, G., Tegel, W., Keßler, J., Höller, S., Kaps, S., Hertel, M., Dulamsuren, C., Seifert, T., Hirsch, W., Seim, A., 2021. Tree mortality of European beech and Norway spruce induced by 2018–2019 hot droughts in central Germany. *Agric. For. Meteorol.* 307, 108482. <https://doi.org/10.1016/j.agrformet.2021.108482>.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, R.C., 2011. A large and persistent carbon sink in the world's forests. *Science* 333, 988–993. <https://doi.org/10.1126/science.1201609>.
- Peltier, D.M.P., Ogle, K., 2020. Tree growth sensitivity to climate is temporally variable. *Ecol. Lett.* 23, 1561–1572. <https://doi.org/10.1111/ele.13575>.
- Ponocná, T., Spyt, B., Kaczka, R., Büntgen, U., Tremli, V., 2016. Growth trends and climate responses of Norway spruce along elevational gradients in East-Central Europe. *Trees* 30, 1633–1646. <https://doi.org/10.1007/s00468-016-1396-3>.
- Popa, A., Popa, I., Badea, O., Bosela, M., 2024a. Non-linear response of Norway spruce to climate variation along elevational and age gradients in the Carpathians. *Environ. Res.* 119073. <https://doi.org/10.1016/j.envres.2024.119073>.
- Popa, A., Popa, I., Roibu, C.-C., Badea, O.N., 2022. Do different tree-ring proxies contain different temperature signals? A case study of norway spruce (*Picea abies* (L.) Karst) in the Eastern Carpathians. *Plants* 11, 2428. <https://doi.org/10.3390/plants11182428>.
- Popa, A., Van Der Maaten, E., Popa, I., Van Der Maaten-Theunissen, M., 2024b. Early warning signals indicate climate change-induced stress in Norway spruce in the eastern Carpathians. *Sci. Total Environ.* 169167. <https://doi.org/10.1016/j.scitotenv.2023.169167>.
- Popa, I., Kern, Z., 2009. Long-term summer temperature reconstruction inferred from tree-ring records from the Eastern Carpathians. *Clim. Dyn.* 32, 1107–1117. <https://doi.org/10.1007/s00382-008-0439-x>.
- Popa, A., van der Maaten-Theunissen, M., Popa, I., Badea, O., van der Maaten, E., 2024. Spruce suffers most from drought at low elevations in the Carpathians, though shows high resilience. *For. Ecol. Manage.* 571, 122201. <https://doi.org/10.1016/j.foreco.2024.122201>.
- Pretzsch, H., 2021. Trees grow modulated by the ecological memory of their past growth. Consequences for monitoring, modelling, and silvicultural treatment. *For. Ecol. Manage.* 487, 118982. <https://doi.org/10.1016/j.foreco.2021.118982>.
- Primicia, I., Camarero, J.J., Janda, P., Čada, V., Morrissey, R.C., Trotsiuk, V., Bače, R., Teodosiu, M., Svoboda, M., 2015. Age, competition, disturbance and elevation effects on tree and stand growth response of primary *Picea abies* forest to climate. *For. Ecol. Manage.* 354, 77–86. <https://doi.org/10.1016/j.foreco.2015.06.034>.
- R Core Team, 2023. *R: a Language and Environment for Statistical Computing*.
- Rehse, R., Mette, T., Menzel, A., Buras, A., 2017. Soil properties affect the drought susceptibility of Norway spruce. *Dendrochronologia* 45, 81–89. <https://doi.org/10.1016/j.dendro.2017.07.003>.

- Rinn, F., 2012. *TSAPWin Scientific: Time Series Analysis and Presentation for Dendrochronology and Related Applications*. RINNTECH, D-69124, Heidelberg, Germany.
- Rocha, E., Gunnarsson, B., Björklund, J., Zhang, P., Linderholm, H.W., 2021. A Norway spruce tree-ring width chronology for the Common Era from the Central Scandinavian Mountains. *Dendrochronologia* 70, 125896. <https://doi.org/10.1016/j.dendro.2021.125896>.
- Rossi, S., Deslauriers, A., Anfodillo, T., Carraro, V., 2007. Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. *Oecologia* 152, 1–12. <https://doi.org/10.1007/s00442-006-0625-7>.
- Rossi, S., Deslauriers, A., Gričar, J., Seo, J.-W., Rathgeber, C.B., Anfodillo, T., Morin, H., Levanič, T., Oven, P., Jalkanen, R., 2008. Critical temperatures for xylogenesis in conifers of cold climates. *Global Ecology and Biogeography* 17, 696–707. <https://doi.org/10.1111/j.1466-8238.2008.00417.x>.
- Savva, Y., Oleksyn, J., Reich, P.B., Tjoelker, M.G., Vaganov, E.A., Modrzyński, J., 2006. Interannual growth response of Norway spruce to climate along an altitudinal gradient in the Tatra Mountains. *Poland. Trees* 20, 735–746. <https://doi.org/10.1007/s00468-006-0088-9>.
- Schmid, G., Hilmers, T., Uhl, E., Pretzsch, H., 2022. The Past Matters: previous Management Strategies Modulate Current Growth and Drought Responses of Norway Spruce (*Picea abies* H. Karst.). *Forests* 13, 243. <https://doi.org/10.3390/f13020243>.
- Schuld, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T.E.E., Hauck, M., Hajek, P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübke, T., Nelson, D.B., Rammig, A., Rigling, A., Rose, L., Ruehr, N.K., Schumann, K., Weiser, F., Werner, C., Wohlgenuth, T., Zang, C.S., Kahmen, A., 2020. A first assessment of the impact of the extreme 2018 summer drought on Central European forests. *Basic Appl Ecol* 45, 86–103. <https://doi.org/10.1016/j.baec.2020.04.003>.
- Schurman, J.S., Babst, F., Björklund, J., Rydval, M., Bače, R., Čada, V., Janda, P., Mikolas, M., Saulnier, M., Trotsiuk, V., Svoboda, M., 2019. The climatic drivers of primary *Picea* forest growth along the Carpathian arc are changing under rising temperatures. *Glob. Change Biol.* 25, 3136–3150. <https://doi.org/10.1111/gcb.14721>.
- Schuster, R., Oberhuber, W., 2013. Drought sensitivity of three co-occurring conifers within a dry inner Alpine environment. *Trees* 27, 61–69. <https://doi.org/10.1007/s00468-012-0768-6>.
- Schwartz, M.D., Ahas, R., Aasa, A., 2006. Onset of spring starting earlier across the Northern Hemisphere. *Glob. Chang. Biol.* 12, 343–351. <https://doi.org/10.1111/j.1365-2486.2005.01097.x>.
- Seifert, T., Müller-Starck, G., 2009. Impacts of fructification on biomass production and correlated genetic effects in Norway spruce (*Picea abies* [L.] Karst.). *Eur. J. Forest Res.* 128, 155–169. <https://doi.org/10.1007/s10342-008-0219-5>.
- Selås, V., Piovesan, G., Adams, J.M., Bernabei, M., 2002. Climatic factors controlling reproduction and growth of Norway Spruce South. *Norway* 32, 9.
- Senf, C., Buras, A., Zang, C.S., Rammig, A., Seidl, R., 2020. Excess forest mortality is consistently linked to drought across Europe. *Nat. Commun.* 11, 6200. <https://doi.org/10.1038/s41467-020-19924-1>.
- Shestakova, T.A., Gutiérrez, E., Voltas, J., 2018. A roadmap to disentangling ecogeographical patterns of spatial synchrony in dendrosciences. *Trees* 32, 359–370. <https://doi.org/10.1007/s00468-017-1653-0>.
- Sidor, C.G., Cuciurean, C.I., Popa, I., Leca, Ștefan, Vlad, R., Badea, O., 2022. Broad-leaved tree growth modulated by industrial air pollution in the northern Romania (Baia Mare Region). *Forests* 13, 807. <https://doi.org/10.3390/f13050807>.
- Sidor, C.G., Popa, I., Vlad, R., Cherubini, P., 2015. Different tree-ring responses of Norway spruce to air temperature across an altitudinal gradient in the Eastern Carpathians (Romania). *Trees* 29, 985–997. <https://doi.org/10.1007/s00468-015-1178-3>.
- Speer, J.H., 2010. *Fundamentals of Tree-Ring Research*. University of Arizona Press.
- Spiecker, H., 2004. *Norway Spruce Conversion: Options and Consequences*. Leiden.
- Spinoni, J., Antofie, T., Barbosa, P., Bihari, Z., Lakatos, M., Szalai, S., Szentimrey, T., Vogt, J., 2013. An overview of drought events in the Carpathian Region in 1961–2010. *Adv. Sci. Res.* 10, 21–32. <https://doi.org/10.5194/asr-10-21-2013>.
- Spinoni, J., Szalai, S., Szentimrey, T., Lakatos, M., Bihari, Z., Nagy, A., Németh, Á., Kovács, T., Mihic, D., Dacic, M., Petrovic, P., Krzić, A., Hiebl, J., Auer, I., Milkovic, J., Štěpánek, P., Zahradníček, P., Kilar, P., Limanowka, D., Pyrc, R., Cheval, S., Birsan, M.-V., Dumitrescu, A., Deak, G., Matei, M., Antolovic, I., Nejedlík, P., Štastný, P., Kajaba, P., Bochníček, O., Galo, D., Mikulová, K., Nabyvanets, Y., Skrynyk, O., Krakovská, S., Gnatiuk, N., Tolasz, R., Antofie, T., Vogt, J., 2015. Climate of the Carpathian Region in the period 1961–2010: Climatologies and trends of 10 variables: climate change in the Carpathian Region. *Int. J. Climatol.* 35, 1322–1341. <https://doi.org/10.1002/joc.4059>.
- Spinoni, J., Vogt, J.V., Naumann, G., Barbosa, P., Dosio, A., 2018. Will drought events become more frequent and severe in Europe?: Future drought events in Europe. *Int. J. Climatol.* 38, 1718–1736. <https://doi.org/10.1002/joc.5291>.
- Stanescu, V., Sofletea, N., Popescu, O., 1997. *Flora forestiera lemnoasa a Romaniei [Woody forest flora of Romania]*. Editura Ceres. Bucuresti, Romania, p. 451 [in Romanian].
- Știrbu, M.-I., Roibu, C.-C., Carrer, M., Mursa, A., Unterholzner, L., Prendin, A.L., 2022. Contrasting climate sensitivity of *Pinus cembra* tree-ring traits in the Carpathians. *Front. Plant Sci.* 13, 855003. <https://doi.org/10.3389/fpls.2022.855003>.
- Svobodová, K., Langbehn, T., Björklund, J., Rydval, M., Trotsiuk, V., Morrissey, R.C., Čada, V., Janda, P., Begović, K., Ágh-Lábúsová, J., Schurman, J.S., Nováková, M., Kozák, D., Kameniar, O., Synek, M., Mikoláš, M., Svoboda, M., 2019. Increased sensitivity to drought across successional stages in natural Norway spruce (*Picea abies* (L.) Karst.) forests of the Calimani Mountains, Romania. *Trees* 33, 1345–1359. <https://doi.org/10.1007/s00468-019-01862-1>.
- Synek, M., Janda, P., Mikoláš, M., Nagel, T.A., Schurman, J.S., Pettit, J.L., Trotsiuk, V., Morrissey, R.C., Bače, R., Čada, V., Brang, P., Bugmann, H., Begović, K., Chaskovskyy, O., Dušátko, M., Franković, M., Kameniar, O., Knř, T., Kozák, D., Langbehn, T., Málek, J., Rodrigo, R., Saulnier, M., Teodosiu, M., Vostarek, O., Svoboda, M., 2020. Contrasting patterns of natural mortality in primary *Picea* forests of the Carpathian Mountains. *For. Ecol. Manage.* 457, 117734. <https://doi.org/10.1016/j.foreco.2019.117734>.
- Tremli, V., Kašpar, J., Kuželová, H., Gryc, V., 2015. Differences in intra-annual wood formation in *Picea abies* across the treeline ecotone, Giant Mountains, Czech Republic. *Trees* 29, 515–526. <https://doi.org/10.1007/s00468-014-1129-4>.
- Tumajer, J., Altman, J., Štěpánek, P., Tremli, V., Doležal, J., Cienciala, E., 2017. Increasing moisture limitation of Norway spruce in Central Europe revealed by forward modelling of tree growth in tree-ring network. *Agric. For. Meteorol.* 247, 56–64. <https://doi.org/10.1016/j.agrformet.2017.07.015>.
- Tumajer, J., Begović, K., Čada, V., Jenicek, M., Lange, J., Mašek, J., Kaczka, R.J., Rydval, M., Svoboda, M., Vlček, L., Tremli, V., 2023. Ecological and methodological drivers of non-stationarity in tree growth response to climate. *Glob. Chang. Biol.* 29, 462–476. <https://doi.org/10.1111/gcb.16470>.
- UNEP (Ed.), 2008. *Carpathians Environment Outlook 2008*. UNEP, New York, NY.
- Unterholzner, L., Castagneri, D., Cerrato, R., Știrbu, M.-I., Roibu, C.-C., Carrer, M., 2024. Climate response of a glacial relict conifer across its distribution range is invariant in space but not in time. *Sci. Total Environ.* 906, 167512. <https://doi.org/10.1016/j.scitotenv.2023.167512>.
- Uyanik, G.K., Güler, N., 2013. A study on multiple linear regression analysis. *Procedia - Soc. Behav. Sci.* 106, 234–240. <https://doi.org/10.1016/j.sbspro.2013.12.027>.
- Valipour, M., Bateni, S.M., Jun, C., 2021. Global surface temperature: a new insight. *Climate* 9, 81. <https://doi.org/10.3390/cli9050081>.
- van der Maaten-Theunissen, M., Kahle, H.-P., van der Maaten, E., 2013. Drought sensitivity of Norway spruce is higher than that of silver fir along an altitudinal gradient in southwestern Germany. *Ann. For. Sci.* 70, 185–193. <https://doi.org/10.1007/s13595-012-0241-0>.
- Vitali, V., Büntgen, U., Bauhus, J., 2017. Silver fir and Douglas fir are more tolerant to extreme droughts than Norway spruce in south-western Germany. *Glob. Change Biol.* 23, 5108–5119. <https://doi.org/10.1111/gcb.13774>.
- Von Felten, S., Hättenschwiler, S., Saurer, M., Siegwolf, R., 2007. Carbon allocation in shoots of alpine treeline conifers in a CO₂ enriched environment. *Trees* 21, 283. <https://doi.org/10.1007/s00468-006-0118-7>.
- Wang, Q., Fan, X., Wang, M., 2014. Recent warming amplification over high elevation regions across the globe. *Clim. Dyn.* 43, 87–101. <https://doi.org/10.1007/s00382-013-1889-3>.
- Wild, M., Ohmura, A., Makowski, K., 2007. Impact of global dimming and brightening on global warming. *Geophys. Res. Lett.* 34, L04702. <https://doi.org/10.1029/2006GL028031>.
- 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., Smljanic, M., 2020. Global assessment of relationships between climate and tree growth. *Glob. Change Biol.* 26, 3212–3220. <https://doi.org/10.1111/gcb.15057>.
- Zhang, T., Niinemets, Ü., Sheffield, J.W., 2018. Shifts in tree functional composition amplify the response of forest biomass to climate. *Nature* 556, 99–102. <https://doi.org/10.1038/nature26152>.