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Adaptation and resilience of Norway spruce forest ecosystems in the northern part of Eastern Carpathians in the context of climate change

SUMMARY

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PhD THESIS

Adaptation and resilience of Norway spruce forest ecosystems in the northern part of Eastern Carpathians in the context of climate change

Adaptarea și reziliența ecosistemelor forestiere de molid din nordul Carpaților Orientali în contextul schimbărilor climatice

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Defense committee:

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Date, time, and location of the public defense of the doctoral thesis: September 23, 2024, 11:00, room S.I.2, S building, at the Faculty of Forestry and Forest Exploitation in Brașov.

Any feedback or comments on the content of the thesis should be sent electronically, in a timely manner, to andrei-i.popa@unitbv.ro.

We also invite you to attend the public defense session of the doctoral thesis.

Thank you.

"In a forest of a hundred thousand trees, no two leaves are alike, and no two journeys are alike. Find your own path."

Shirley Bassey

CONTENT

ACKNOWLEDGMENT

This Ph.D. thesis is the result of my research conducted at the National Institute for Research and Development in Forestry "Marin Drăcea", Research-Development and Experimentation-Production Station Câmpulung Moldovenesc. In this thesis, I analyzed the annual growth patterns of Norway spruce in managed forests in the Eastern Carpathians along elevational and age gradients to increase the understanding of how this species grows at the southeasternmost edge of its natural distribution and how climate change has affected it. This research would not have been possible without the help, support, and encouragement of a large number of people. In the following, I would like to thank them and to show my gratitude.

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Andrei Popa,

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LIST OF ABBREVIATIONS

$\hat{a}_C$ – growth synchrony;

adj r^2 – adjusted explained variance;

AGR – average growth rate;

ANCOVA – analysis of covariance;

ANOVA – Analysis of variance;

AR1 – first-order autocorrelation;

BAI – basal area increment;

BI – image-based blue reflectance - blue intensity;

Cond. R^2 – coefficient of variation for fixed and random effects;

CRU – Climatic Research Unit;

CSD – critical slowing down;

CWB – climatic water balance;

CWB_{after} – the mean of climatic water balance in two years after the drought years;

CWB_{before} – the mean of climatic water balance in two years before the drought years;

DBH – diameter breast height;

DOY – day fo the year;

E-OBS – daily gridded meteorological database;

EPS – expressed population signal;

EWS – Early-Warning Signals;

GAMM – Generalized Additive Mixed Model;

GAMs – generalized additive models;

GDP – Gross domestic product;

Gini – Gini coefficient for ring width indices;

ICC –intra-class correlation coefficient;

ICP Forests – International Cooperative Programme on Assessment and Monitoring of Air Pollution Effects on Forests;

IPCC – Intergovernmental Panel on Climate Change;

LMMs – linear mixed-effect models;

LULUCF – Land-Use, Land-Use Change, and Forestry;

MAP – mean annual precipitation;

Marg. R^2 – coefficient of variation for fixed effects;

MAT – mean annual temperature;

MSR_{OOB} – mean of squared residuals for out-of-bag principle in random forest analisys;

MXD – maximum latewood density;

OOB – out-of-bag principle;

PC1 – first principal component;

PC2 – second principal component;

PCGA – Principal Component Gradient Analysis;

PET – potential evapotranspiration;

r – coefficient of correlation;

R^2 – coefficient of determination;

rbar – interseries correlation;

RFA – random forest analysis;

RWI – residual tree ring index chronologies;

SD – standard deviation;

SPEI – Standardized Precipitation-Evapotranspiration Index;

TRI – tree ring-width index series;

TRW – tree-ring width;

TSCS – temporal shifts of climate sensitivity;

VI – variable importance;

VIF – variance inflation factor;

σ^2 – variance of residuals;

%IncMSE – Increased Mean Square Error;

%VarExp – percent of variance explained by random forest moldels;

1. INTRODUCTION

Global climate change, an important challenge in the twenty-first century, demands immediate attention from human society. Mitigating the adverse effects of climate change, achieving carbon neutrality, and preserving biodiversity remain key priorities on public and policy agendas at the European and global levels. The main effects of climate change are related to an increase in the frequency of extreme climatic events. For example, recent studies have revealed that at the European level, a significant increase in the intensity and frequency of drought has occurred in recent decades (Ionita and Nagavciuc, 2021). The primary driver of these extreme climatic events is global warming. It was reported that at the end of 2023, the global mean temperature would have increased by 1.8°C compared to the preindustrial period (United Nations Environment Programme, 2023). Along with these more intense and frequent drought events, other extreme events (e.g., heat waves, storms, floods) will continue to have a significant impact on Europe's society and environment.

In this challenging context, forests are among the most vulnerable ecosystems. Multiple studies have shown that drought-induced tree mortality can be observed at global scales (Allen et al., 2015). At the European scale, recent drought events (e.g., in 2018) have had a devastating effect on forest growth, with mortality rates surpassing those of previous drought events (Schuldt et al., 2020). Alongside mortality events due to extreme climatic events (e.g., drought, heat waves), changes in climatic conditions (e.g., increased mean annual temperature or reduced annual precipitation) interfere with trees' physiology and capacity to store carbon, and thus their ability to provide ecosystem services. Large-scale forest decline has led to increased attention in the triggering mechanisms of these events. A comprehensive understanding of long-term trends in forest growth and of responses to extreme events, or to climate in general, represents a starting point for predicting the future conditions of forest ecosystems, and thus a basis for climate-smart forest management.

Although forests are prone to be drastically affected in current extreme climatic scenarios, they also represent a key instrument for mitigating the negative effects of global challenges such as climate change, extreme events, biodiversity loss, or land degradation. At the European level, forests sequester 10% of gross greenhouse gas emissions (FOREST EUROPE, 2020). However, the European Union Strategy on Adaptation to Climate Change (2021), based on the European Green Deal, stipulates that European countries achieve climate neutrality by 2050. Specifically, the European Union's target is to sequester around 310 million metric tons of CO2 in natural sinks, as set out in the revised LULUCF Regulation (Land-Use, Land-Use Change, and Forestry). To achieve these goals, sustainable forest management practices in accordance with actual climatic challenges need to be implemented. Climate-smart forestry, a recent concept, emphasizes the need to implement "sustainable adaptive forest management and governance to protect and enhance the potential of forest to adapt to, and mitigate climate change" (Bowditch et al., 2020). These adaptive forest practice measures require updated and regional relevant knowledge of actual forest status and how tree species react to new environmental conditions. Past information on tree species' adaptability, growth conditions, and resilience may be outdated in the actual context of rapid changes in environmental conditions (Kijowska-Oberc et al., 2020).

In Europe, forests cover up to 32% of the land surface (Hanewinkel et al., 2013). Moreover, the forest sector contributes around 0.7% of Europe's GDP (European Environment Agency, 2024). One of the most commercially important coniferous species is Norway spruce (*Picea abies* (L.) Karst.) (Caudullo et al., 2016). This species is highly popular in forestry due to the large amount of its wood used for construction, pulpwood for paper, and furniture. The ability of Norway spruce to grow rapidly and to produce quality wood under various environmental conditions makes it one of the most widespread tree species in managed forests. In Europe, spruce was largely cultivated both inside and outside its natural habitats in even-aged mono-specific forests.

In terms of natural species occurrence, Norway spruce can be found from sea level up to the timberline at 2400 m a.s.l. (Caudullo et al., 2016). In Europe, the Carpathians represent the southeasternmost part of the natural distribution of this coniferous species (Caudullo et al., 2017). Spruce is found in the Carpathians in various proportions, from more than 80% in the Western Carpathians to less than 70% in the Eastern Carpathians and to around 30% in the Southern Carpathians (Kholiavchuk et al., 2023). In Romania, Norway spruce is the most common coniferous species, with 19.49% of total forest and 23.78% of total wood volume, according to the National Forest Inventory, second cycle (https://roifn.ro/site/rezultate-ifn-2/).

In recent decades, Norway spruce has faced large-scale dieback events in Central Europe (T. Hlásny et al., 2021; Netherer et al., 2019). These unprecedented events were mainly caused by drought-induced stress that affected trees' ability to resist bark-beetle attacks (Netherer et al., 2015). The large areas of spruce forests affected in the last decade represent substantial economic and ecological losses. In addition, the large quantity of wood harvested in a short time led to an imbalance in the economic market. Under current climatic scenario projections, it is expected that larger parts of Europe will be affected by bark beetle attacks in the near future (Hlásny et al., 2021). However, at present, spruce dieback in Eastern Europe has been reported at lower scales compared to that in the central parts of Europe (Synek et al., 2020). In view of this, there is an urgent need for updated information on the status of Norway spruce forests in Eastern Europe to fully understand and better predict the future of spruce-based forests in the Carpathians.

Seasonality in climatic conditions induces variability in the growth patterns of trees (Fritts, 1976). At the same time, other factors, such as disturbance events, forest management interventions, and genetic potential, are likely to contribute to tree growth patterns. The radial growth of trees (secondary growth) is recorded with annual resolution in tree rings. The information captured in tree rings has already been used at a global scale to highlight the consequences of global warming on forest ecosystems, including mortality events (Cailleret et al., 2019), changes in carbon and water dynamics (Babst et al., 2019), and responses to past climatic variability (Esper et al., 2016). Although significant achievements in assessing the growth patterns or resilience of forests based on tree rings have been made at European or global scales, it has been shown that local/regional conditions have a defining impact on tree response to climate (Lebourgeois et al., 2014). Thus, studies conducted at regional levels are likely to highlight important particularities in the resilience and adaptability of trees to climate change.

Studies on the influence of climatic factors on spruce growth have been conducted in the majority of the montane areas in Europe, from Southern Europe (Begović et al., 2020), to the Alps (Schuster and Oberhuber, 2013), Central Europe (Bošel'a et al., 2014), and Eastern Europe (Schurman et al., 2019; Sidor et al., 2015). Most of the studies concluded that at lower elevations, spruce growth is mainly limited by water availability, while at higher elevations, growing-season temperatures and length are its primary drivers. In the context of climate change, the limiting factors of tree growth are likely to change, and the climate–growth relationships are therefore not stable in time (Wilmking et al., 2020). The non-stationarity phenomenon has already been reported at a global scale (Jevšenak et al., 2024). Therefore, past knowledge about the limiting factors that constrain spruce growth may be outdated, and to be able to configure an adaptative, climate-smart, and sustainable forest management, actual information is needed.

In the Carpathians, dendrochronological studies have been conducted for over two decades (Popa, 2004). Due to the fact that spruce is one of the main coniferous species in the region, the growth patterns and response to the climate of this species have been analyzed (Schurman et al., 2019; Sidor et al., 2015). However, most of the recent studies were conducted in primary forests (Schurman et al., 2019). Based on this, a knowledge gap related to the growth conditions of spruce in managed forests was identified. At the Carpathian level, the majority of forests are managed, and in the context of climate change, these forests are most vulnerable. Through the complex and novel methodology applied in this Ph.D. thesis, important imputes were obtained for use in different conceptual frameworks to facilitate the development of sustainable management practices.

The research in this thesis was conducted on a newly established tree-ring network consisting of 158 stands of even-aged managed spruce forests of various ages distributed along an elevational gradient (from 475 m a.s.l. up to the timberline at 1675 m a.s.l.) in the Eastern Carpathians. A total of 3032 cores were analyzed. Based on different specific objectives, raw measurements of tree ring widths, detrended indices, or basal area increments series were used. For the statistical analysis, classical approaches (Pearson or Spearman correlation) were used in conjunction with new, innovative methods based on machine learning techniques (e.g., Random Forest Analysis), linear mixed-effect models (LMMs), or generalized additive models (GAMs). More importantly, within the thesis, a new methodology was developed to analyze the non-stationarity of climate–growth relationships based on linear regression of correlation coefficients between radial growth and climatic factors.

2. AIM AND OBJECTIVES OF THE RESEARCH

This Ph.D. thesis presents a comprehensive assessment of Norway spruce (*Picea abies* (L.) H. Karst.) growth dynamics in the Eastern Carpathians (Romania) using tree ring data from managed forests distributed along elevational and age gradients. The aim of the research is to update the knowledge on the resilience and adaptability of Norway spruce-managed ecosystems to climate change as scientific support for climate-smart forestry.

The general and specific research objectives of this Ph.D. thesis are:

GO1. Quantification of Norway spruce growth dynamics in the last century, with a specific focus on:

SO1.1 Long-term growth trends based on basal area increment;

SO1.2 Changes in growth sensitivity and growth synchrony;

SO1.3 Early warning signals of Norway spruce decline;

GO2. Evaluation of resilience components in drought years, with a specific focus on:

SO2.1 Variability of resilience components along elevational gradients;

SO2.2 Influence of tree age on growth response to drought;

SO2.3 Impact of water availability before, during, and after drought on resilience components;

GO3. Climate–growth relationships of Norway spruce, with a specific focus on:

SO3.1 Temporal shifts in spruce climate sensitivity;

SO3.2 Non-linearity in spruce response to climate;

SO3.3 Climatic signals captured through different tree ring proxies (TRW, BAI, and BI).

3. OUTLINE OF THE RESEARCH

This Ph.D. thesis is structured as five manuscript-style chapters (Chapters 4-8). Three chapters (Chapters 4, 7, and 8) have been published in ISI-indexed peer-reviewed journals, and two (Chapters 5 and 6) are currently under revision. Information related to publication dates, journals, and co-authors is presented at the beginning of each chapter.

In Chapter 4, the growth dynamics of Norway spruce were assessed based on a tree-ring network consisting of 157 Norway spruce chronologies (comprised by more than 3000 trees) of different ages distributed along elevational transects in the Eastern Carpathians, Romania. The BAI chronologies at stand level were used to analyze the long-term trends in growth rates at the elevational-class level. Furthermore, the early warning signals of climate-change-induced stress were evaluated, namely: (1) growth decline, (2) increased sensitivity of tree growth (statistically assessed through the first-order autocorrelation and standard deviation), and (3) increased growth synchrony. A pronounced growth decline was observed to have occurred over the last two decades, which was strongest in younger stands and at lower elevations. However, the growth sensitivity and synchrony did not show consistent patterns, suggesting that forest decline may not be immediately imminent. Overall, our findings highlight an increased vulnerability of spruce in the Eastern Carpathians. With ongoing climate change, spruce dieback may be expected in this part of Europe as well.

The content of this chapter was published in the *Science of The Total Environment Journal* (Andrei Popa, Ernst van der Maaten, Ionel Popa, Marieke van der Maaten-Theunissen, 2024a, *Early warning signals indicate climate change-induced stress in Norway spruce in the Eastern Carpathians,* Science of The Total Environment, Volume 912, 169167, https://doi.org/10.1016/j.scitotenv.2023.169167, Q1; IF=8.2) and general objective 1 (GO.1) and its specific objectives (SO1.1 -1.3) were fully achieved.

In Chapter 5, a comprehensive analysis of spruce resilience was conducted, in the context of the increased intensity and frequency of drought in recent decades and the large-scale dieback of Norway spruce in Central Europe. Differences between resilience components (e.g., resistance, recovery, resilience, recovery period) were analyzed along elevational and age gradients. The "line of full resilience" concept was used in an integrated interpretation of resilience components. The influence of water availability before, during, and after drought events on the resilience components of spruce was assessed using linear mixed-effect models. The results showed that spruce at low elevations (<800 m a.s.l.) displayed the lowest resistance to drought, but that this was associated with a high recovery rate, while the increased resistance at high elevations (>1400 m a.s.l.) was associated with a low recovery rate. Regarding the age of trees, it was shown that older trees needed the longest time to recover from drought events. The severity of the drought was found to have the highest impact on spruce resilience. Overall, the obtained results offer current knowledge about the ability of one of the most important coniferous species in Europe to cope with drought—information that could be integrated into the sustainable forest management of this vulnerable species.

The content of this chapter was presented in Andrei Popa, Marieke van der Maaten-Theunissen, Ionel Popa, Ovidiu Badea, Ernst van der Maaten, *Spruce suffers most from drought at low elevations in the Carpathians, though shows high resilience,* (Forest Ecology and Managemnet, Q1, IF=3.7, under review) and general objective 2 (GO. 2) and its specific objectives (SO2.1 -2.3) were fully achieved.

In Chapter 6, it was assessed spruce's response to climate in the context of climate change. Across much of Europe, climate change has caused a major change in spruce growth conditions and, implicitly, in its response to climate. Studying temporal shifts of climate sensitivity (TSCS) over time may elucidate the degree to which spruce may be vulnerable to climate-change induced decline in upcoming decades. TSCS was mathematically defined as the slope parameter of the regression of spruce climate sensitivity (the correlation coefficient) over time. Given the often-observed contrasting shift of climate sensitivity at low versus high elevations, studying the potentially divergent TSCS along elevational and spatial gradients was of particular interest. Analyses revealed several indications of TSCS for spruce in the Eastern Carpathians. At high elevations (>1100 m a.s.l.), it was found that the positive link between summer temperatures and spruce growth decreased significantly over the study period. In turn, trees at these elevations exhibited an increasingly positive relationship with late winter temperatures over time. At low elevations (<800 m a.s.l.), the signal of positive summer Standardized Precipitation-Evapotranspiration Index (SPEI) correlation became more frequent among sites toward 2021, while the strength of the positive winter SPEI correlation from the previous growing season weakened. At the same time, results revealed that TSCS was significantly driven by an elevational climate gradient and a longitudinal continentality gradient. Overall, the study’s findings indicate that Norway spruce is becoming increasingly affected by water limitation under climate change at low elevations, highlighting a potentially rising risk of the decline of this species in the Eastern Carpathians.

The content of this chapter was presented in Andrei Popa, Jernej Jevšenak, Ionel Popa, Ovidiu Badea, Allan Buras, *In pursuit of change: Divergent temporal shifts in climate sensitivity of Norway spruce along an elevational and continentality gradient in the Carpathians*, (Agricultural and Forest Meteorology, Q1, IF=5.6, under review) and specific objective 3.1 (OS3.1) was fully achieved.

In Chapter 7, it was analyzed the non-linearity in the climate response of spruce. Trees’ growth dynamics and biomass accumulation are determined mainly by environmental constraints, inter-tree competition, and disturbance regimes. Usually, climate–growth relationships are assessed by linear correlation due to the simplicity and straightforwardness of modeling. However, applying this method may bias results since the ecological and physiological responses of trees to environmental factors are non-linear and usually bell-shaped. A non-linear assessment of climate–growth relationships using machine-learning techniques for spruce was applied. Results showed that non-linearity in the climate–growth response of spruce was season-specific: temperatures from the previous autumn and current growing season, along with water availability during winter, induced a bell-shaped response. Moreover, it was found that at low elevations, spruce growth was strongly limited by water availability, while winter temperatures are likely to have had a slight influence along the entire elevational gradient. Furthermore, at lower elevations, younger trees were more drought-sensitive compared to older trees.

Overall, the obtained results shed new light on the response of spruce to climate in the Carpathians, which may aid in management decisions.

The content presented in this chapter was published in the *Environmental Research Journal* (Andrei Popa, Ionel Popa, Ovidiu Badea, Michal Bosela, 2024b, *Non-linear response of Norway spruce to climate variation along elevational and age gradients in the Carpathians*, Environmental Research, 119073, https://doi.org/10.1016/j.envres.2024.119073, Q1; IF=7.7) and specific objective 3.2 (OS3.2) was full achieved.

In Chapter 8, it was assessed the climate–growth relationships based on different tree-ring parameters. Tree-ring parameters offer valuable knowledge regarding how trees respond and adapt to environmental changes. Trees encode all environmental changes in different tree-ring parameters. This study analyzed how air temperature is encoded in different Norway spruce tree-ring proxies along an elevational gradient in an intramountain valley of the Carpathians. The climate–growth relationship was analyzed for two contrasting altitudes: low elevation, i.e., below 1000 m a.s.l., and high elevation, i.e., above 1500 m a.s.l. Two local weather stations, one in the valley and the other in the upper part of the mountains, provided daily temperatures (Joseni, 750 m a.s.l., and Bucin, 1282 m a.s.l., respectively). The bootstrap Pearson correlation between cumulative daily temperature data and three tree-ring proxies (tree-ring width – TRW, basal area increment – BAI, and blue intensity – BI) was computed for each series. The results show that elevation modulates the climate response pattern in the case of BI, and remains relatively similar for TRW and BAI. The winter temperatures' positive influence on spruce growth was observed in both TRW and BAI chronologies. Additionally, the BAI chronology revealed a positive relationship with summer temperature. The highest correlation coefficient ($r = 0.551$, $p < 0.05$, $n = 41$) was recorded between BI residual chronology from high elevation series and summer/autumn temperatures from the higher-elevation weather station for a cumulative period of 59 days (the second half of August to the beginning of October). Our results show that, in this intramountain valley of the Eastern Carpathians, different tree-ring proxies capture different climatic signals.

The content presented in this chapter was published in the Plants (Andrei Popa, Ionel Popa, Cătălin-Constantin Roibu, Ovidiu Nicolae Badea, 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, 18: 2428. https://doi.org/10.3390/plants11182428, Q1; IF = 4.5) and specific objective 3.3 (OS3.3) was full achieved.

4. GROWTH DYNAMICS OF NORWAY SPRUCE IN EASTERN CARPATHIANS IN RELATION TO ELEVATION AND AGE

Andrei Popa, Ernst van der Maaten, Ionel Popa, Marieke van der Maaten-Theunissen, 2024a, *Early warning signals indicate climate change-induced stress in Norway spruce in the Eastern Carpathians*, Science of The Total Environment, Volume 912, 169167, https://doi.org/10.1016/j.scitotenv.2023.169167, Q1; IF=8.2

4.1 Introduction

Climate change is affecting forest ecosystems all around the globe, in particular through warming as well as increases in drought frequency and intensity. Warming, coupled with severe droughts during the vegetation period, leads to stressed conditions for forest ecosystems. Impacts range from effects on the provisioning of ecosystem services such as carbon sequestration (Kolus et al., 2019) to tree mortality (Camarero et al., 2015). The constant warming trend in the last decades has led to increased evaporative losses due to an intensification of transpiration and respiration, and eventually to tree mortality when coupled with water deficit. Large-scale forest decline led to an increased attention to physiological mechanisms of trees to cope with drought and their effects on tree survival capacity. Namely, understanding how tree species are affected by climate change is important for sustainable forest management and increasing the ability to mitigate environmental changes.

Forest decline and dieback is a phenomenon resulting from a cumulus of factors contributing at different time and spatial scales (McDowell et al., 2008), making it difficult to predict. Tree mortality represents one of the main drivers that contributes to forest dynamics. Extreme events with short duration (e.g., storms, fire) cause perturbation rapidly, with visible effects at the ecosystem level (Seidl et al., 2011). A stressful condition in the long term (e.g., heat waves, drought) first induces changes at the physiological level (e.g., hydrological conductance, transpiration, photosynthesis) before decline and mortality occur (McDowell et al., 2013). Early warning signals (EWS), as proposed by Scheffer et al., (2009), characterize systems under critical transitions. The reduction of resilience capacity of a system, after a perturbation, can be associated with the critical slowing down (CSD) of the system (Dakos et al., 2012). This process of CSD has been identified in populations under increasing stress levels before extinction. The reduction of biomass accumulation processes in forest ecosystems can be associated with a CSD (Cailleret et al., 2019). Usually, CSD of tree growth is associated with an increase in autocorrelation and variability as well as a decrease in synchrony with the environment, but variable responses in time and space are possible (Cailleret et al., 2019).

Growth synchrony can be used as an EWS to predict stressful conditions in forest ecosystems (Shestakova et al., 2018). As a result of a change in temperature and moisture regime, forests' growth synchrony was reported to become higher along wide distances (Shestakova et al., 2016). Spatial synchrony in tree growth and identification of exogenous determining factors represents a key factor in forecasting the effects of climate change on forest ecosystems and, at the same time, can serve as an important EWS (Shestakova et al., 2018).

Norway spruce (*Picea abies* (L.) Karst.) is a major coniferous species in Europe, which is fast-growing and with a long tradition of cultivation in European forestry (Klimo et al., 2000). The species covers a large area along an altitudinal range from sea level to 2,400 m a.s.l. (Caudullo et al., 2016) and has substantial economic value due to its ability to produce high-quality wood in moderate-quality environments. In the actual context of climate change, especially the increase in drought severity and frequency, Norway spruce is likely to be at risk. Norway spruce is known as a drought-sensitive species (Lévesque et al., 2013; van der Maaten-Theunissen et al., 2013; Vitali et al., 2017). Severe drought events in critical moments during the vegetation period contribute to a reduction of the resilience of Norway spruce and its ability to resist bark-beetle attacks (Netherer et al., 2015; Ryan et al., 2015).

In recent years, extreme heat and drought events in Central Europe were triggering factors for large-scale dieback of Norway spruce forests (Hlásny et al., 2021; Netherer et al., 2019). In eastern parts of Europe, no extensive Norway spruce decline has been recorded so far (Synek et al., 2020). The main risk for Norway spruce in this area are storms, which may cause crown damage, stem breakage and uprooting, whereas at a smaller scale, bark-beetle attacks are important disturbing agents (Synek et al., 2020). Considering the faith of Norway spruce in Central Europe, the question arises how the future of the species in Eastern Europe may look like. Therefore, this study evaluates EWS using a new tree-ring network established using ring-width measurements from over 3000 Norway spruce trees from 157 moderate to highly productive stands. Study stands are of different age and distributed along an elevational gradient in the Eastern Carpathians, falling within the natural distribution of Norway spruce. The study aims to highlight changes in growth trends, sensitivity, and synchrony as a result of climate change.

We hypothesize that: (i) Norway spruce at lower elevations shows a decreasing trend in basal area increment, whereas at intermediate and higher elevations, trends increase, (ii) old stands are characterized by a stronger growth decline compared to younger stands, and (iii) for all stands, growth synchrony increased during the last decades.

4. 2 Material and Methods

4.2.1 Study area

In the Eastern Carpathians in Romania, the largest continuous Norway spruce forests of Eastern Europe are located (Ichim, 1990). Here, within the natural distribution range of Norway spruce, the study area is located along a latitudinal (46°36′23″ N to 47°53′56″ N and 24°55′24″ E to 26°00′46″ E) and elevational gradient (from 475 m a.s.l. to the timberline, i.e. up to 1,675 m a.s.l.; Fig. 4.1). To investigate the growth dynamics of Norway spruce, 157 even-aged managed forest stands were sampled. Most stands were pure Norway spruce stands whereas others were spruce-dominated stands with at least 80% of spruce and an admixture of other species; mean age varied from 40 to 180 years. In mixture, spruce was mainly accompanied by European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) at lower and intermediate elevations, and by rowan (*Sorbus aucuparia* L.) and birch (*Betula pendula* L.) at higher elevations. The mean annual temperature ranges from 6.8°C at low elevations to 3.2°C at high elevations, while annual precipitation sums vary from 620 to 870 mm, respectively.

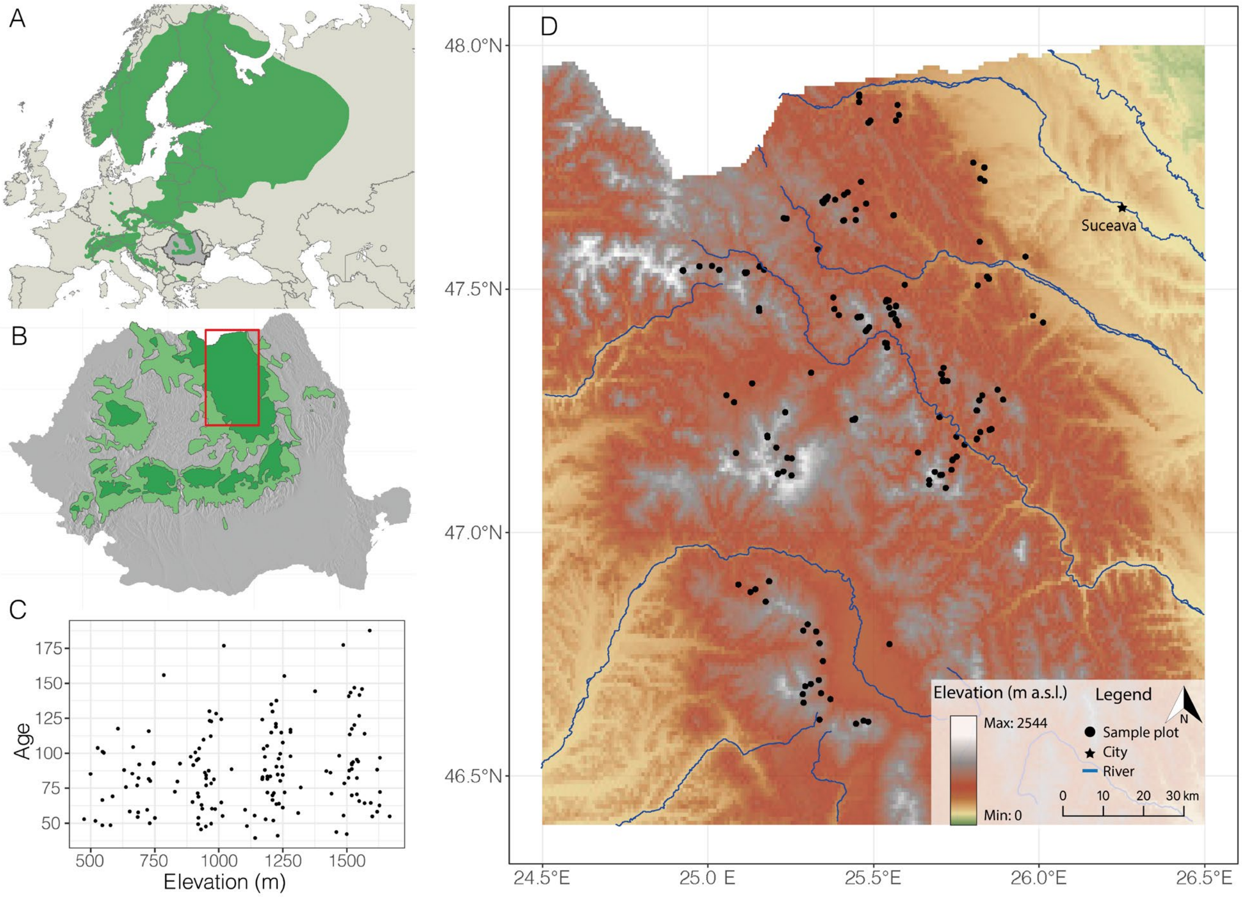

Figure 4.1 Norway spruce distribution in A. Europe (dark green colour) (Caudullo et al., 2017) and B. Romania (natural distribution – dark green, artificial distribution – light green, study area – red box) (Stanescu et al., 1997); C. Average age and elevation of the sampled trees and stands, resp.; D. Location of the studied stands in the Eastern Carpathians (black circles).

4.2.2 Growth data

During 2021 and 2022, at least 20 dominant trees with no visible signs of damage were sampled in each stand. Thereby, hold-over trees were excluded. Per tree, one increment core was collected at breast height (1.3 m) with an increment borer. Stem diameter (diameter breast height; DBH) was measured using a diameter tape. Cores were prepared following standard dendrochronological procedures (Speer, 2010) and scanned with a Epson Expression 12000 XL scanner with 2400 dpi true resolution. Ring-width measurements were made on the images in the software CooRecorder/CDendro (Version 9.6, Cybis Elektronik & Data AB, Sweden), whereafter they were visually and statistically cross-dated (Grissino-Mayer, 2001). In the case of cores without the pith, the age of the trees was estimated based on an estimation of the missing number of rings by fitting a geometric pith locator to the innermost rings.

During the validation processes, a tree was excluded from further analyses if its age differed by more than 30 years from average stand age. The final database consisted of 3012 validated cores. Due to the fact that during sampling in 2021 radial growth was not yet finished, this year was excluded from analysis for 11% of the plots.

Growth trends were quantified using basal area increment (BAI). BAI was calculated for each year based on annual ring widths (TRW) and DBH.

Individual BAI series were detrended by a double detrending process: First, a Hugershoff equation, and thereafter a cubic-smoothing spline of 30 years with a 50% frequency cut-off was applied. By this, trends induced by stem size as well as the influence of silvicultural interventions, competition and disturbances are eliminated (Cook and Kairiukstis, 1990; Thurm et al., 2016). For each plot, mean chronologies of BAI and BAI indices were calculated using a bi-weight robust mean in order to reduce the influence of the outliers (Cook and Kairiukstis, 1990).

To analyze possible differences in growth patterns in relation to elevation, plots were grouped into four elevational classes: <800 m a.s.l. (30 plots and 549 trees), 800-1100 m a.s.l. (40 plots and 782 trees), 1100-1400 m a.s.l. (45 plots and 884 trees) and >1,400 m a.s.l. (42 plots and 797 trees). Average BAI for each elevation class was calculated and smoothed with a Generalized Additive Mixed Model (GAMM), whereby mean BAI at stand level was modelled as a smooth function of year with plot as random effect.

4.2.3 Early warning signals

In this study, we focus on three widely used EWS of climate change-induced stress: (i) negative trends in BAI, (ii) an increase in the sensitivity of tree growth (assessed over first-order autocorrelation and standard deviation), and (iii) an increase in growth synchrony (Cailleret et al., 2019; Camarero et al., 2015; Shestakova et al., 2018). The onset of the continuous warming trend occurred in the 1980s (Fig. 2A). Hence, EWS were analyzed for three periods, namely a pre-, early and late warming period (i.e. 1962-1981, 1982-2001, and 2002-2021, respectively), to study possible effects of recent warming. In the early and late warming period, all stands were considered, whereas in the pre-warming period, only older stands could be considered which chronologies dated back sufficiently long.

Growth trends were assessed based on raw BAI chronologies. The significance of the trend for each plot and period was tested using the Mann-Kendall trend test. Tau values <0 indicate a negative and >0 a positive trend. The change in growth sensitivity was quantified based on two statistical parameters: first-order autocorrelation (AR1) and standard deviation (SD). AR1 and SD were calculated at the tree level and averaged for each stand. For each period, a linear model was computed and the R^2 and the p values were used to evaluate the fitted model. To compare the differences between the periods, analysis of covariance (ANCOVA) was applied. ANCOVA is a statistical method that enables to test differences in slopes and intercepts of linear regression models by examining the effect of a categorical on a dependent variable while controlling for the impact of a continuous covariable. The EWS statistics tau values, AR1, and SD were used as dependent variables, while the period (pre-, early, late warming period) was used as a categorial variable, and mean stand age as a covariate. In order to apply ANCOVA, normality of the regression residuals was checked using the Shapiro–Wilk test, whereas the homogeneity of variances was checked by Levene's test. A nonsignificant value of the Shapiro-Wilk test and Levene's test would confirm the general assumption of the ANCOVA model. In case our ANCOVA model indicated significant differences between the three considered periods, a Tukey-Kramer HSD test was used as post-hoc test.

Growth synchrony was assessed using two methods. Firstly, Pearson correlations between mean chronologies of BAI indices among all plots (cross-correlation) within an elevation class were calculated. As a second method, a variance-covariance model was applied on the BAI index chronologies. The homoscedastic variant of the full model defined by Shestakova et al., (2014) was used, with elevational class as grouping variable. Growth synchrony was assessed within the elevational classes for all periods.

All data processing and analysis was done in R (R Core Team, 2023), using the packages "dplR" (Bunn, 2008), "mgcv" (Wood and Wood, 2015), "trend" (Pohlert et al., 2016), and "DendroSync" (Alday et al., 2018).

4.3 Results

4.3.1 Long-term growth trends of Norway spruce

Trees from lower elevations have higher growth rates (Fig. 4.2). At the same time, the BAI at elevations below 800 m shows more fluctuations in the last century compared with that at higher elevations. BAI shows an increasing trend until 2002 for all elevational classes (Fig. 4.2). In 2003, a major reduction in BAI was recorded at all elevations, which is inversely proportional to elevation, i.e. the highest reduction was observed at low elevation. The year 2003 was one of the driest in the study area, with SPEI12 below -2. Even though growth recovery can be observed after 2003 at low elevation, the year can be considered the starting point of long-term growth reductions in Norway spruce in the study area.

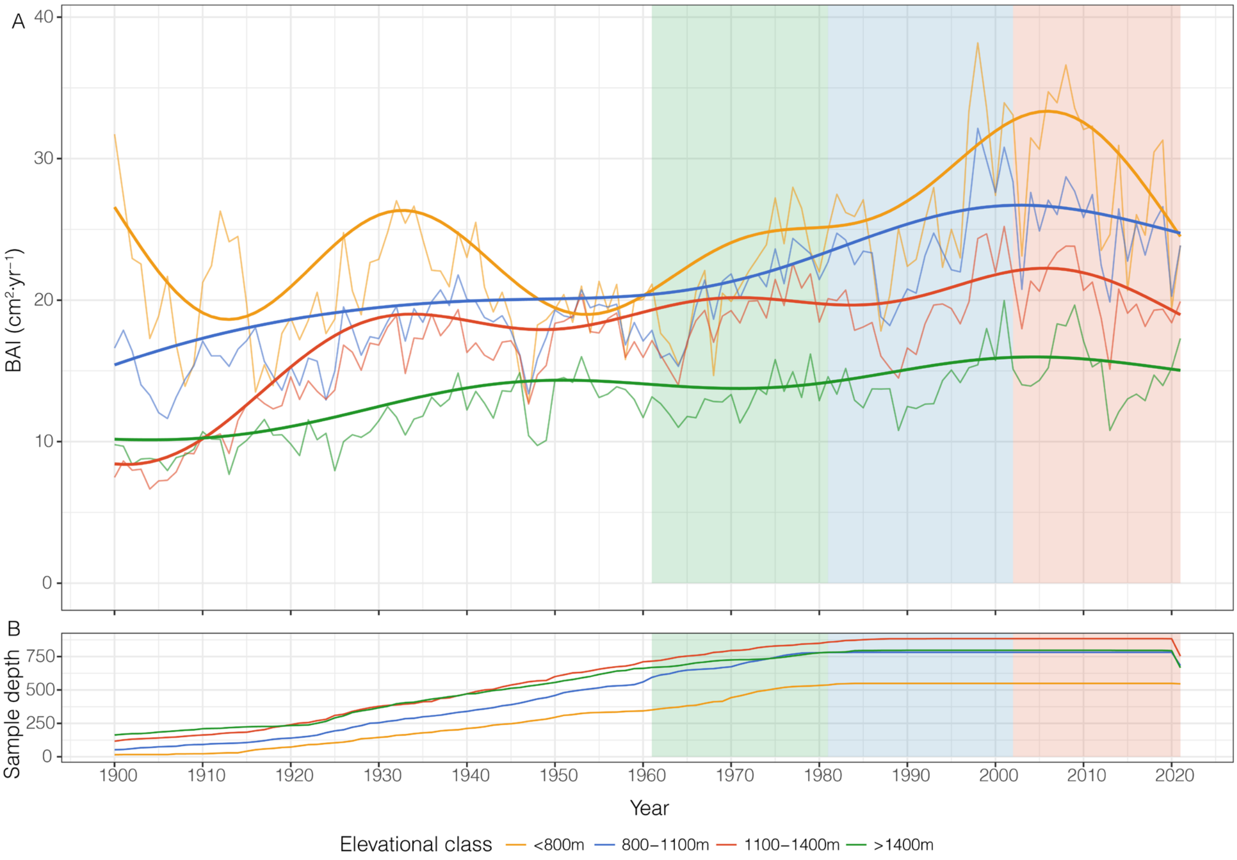

Figure 4.2 A. Time series of basal area increment and smoothed trend lines calculated using a GAMM for the four elevational classes; B. the sample depth, i.e. the number of trees in each year included in the analyses. The shaded areas in green, blue, and red represent the study periods pre-warming: 1962-1981, early warming: 1982-2001, and late warming: 2002-2021, respectively.

A recent change from positive to negative BAI trends can be observed for all elevations (Fig. 4.3) with our ANCOVA models showing significant differences between periods. A significant difference ($p < 0.01$) induced by the covariate mean stand age, was found only at an elevation <800m. Recent growth decline is particularly pronounced in younger trees, except for sites >1400 m, where growth decline is not indicated to change with age (Fig. 4.3). Age-related trends were, however, only significant at lower elevations. The biggest change in tau values between the analyzed periods was recorded for younger to middle-aged stands. At low elevation (<800m), post-hoc tests indicated significant differences in tau values between all three periods, whereas tau values in the pre-warming and early periods differed from the late period at all other elevations. These consistent negative trends in BAI in the last two decades represent a clear EWS of Norway spruce decline.

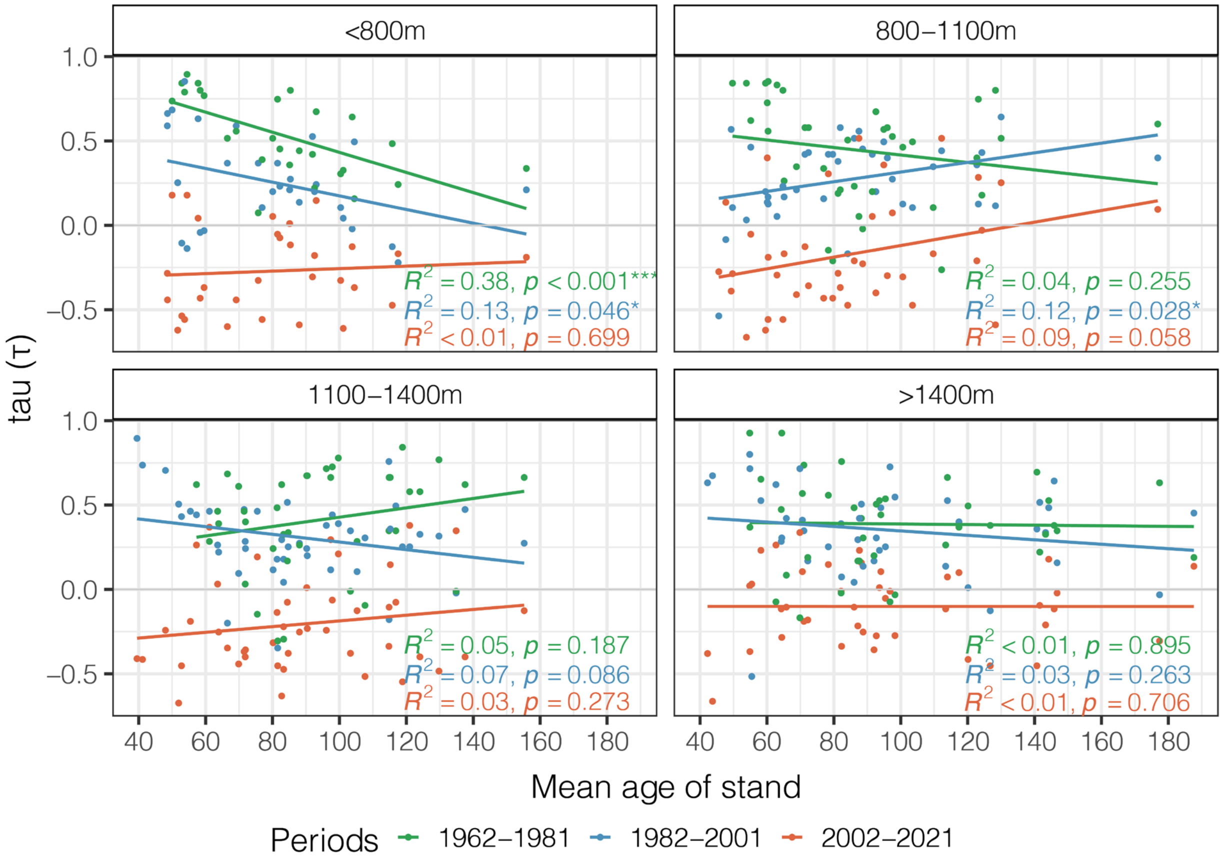

Figure 4.3 The Mann-Kendall tau coefficients for all studied stands in the three investigated periods (pre-warming: 1962-1981 in green, early warming: 1982-2001 in blue, and late waring: 2002-2021 in red) in relation to mean stand age. Negative tau values indicate growth decline

4.3.2 Changes in growth sensitivity and synchrony

ANCOVA analysis showed that there were significant differences ($p < 0.001$) in AR1 between the three considered periods. AR1 decreased in the late warming period for most of the stands below 1400 m compared to the pre-warming or early warming periods, indicating a reduction in the influence of previous-year conditions on current years' growth. At higher elevations, AR1 slightly increased in the last 20 years compared to the previous two considered periods. All differences between the late warming and the pre- or early warming period were found to be significantly different. Even though, according to the ANCOVA analysis, the covariate variable (mean stand age) did not have any significant influence on the model, a higher AR1 for older stands compared with younger stands was found in the pre-warming and early warming periods at an elevation between 800-1100 m. An opposite situation of slightly higher AR1 was observed for younger stands in the late warming period in all stands except those in the elevation band of 800-1100 m.

The growth variability quantified through the SD of BAI has only slightly increased over time. Results of ANCOVA analysis showed significant differences ($p < 0.05$) between periods, but for only between the pre-warming and late warming period in some elevational classes. The SD of BAI is higher for older stands compared to younger stands in all periods, except for young stands at low elevation in the late warming period. Furthermore, an inverse relationship can be observed between the SD of BAI and elevation, namely, the variability decreases with elevation. Specifically, at lower elevations, the variability is higher, compared with higher elevations.

The growth synchrony ($\hat{a}_C$) between stands at elevations <800 m is highest in all periods (Fig. 4.4). The variance-covariance model shows an increase in growth synchrony from pre-warming to the warming periods. For elevation >1400m, a continuous increase in growth synchrony was observed, while for lower elevation a decrease was observed in late warming period. The highest reduction is recorded between 800-1400 m (23%), which is considered the optimal elevation for Norway spruce in Eastern Europe.

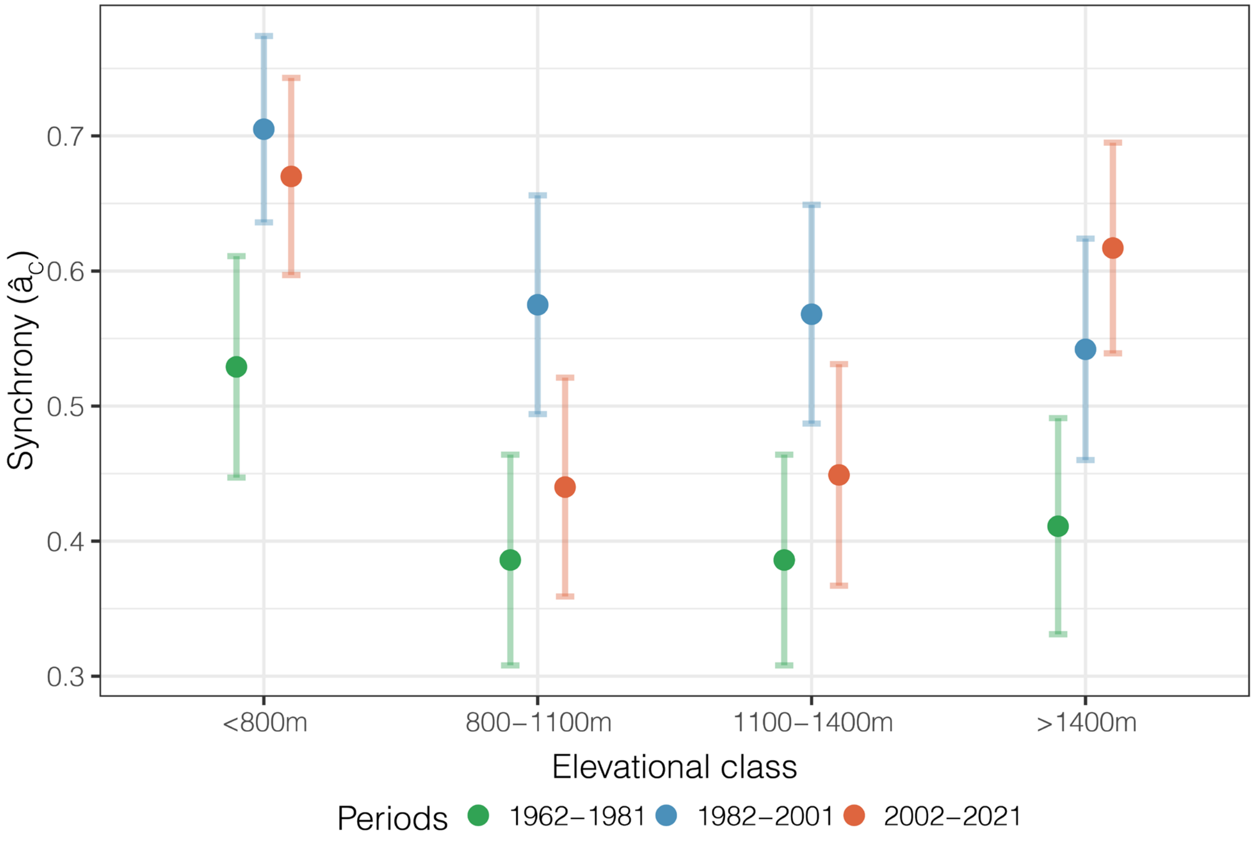

Figure 4.4 Growth synchrony based on the variance-covariance model for the four elevational classes in the three investigated periods (pre-warming: 1962-1981 in green, early warming: 1982-2001 in blue, and late warming: 2002-2021 in red)

4.4 Discussion

4.4.1 Growth decline of Norway spruce in the Eastern Carpathians

Whereas studies on Norway spruce in the Carpathians mainly reported increasing growth trends so far (Schurman et al., 2019), our study is among the first ones that highlight widespread negative trends (Bosela et al., 2021). We observed a reduction in BAI of Norway spruce, particularly at lower elevations, during the last two decades, indicating growth decline. The year 2003 can be considered as the starting point of decline in the Eastern Carpathians. Hartl-Meier et al. (2014) reported that Norway spruce in the European Alps, showed growth reductions of >50% in 2003 (compared with the average growth of the previous 5 years) at elevations <800 m, but no growth losses at elevations >1400 m. The 2003 drought was reported by multiple studies as a severe drought that seriously affected Norway spruce forests across Europe (Boden et al., 2014; Bosela et al., 2019; Vitali et al., 2017).

Although no large-scale forest dieback has been observed in Norway spruce in eastern parts of Europe so far (Synek et al., 2020), the observed negative trends in BAI are a clear EWS that these forests are at risk; i.e. negative BAI trends are an indicator of tree mortality.

4.4.2 Younger stands are more prone to climate change

While previous literature indicated that larger trees (i.e. older trees in managed stands) tend to be more sensitive to drought due to hydraulic conductance constraints, our study revealed a different pattern. Namely, younger to middle-aged stands (i.e. smaller trees) tended to be more affected, as they displayed a more pronounced growth decline as compared to older stands in the late warming period, especially at elevations between 800 and 1400 m. It could be related to the fact that younger trees have a smaller rooting system and are thus more dependent on surface soil water. The increased temperatures lead to higher evaporation in the upper layers of the soil and could lead to a stressed condition for young trees. In contrast, older trees have a bigger and more developed rooting system, enabling them to access deeper soil water. As, at elevations >1400 m there were no differences in BAI trends between young and old stands in the late warming period, water availability may still suffice here. On the other hand, the growth trends of healthy trees are typically characterized by BAI curves that exhibit a continuously increasing trend that may flatten at older age. This pattern is influenced by water and nutrient transport strategies and the increased metabolic costs associated with tree size. Considering age-related growth dynamics, it is important to note that younger to middle-aged trees tend to display an increasing BAI trend that gradually flattens as they grow older. This can result in a transition from an increasing trend to no trend between the analyzed periods.

4.4.3 Unambiguous trends in other early-warning signals

Assessing forest health can be challenging (Trumbore et al., 2015). Nevertheless, the state of forest ecosystems can be addressed by quantifying the health and conditions of its primary contributors, in terms of size and biomass, namely the trees. Recent studies revealed that most living organisms or systems show EWS before reaching a critical tipping point in their existence (Dakos et al., 2012; Scheffer et al., 2009). Studies on declining trees suggested that along with growth decline, changes in AR1 and SD of growth series can be used as valuable EWS (Cailleret et al., 2019; Camarero et al., 2015; Gazol et al., 2020). Camarero et al. (2015) reported an increase in AR1 and SD in declining trees. However, in our tree-ring network, a decrease in AR1 at lower and intermediate elevations as well as small increases in SD at all elevations, were found. This may indicate that spruce forests in the Eastern Carpathians are not yet severely affected, though the decline has begun (cf. Fig. 4.3).

That SD is highest at low elevations, may indicate that these trees are more stressed than at other elevations. High values for growth synchrony for Norway spruce forests at elevations <800 m underline this (Fig. 4.4; cf. Shestakova et al., 2016, 2014). It is most likely that water availability is limiting growth at these elevations (Sidor et al., 2015). Also in other regions of Europe, strong relationships between growth of Norway spruce and water availability were found (van der Maaten-Theunissen et al., 2013; Vitali et al., 2017; Vitasse et al., 2019).

The increase in growth synchrony in the early and late warming periods compared to the pre-warming period suggests increased stress for Norway spruce in the Eastern Carpathians along the entire elevational gradient. An unexpected finding at lower elevations (<800 m) is the small decrease in the growth synchrony ($\hat{a}_c$) in the later warming period, which may highlight that conditions were so stressful for a longer period of time that trees are starting to show independent growth patterns (Buras et al., 2023). The same may also hold true for elevations between 800 and 1400 m, where an âc reduction in the late period was even more pronounced. However, given that growing conditions at these elevations seem rather optimal for the growth of Norway spruce, it may also be that factors other than climate are interacting. More studies are needed in this respect, for example, studies focusing on temporal changes in the climate sensitivity of tree growth.

4.5 Conclusion

Overall, our results point out that Norway spruce in the Eastern Carpathians shows growth decline since 2003, especially at lower elevations. The negative trends in BAI in the last two decades represent a clear EWS of climate-induced stress. Even if the Norway spruce forests in the Eastern Carpathians look healthy and productive, our results indicate an increased vulnerability of this species. Surprisingly, younger trees were suggested to be more affected by ongoing climate change. Our results represent a starting point for further research to fully understand the complexity of climate change effects on Norway spruce forests in the region.

5. RESILIENCE COMPONENTS OF SPRUCE IN DROUGHT YEARS ALONG ELEVATIONAL AND AGE GRADIENTS

Andrei Popa, Marieke van der Maaten-Theunissen, Ionel Popa, Ovidiu Badea, Ernst van der Maaten, *Spruce suffers most from drought at low elevations in the Carpathians, though shows high resilience,* Forest Ecology and Management, Q1, IF=3.7 (under review)

5.1 Introduction

Droughts, natural phenomena characterized by a prolonged period of low water availability in the soil, stem from reduced precipitation levels coupled with higher atmospheric evaporation (Lloyd-Hughes, 2014). They may severely impact forest ecosystems, e.g., by compromising their capacity to provide ecosystem services such as a reduction of forest productivity, and may eventually trigger forest mortality.

In ecological studies, ecological stability is a wide and largely debated term (Van Meerbeek et al., 2021). Typically, a slowing down of processes is associated with early warning signals leading to the loss of stability (Scheffer et al., 2009). In the actual climate change context, much attention was dedicated to quantifying tree resilience to drought (Lloret et al., 2011; Schwarz et al., 2020). Resilience is defined as the ability of trees to achieve pre-drought growth rates after an extreme drought event (Lloret et al., 2011). Along with this indicator, resistance, and recovery are defined as the capacity to maintain growth levels during drought and the ability to restore growth after the extreme event, respectively (Lloret et al., 2011). Thurm et al. (2016) introduced another resilience component to tree-ring science known as the recovery period, which is defined as the period within which the trees are able to restore their growth levels to pre-drought ones. The latter indicator offers valuable information related to tree response to drought and the lagged effect of drought. In addition, a recently developed method proposed by Schwarz et al. (2020), known as the concept of the "line of full resilience," offers an integrative approach to interpret tree resilience components, making comparisons between different tree species or tree categories (e.g., elevational or age classes) easier. Any deviation from the theoretical model, which assumes a full recovery after a growth reduction, indicates a potential problem during extreme droughts. Similarly, low drought resilience of trees is related to a higher mortality risk in the future (DeSoto et al., 2020).

The vast majority of studies on spruce focused on the central or northern part of the distribution area, where negative impacts of climate change prevail. In Eastern Europe, no large-scale dieback events have been reported yet (Synek et al., 2020). However, Popa et al. (2024a) shows that in the Eastern Carpathians, spruce decline has begun, especially at lower elevations (<800 m). To improve our knowledge on the ecological stability of these forest ecosystems, this study assesses the resilience components (i.e. resistance, recovery, resilience, and recovery period) of spruce using a large dendrochronological network in the Eastern Carpathians, consisting of more than 3,000 trees from 158 plots of different age distributed along elevational gradients. We address the following research questions:

(Q1) How do resistance and resilience to drought differ with elevation?

(Q2) How does tree age influence growth responses to drought?

(Q3) What is the influence of water availability before, during, and after a drought on growth resilience?

5.2 Material and Methods

5.2.1 Climatic data and drought year selection

We downloaded maximum and minimum temperature as well as precipitation data at the daily level for each plot from 1950 to 2021 from the Easyclimate database using the "easyclimate" R package (Cruz-Alonso et al., 2023). Daily climate data were aggregated into monthly data by averaging daily temperatures and calculating sums of daily precipitation per month and year. Further, potential evapotranspiration (PET) was calculated according to the Hargreaves method (Droogers and Allen, 2002) while using the climate data described before as well as plot latitude and estimated solar radiation. As an indicator of water availability, we calculated the climatic water balance as a difference between precipitation and PET. The PET values were calculated using the "SPEI" R package (Beguería et al., 2017).

In the selection of drought years and further analyses, we used the average climatic water balance between February and July (referred to as CWB) based on the fact that in mountainous areas, radial growth of spruce takes place until early/late July (Treml et al., 2015). To identify the most common drought years, the top three years with the lowest value of CWB were selected at the plot level. At the elevational band level and for the entire network, the percentage of plots that faced a drought in the last seven decades was calculated. We selected the three most frequent drought years in the network for further analysis.

5.2.2 Resilience components and statistical analysis

To address our research questions, we calculated the resilience components resistance, recovery, and resilience (after Lloret et al., 2011) and the recovery period (Schwarz et al., 2020; Thurm et al., 2016) for the three most frequent droughts years in the network. All resilience components were calculated on raw tree-ring widths at the tree level but only for plots that actually faced a drought in those years. The pre- and post-drought periods were set to two years because this period is likely to best capture the previous and post conditions and to minimize the influence of other disturbance events (Vitali et al., 2017). The maximum length of the recovery period was set to 10 years (Schwarz et al., 2020). All resilience components were calculated using the "pointRes" R package (van der Maaten-Theunissen et al., 2021, 2015).

We determined the significance of the differences in resilience components along the elevational (Q1) and age (Q2) gradients using the Kruskal-Wallis test and pairwise Wilcoxon tests as post-hoc test. The tests were applied using the "rstatix" R package (Kassambara, 2021).

For each of the three most frequent drought years at the elevational bands and age class levels, we fitted an exponential model (Eq. 5.1) named 'the line of actual resilience':

$$Recovery \ = b * Resistance^{z} \qquad \text{(Eq. 5.1)}$$

The intersection point between the theoretical line and the fitted line represents the value of resistance that trees need to have during the drought year to be able to recover fully. To assess the deviation from the 'line of full resilience' of the 'actual lines of resilience', we computed an ANOVA (Rutherford, 2011). Fitted models for the 'line of actual resilience' were calculated using the "nls2" R package (Huet et al., 2004), and the confidence interval was calculated using 2000 bootstrap repetitions using the "boot" R package (Canty and Ripley, 2017).

To quantify the influence of water availability on resilience components (Q3), we used the climatic water balance since it is a better indicator of water availability and allows for comparability between sites, opposite of SPEI, which is standardized within site and period (Zang et al., 2020). We defined CWB before the drought as the mean of CWB in two years before the drought years, and similarly, the CWB after the drought using two years after the drought years.

To assess how water availability before, during, and after an extreme drought event influences the resilience components of spruce (Q3), we used linear mixed-effects models (LMMs). For each response variable (i.e. resistance, recovery, resilience, and recovery period), we computed multiple LMMs varying the explanatory variables (i.e. CWB before the drought, CWB during drought, and CWB after the drought). In the case of resistance, only the influence of CWB before and during the drought were considered. The plot was used as a random effect. Trees that had a resistance >1 or a recovery period >10 were not included in the model of the recovery period. Response variables were log-transformed before analysis to correct for heteroscedasticity, and explanatory variables were scaled by subtracting the mean values and dividing by standard deviation to allow for the comparison of variables' effects. The variance inflation factor (VIF) was calculated to assess the correlation between explanatory variables (O'Brien, 2007). The LMMs were fitted using the "lme4" R package (Bates et al., 2009), and the estimated plots (Fig. 5.5) were made using the "sjPlot" R package (Lüdecke and Lüdecke, 2015). All data processing and analysis was done in R (R Core Team, 2023).

5.3 Results

5.3.1 Resilience along elevational and age gradients

In all three drought years, the resistance of spruce increased with elevation (Fig. 5.1). Significant differences between elevational bands were found (Fig. 5.1). The highest mean growth loss (26%) was recorded in 2012 at lower elevations, followed by a growth loss of 24.3% in 1987. Recovery showed higher values at low elevations in all drought years, with significant differences compared to other elevational bands. Resilience of spruce from elevations >1400m differed significantly from resilience at other elevations. For trees that faced a growth reduction, the longest recovery time was 5.1±2.5 years at elevations >1400m in 2012, while the fastest recovery occurred at elevations <800m in 2015 (1.7±1.2 years).

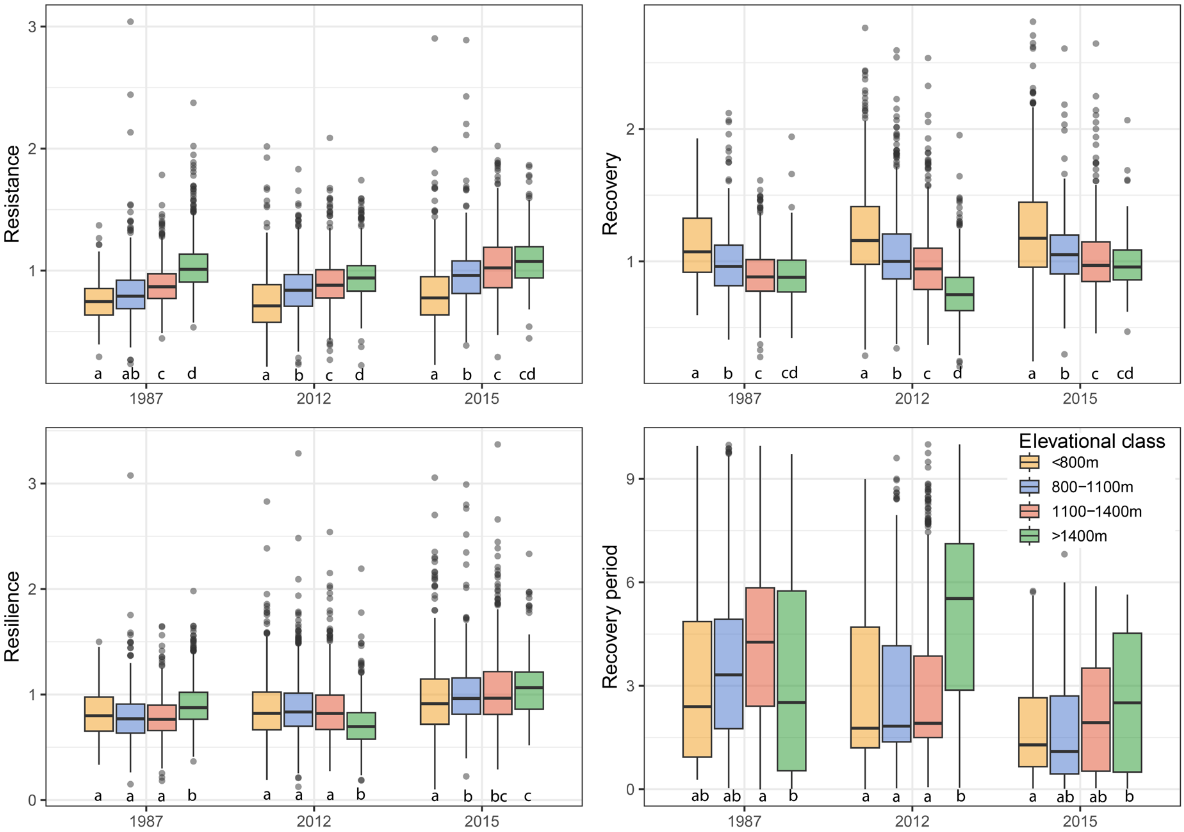

Figure 5.1 Spruce resilience components in relation to elevational classes for the three most common drought years in the study area. Letters indicate significant differences between elevational classes based on pairwise Wilcoxon tests.

5.3.2 Effects of water availability on spruce resilience

When examining the effect of water availability, we found significant but diverse effects on the resilience components of CWB before, during, and after an extreme drought (Table 5.1). Specifically, CWB during the drought positively influenced resistance and resilience ($p < 0.001$), but no significant effect was observed for recovery. Conversely, for the recovery period, a negative influence of the CWB during the drought was observed. Water availability from two years before the drought (CWB_{before}) has a smaller influence on spruce resilience components (estimates closer to 0, Table 5.1). Still, CWB_{before} negatively influenced spruce's resistance, recovery, and resilience, but at a lower rate compared to water availability from two years after the drought event (CWB_{after}). Furthermore, we identified a positive and significant influence ($p < 0.001$) of CWB_{before} and CWB_{after} on the recovery period.

The resistance and resilience of spruce increased with increasing CWB in the drought year (Fig. 5.2), indicating that the drought intensity severely affected the ability to maintain growth levels. On the opposite, the resilience components decreased with the increase in water availability before the drought. Interestingly, we observed a decrease in recovery and resilience (directly related to recovery) along the sites with higher water availability. These facts are related to the higher recovery rates shown by spruce at lower elevations (sites with lower CWB) compared to the lower recovery of spruce at higher elevations. A longer recovery period was observed for sites with low CWB during drought. However, a longer recovery period was associated with sites that showed a higher CWB before or after the drought. The sites with the highest water availability are at higher elevations, where the longest period of recovery was reported (Fig. 5.1).

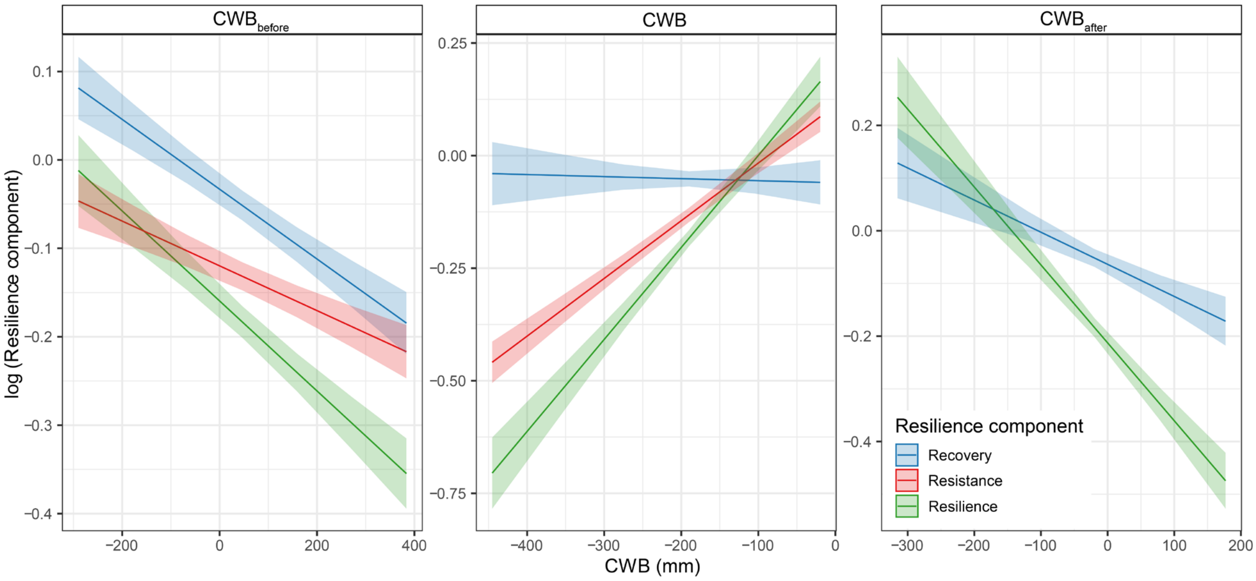

Figure 5.2 Effect of water availability on resilience components based on linear mixed-effect models (Table 5.1). One linear mixed-effect model was fitted for each (log-transformed) resilience component.

5.3.3 Line of full resilience

In all selected drought years, significant deviations were observed between the fitted 'line of actual resilience' and the hypothetical line across all elevations, as determined by an ANOVA ($p < 0.01$) (Fig. 5.3). Specifically, for elevations >1400 m, trees that showed resistance values below 1.014 in 2015, 1.215 in 1987, and 1.653 in 2012, did not have a recovery rate high enough to achieve a full resilience of 1. On the contrary, at elevations <800m, trees with lower resistance were able to recover fully. Concretely, trees with resistance above 0.853 (for 2015) to 0.963 (for 1987) had recovery rates high enough to gain full resilience within two years. In relation to age, only in 2015, trees with resistance <1 (values from 0.870 for older trees to 0.956 for younger ones) had recovery rates that led to full resilience. Conversely, in 1987 and 2012, full resilience was obtained only by trees that did not record any growth reduction (resistance >1). Overall, older trees showed resistance values accompanied by recovery rates that were not high enough to assure full resilience.

Table 5.1 Linear mixed-effect model results for predicting resilience components based on water availability (CWB before, during, and after the drought years). Estim. represents the model estimates, σ^2 variance of residuals, VIF variable inflation factor, τ variance caused by random effects, ICC intra-class correlation coefficient, N number of plots, Marg. R^2 coefficient of variation for fixed effects, Cond. R^2 coefficient of variation for fixed and random effects.

	Resistance				*Recovery*				*Resilience*				*Recovery period*			
Predictors	*Estim.*	*std. Error*	*p*	*VIF*	*Estim.*	*std. Error*	*p*	*VIF*	*Estim.*	*std. Error*	*p*	*VIF*	*Estim.*	*std. Error*	*p*	*VIF*
(Intercept)	-0.132	0.008	<0.001	-	-0.052	0.009	<0.001	-	-0.183	0.009	<0.001	-	0.719	0.028	<0.001	-
CWBbefore	-0.028	0.004	<0.001	1.026	-0.044	0.005	<0.001	1.198	-0.057	0.006	<0.001	1.232	0.108	0.031	<0.001	1.692
CWB	0.109	0.007	<0.001	1.026	-0.004	0.012	0.74	2.218	0.174	0.013	<0.001	2.434	-0.529	0.065	<0.001	5.478
CWBafter	-	-	-	-	-0.060	0.011	<0.001	2.506	-0.146	0.013	<0.001	2.773	0.639	0.067	<0.001	6.242
Random Effects																
σ^2	0.05				0.07				0.09				1.08			
τ	0.01				0.01				0.01				0.05			
ICC	0.14				0.12				0.1				0.05			
N plots	158				158				158				158			
Obs.	6147				6147				6147				2630			
Marg. R^2 / Cond.R^2	0.118 / 0.241				0.116 / 0.225				0.060 / 0.156				0.075 / 0.117			

5.4 Discussion

5.4.1 Spruce at low elevation shows the lowest resistance

Following drought years, characterized by low tree resistance and consequent growth decline, the potential for recovery typically increases; however, trees that showed a high resistance are likely to show lower recovery rates (Schmucker et al., 2023). A similar pattern was observed in our tree-ring network in the Eastern Carpathians. Specifically, we observed that at low elevations, spruce exhibited low resistance, but the recovery was higher compared to the situation at higher elevations, where high resistance was associated with a lower recovery. This trend aligns with findings from other studies, which also reported low resistance (i.e. substantial growth loss) associated with a higher recovery rate of spruce at lower elevations (Aldea et al., 2022; Treml et al., 2022) and implies a higher growth variability. In the same study area, Popa et al. (2024a) showed the highest year-to-year growth variability (in terms of basal area increment) to be at low elevation. A higher variability in growth patterns was associated with an increased climate sensitivity and a reduced tree resistance to drought, as confirmed by Popa et al. (2024b).

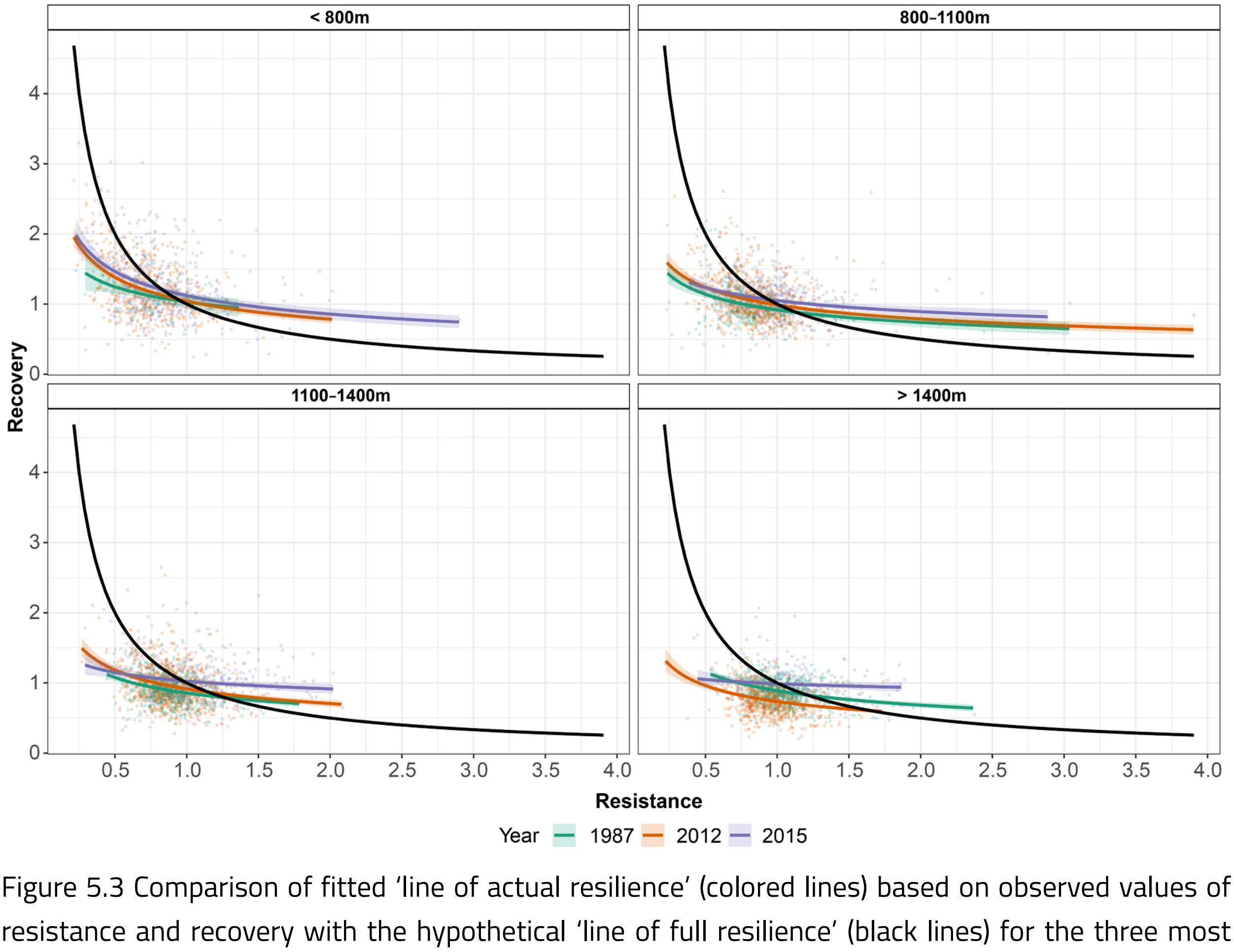

Figure 5.3 Comparison of fitted 'line of actual resilience' (colored lines) based on observed values of resistance and recovery with the hypothetical 'line of full resilience' (black lines) for the three most common drought years for the four elevational bands.

The comparison of the variability of resilience indices along the elevational gradients (Q1) shows significant differences. However, assessing drought tolerance across different elevations poses challenges due to the fact that along the elevational gradient, spruce faces different growth dynamics during the season (e.g., earlier onset of growth at lower elevations). To address these challenges, we used an integrated method for interpreting the tree ring-based resilience indices (Fig. 5.9). The stronger deviation of the fitted 'line of actual resilience' from the 'line of full resilience' observed at higher elevations indicates a lower drought resilience. This method allows a better classification of groups or species in relation to their response to drought. As shown by Schwarz et al. (2020), if the ranking of spruce tolerance to drought was made only considering the resistance index, we may consider that spruce from low elevations is less drought tolerant. But it also showed a higher recovery rate. Thus, spruce from lower elevations is closer to the 'full resilience' compared to spruce from higher elevations.

As spruce from low elevations has experienced more frequent droughts in its development history compared with spruce from high elevations, this can result in higher plasticity and acclimatization to water deficit, suggesting a potentially better adaptation of spruce from lower elevations. At the moment, there are strict regulations related to reproductive material (e.g., seed, seedling, etc.) transfer, most of them based on past or present climatic conditions (Konnert et al., 2015). However, adaptative forest management practices in the context of climate change need to consider the current resilience capacity of species and thus promote the regeneration of forests with better-adapted provenances (Millar et al., 2007). Thus, our results may provide new insights about the capacity of spruce from lower elevations to cope with drought as potential knowledge for adaptative forest management practices.

5.4.2 Older trees need more time to recover

A recent study conducted on a global scale showed that younger trees are less resistant to drought but have a higher capacity to recover after (Au et al., 2022). Our results are in accordance with these findings. Younger trees have shallower, less dense root systems that limit the ability to absorb water during drought periods. In the case of spruce, these limitations are even more pronounced since the root system of spruce is trailing, with a spread more on the horizontal than on the vertical (Caudullo et al., 2016; Ichim, 1990). These limitations could induce less efficient transpiration in younger stands, and trees could experience an increased drought severity (i.e. stronger growth reductions) compared to older stands. The significant differences in growth loss between different age classes in different drought years can have a major impact on carbon stock at the global level. Overall, the ability of young spruce trees to recover after drought events needs further investigation, and it is mandatory to take into account the forest management practices that improve the ability of managed forest ecosystems to better cope with drought.

Conversely, the older stands showed a higher resistance during drought years. The better resistance found in older stands can be related to the forest's structure and tree size. In managed forests, the older the stand is, the bigger the trees are in terms of diameter and height. This implies larger water storage and, due to the large root system, better access to deep soil water compared to younger trees. However, this theory is not fully supported by other studies because a bigger tree would imply a larger canopy and, thus, an increased demand for water in order to maintain transpiration levels (Poorter et al., 2012). Studies (e.g., Bennett et al., 2015; Mathes et al., 2023) showed that older trees are more prone to suffer due to drought and have higher mortality rates. Our results do not fully agree with these results because older spruce from Eastern Carpathians showed a higher resistance to drought. However, in the case of growth losses, the recovery rates are low and recovery periods therefore longer. These aspects may indicate a lower ability of older stands to cope with drought compared to younger stands that were regenerated in recent decades during a period with more frequent droughts and that are likely to react more plastic to these conditions.

5.4.3 Resilience of spruce mainly determined by drought intensity

We found drought intensity to be the most important driver of spruce resilience in the Eastern Carpathians. Our findings are in accordance with other studies that showed that drought characteristics significantly affect tree capacity to maintain growth or to recover after extreme drought events (Aldea et al., 2022; Zhang et al., 2022).

Climatic water balance conditions before and after a drought event are likely to influence the resilience components. Namely, the mathematical calculation of resilience is based on growth conditions before and after (i.e. two years in our study). Favorable growth conditions before the drought event (e.g., high CWB) would lead to an increased growth capacity, surpassing the average conditions; this aspect is likely to increase the vulnerability of the ecosystems to drought events (Zhang et al., 2021). This vulnerability may emerge from an increased leaf area index developed before the drought and, thus, an increased water demand that cannot be compensated (Zhang et al., 2021). At the same time, favorable conditions before a drought event would decrease the probability of trees to be able to recover those highs rates of growth after an extreme event. Our results are in accordance with these findings; resilience components (i.e. resistance, recovery, and resilience) are decreasing with CWB (Fig. 5.2).

5.4.4 Outlook and future perspectives

It is widely known that mixed forests may react better to drought than spruce monocultures (Aldea et al., 2022); however, the economic interest of stakeholders prevents a transition from centuries of spruce monocultures to mixed forest alternatives. However, when taking into account the actual climate scenarios, there is an urgent need for adaptive forest management to cope with the climatic challenges but to continue providing ecosystem services (especially timber production). Our findings offer new insights into the ability of spruce forests in the Carpathians to maintain their growth rates during drought events. Interestingly, our results indicated that younger trees or trees from low elevations have a higher recovery rate. These increased recovery rates may be related to an improved adaptability of spruce to face droughts. Therefore, the use of better-adapted proveniences may represent a potential solution to increase the resilience of spruce monocultures in the future until a smooth transition to mixed forest is made. This study showed different adaptability of spruce along elevational and age gradients, thus representing a starting point for future research in deepening these hypotheses. Linking phenotypes derived from tree rings with associated genetics could validate our findings and fully understand the impact of climate change on spruce-based forests.

6. CLIMATE–GROWTH RELATIONSHIPS OF NORWAY SPRUCE AND NON-STATIONARITY IN THE LAST CENTURY

Andrei Popa, Jernej Jevšenak, Ionel Popa, Ovidiu Badea, Allan Buras, *In pursuit of change: Divergent temporal shifts in climate sensitivity of Norway spruce along an elevational and continentality gradient in the Carpathians*, Agricultural and Forest Meteorology, Q1, IF=5.6 (under review)

6.1 Introduction

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 and high elevations. Furthermore, changes in tree sensitivity to climate have also been observed in temperate forests, 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. 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 (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. In boreal forests, the climate sensitivity of trees to summer temperatures changed significantly under different climate regimes (dry versus wet periods). 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 as to how well that species may cope with ongoing climate change.

To address this research gap, we established a novel method for assessing temporal shifts in climate sensitivity (TSCS) for spruce in the Eastern Carpathians. Our study is based on a large tree-ring network that encompasses more than 3,000 trees from 158 stands, covering a wide range of elevation from 475 to 1,675 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.

6.2 Material and Methods

6.2.1 Tree-growth and climate database

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 (Beguerıa 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 were 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).

6.2.2 Statistical analysis

The climate-growth relationships of spruce were assessed for mean temperature, precipitation, and SPEI. To quantify TSCS, we applied two methods. First, the common overlap period of tree-ring and climate data was split into two periods: 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.

To further investigate TSCS over time, we applied a dynamic method 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.

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. 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. Furthermore, we observed significant outcomes for seasons that are closely related, a pattern that strongly suggests these results are not mere products of chance.

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 a multiple linear regression model (Uyanık and Güler, 2013) and based on the model, 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).

6.3 Results

6.3.1 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. In relation to H1, 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. 6.1 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. 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. 6.5 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. Negative correlations between the current year's spring SPEI values and TRI were observed at elevations below 1,100 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, less than 50% of plots recorded a significant correlation with water availability in the early period, while more than 90% of the plots were significantly influenced by water availability in the late period (Fig. 6.7 SPEI panel).

6.3.2 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. 6.2). For elevations above 1100m, 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 at higher elevations, and with spring (Mar. to Apr.) temperatures at lower elevations.

The correlation between the late autumn/early winter SPEI and TRI decreased substantially, with a stronger change at low elevations (Fig. 6.2 SPEI panel). At the same time, correlations shifted from positive to negative at higher elevations (>1100m), especially during winter and early spring. The correlation intensity between the current summer SPEI and TRI decreased at elevations below 1100m, but for a smaller percentage of plots (less 60%). The positive late summer SPEI correlation at sites below 800m (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. 6.10 SPEI panel). Similar to SPEI patterns, we observed a major TSCS for precipitation.

6.3.3 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. Thus, while high elevations featured a sensitivity increase to winter temperatures, low elevations featured a declining sensitivity. 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. Interestingly, the regression lines quantifying TSCS divergence of the longitudinal gradient were negatively correlated throughout with those from the elevational gradient. Consequently, for winter SPEI and summer SPEI we found positive TSCS in the eastern part of the Eastern Carpathians, which exhibits a drier continental climate, than the 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 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.

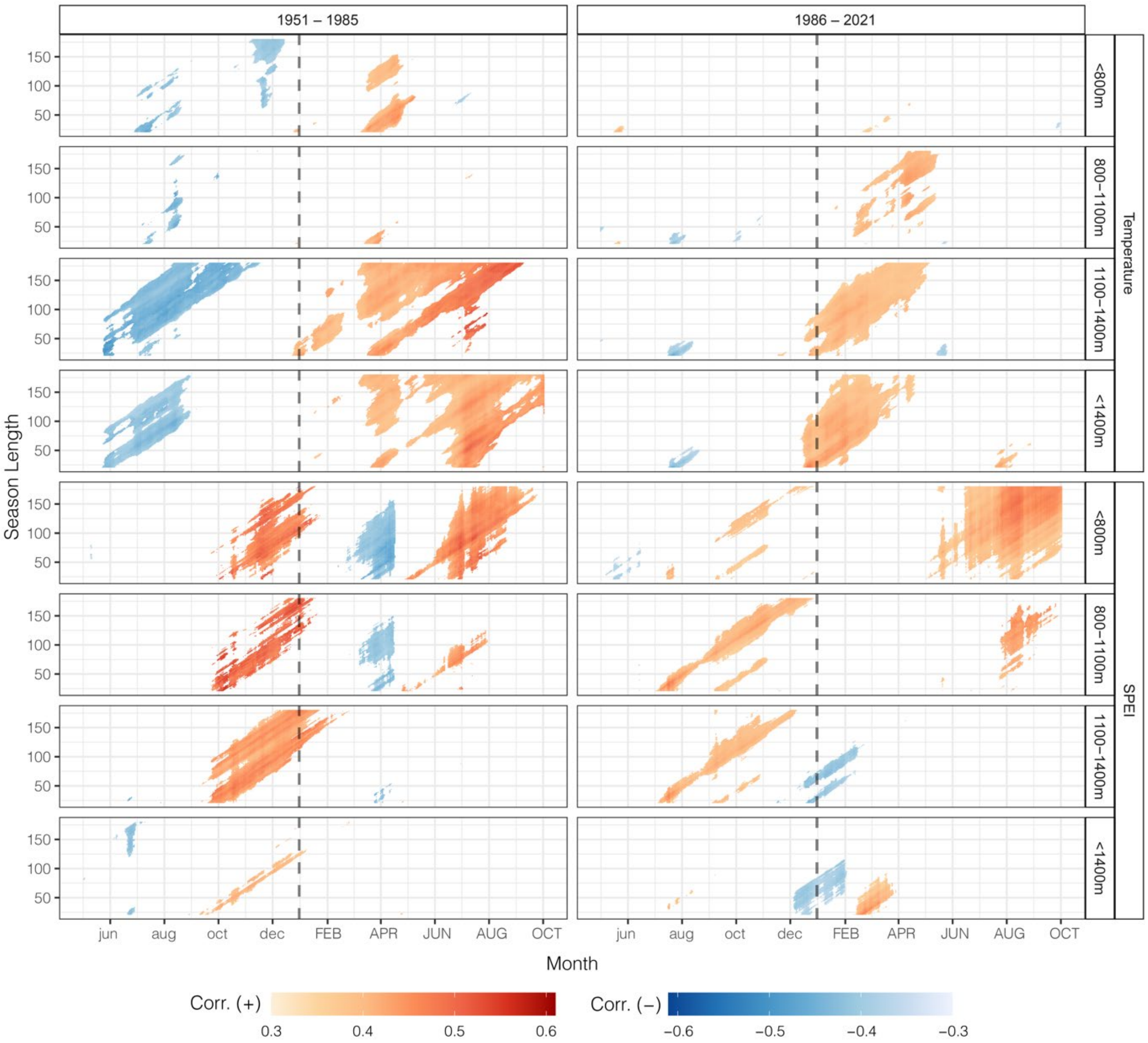

Figure 6.1 Mean temperature and Standardized Precipitation-Evapotranspiration Index (SPEI) correlation coefficients with residual tree ring-width index (TRI) values for different elevational belts in the early (1951 to 1985) and late (1986 to 2021) periods. Only the seasons in which at least 25% of the 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.

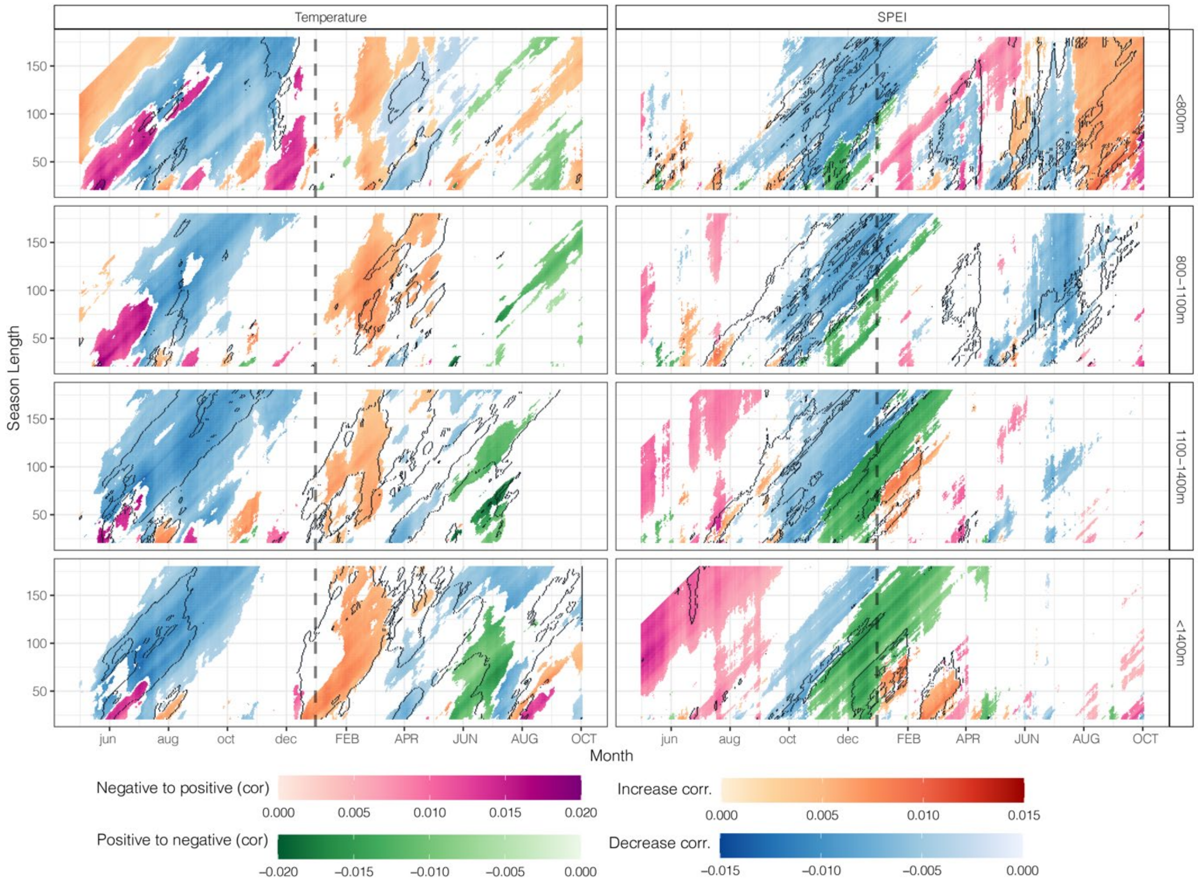

Figure 6.2 Seasons with increasing or decreasing correlations (the positive–positive or negative–negative temporal shifts in climate sensitivity (TSCS) types; red and blue), and seasons with a change in correlation sign (the negative–positive or positive–negative TSCS types; pink and green) for temperature 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 Figure 6.5). The vertical dotted gray line represents the limit between the previous (lowercase letters) and current (uppercase letters) year.

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. 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. 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 less than 10%. 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.

6.4 Discussion

6.4.1 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). 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 (Claudia Hartl-Meier et al., 2014; Sidor et al., 2015). Maximal radial growth rates of spruce are likely to occur from June to July in mountainous areas, 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 1100m. 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). Furthermore, climate warming in mountainous regions has occurred at a rate above the global mean (Wang et al., 2014). Our results mirror observations from other cold-limited environments, namely that climate change is reducing temperature-induced tree growth constraints (Babst et al., 2019). Continuous warming has changed sensitivity to climate across Europe for spruce (Bošel'a et al., 2014; Schurman et al., 2019; Svobodová et al., 2019) and other tree species as well (Unterholzner et al., 2024).

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. 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 leading to a growth reduction, and hence, reduced TRI, in the following year (Hacket-Pain et al., 2019). 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.

6.4.2 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. 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. 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.

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

Our results indicated differences in climate-growth relationships with elevation, 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. 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.

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, 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. 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.

6.5 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.

7. NON-LINEARITY IN CLIMATE RESPONSE OF SPRUCE

Andrei Popa, Ionel Popa, Ovidiu Badea, Michal Bosela, 2024b, *Non-linear response of Norway spruce to climate variation along elevational and age gradients in the Carpathians*, Environmental Research, 119073, https://doi.org/10.1016/j.envres.2024.119073, Q1; IF=7.7

7.1 Introduction

Usually, climate–growth relationships are assessed by linear correlation due to the simplicity and straightforwardness of modeling (Matisons et al., 2021a). However, applying this method may bias results, since the ecological and physiological responses of trees to environmental factors are non-linear, and usually bell-shaped (Wilmking et al., 2020). Under optimal conditions, tree growth follows an asymptotic sigmoid curve consisting of a positive exponential phase and a decreasing relative growth rate. Recently, studies have emphasized the non-linearity of the climate–growth relationships in multiple areas and for several species (Bozkurt et al., 2021; Matisons et al., 2021b). Nevertheless, close-to-linear responses of trees to specific environmental parameters can be found in areas where climate sensitivity is high (e.g., at the timberline) (Wilmking et al., 2020). Thus, the classical approach of assessing the linear climate–growth relationships may be outdated, and new knowledge is required to fully disentangle these complex relationships.

The Eastern Carpathians represent one of the largest and most continuous areas where spruce naturally occurs (Caudullo et al., 2016). Moreover, as spruce is at the southeasternmost edge of its natural range within this area, the region is potentially vulnerable to climate change. To the best of our knowledge, a non-linear assessment of climate–growth relationships using machine-learning techniques for spruce in this area had not been performed prior to this study. To address this knowledge gap, we analyzed a large dendrochronological network from 158 stands, with over 3,000 trees of varying age distributed along an elevational gradient. We aimed to identify to which climatic parameters spruce has a non-linear response. To do so, we addressed the following research question:

Q1: How does the sensitivity of spruce to climate variation change along an elevational gradient?

Q2: Do the climate–growth relationships vary with tree age?

Q3: Are the climate–growth relationships predominantly linear?

7.2 Material and Methods

7.2.1 Climate data

Due to the scarcity of weather stations in the study area and the distribution of the plots along an elevational gradient, we used the European Observation (E-OBS) daily gridded dataset downscaled using WorldClim data. Easyclimate, the downscaled database—initially developed by Moreno and

Hasenauer (2016) and updated for 2022 by Pucher (2023)—includes the minimum and maximum temperature and precipitation since 1950, with a spatial resolution of 1 × 1 km. Climate data were extracted using the "easyclimate" package in R (Cruz-Alonso et al., 2023). The mean daily temperature was derived as the mean of the minimum and maximum temperature. Daily climate data were aggregated for each plot by mean in the case of temperature and summed for precipitation at the seasonal level: previous growing season (previous April–previous August), previous autumn (previous September–previous November), winter (previous December–March), and growing season (April–August).

To quantify the influence of water availability on spruce growth, the Standardized Precipitation-Evapotranspiration Index (SPEI) was used. The SPEI was calculated based on the difference between the monthly precipitation and potential evapotranspiration according to the modified Hargreaves equation (Droogers and Allen, 2002). To analyze the influence of water availability at the season level, the cumulative SPEI for each considered season was computed. The calculation of SPEI values was performed using the "SPEI" package in R (Beguería et al., 2017).

7.2.2 Statistical analysis

To explore the non-linearity of the relationship between RWI and seasonal climate (temperature and SPEI), we performed a random forest analysis (RFA) as a multivariate non-parametric regression method (Breiman, 2001). RFA is a machine-learning technique based on the decision tree algorithm, and combines the bagging principle with random feature selection (Genuer et al., 2010). This method permits the selection and hierarchy of the model predictors based on the variable importance (VI). We used the Increased Mean Square Error (%IncMSE) to measure the variable importance robustly. This statistic defines the increase in the mean square error of the predictions if a variable is permutated. A higher IncMSE signifies a more important predictor.

The RFA model consisted of 150 trees, and each tree grew on a bootstrap sample, with replacement, drawn from the entire dataset. For each individual regression tree, only two-thirds of the dataset is used for training; the remaining constitute out-of-bag (OOB) data that are utilized to estimate the regression error. OOB error can be associated with a form of cross-validation, and itis considered a reliable estimate of the RFA model robustness, thus no additional cross-validation is required (Breiman, 2001; Li et al., 2019). To evaluate our RFA model robustness based on the regression algorithm (for continuous variables), we used the mean of squared residuals (MSR_{OOB}) and percent of variance explained (%VarExp)(Liaw and Wiener, 2002).

Non-linearity in the tree growth response to climate was evaluated using partial dependence plots of RFA. This tool helps to visualize the nature of the relationship between RWI and one climate variable while accounting for the average effect of the other predictors of the model (Friedman, 2001). The RFA was applied to the entire tree-ring network, for each elevation class, and for each age category. The "randomForest" (Liaw and Wiener, 2002) and "pdp" (Greenwell, 2017) R packages were used for the analysis.

All statistical analyses related to our research questions were limited to the years 1950–2020, the common period between the tree-ring dataset and climate data.

7.3 Results

7.3.1 Non-linearity in tree growth and climate relationships

For the entire TRW network, the most important predictor in RFA was the water availability index (SPEI). The most important season, according with IncMSE criteria, is SPEI from the growing season, followed by the previous autumn SPEI (Fig. 7.1). In relation to SPEI from the current growing season, we observed a decrease in variable importance with elevation—that is, higher values at low elevations (<1100 m; IncMSE: 41%) to lower values at high elevations (>1100 m; IncMSE: 29%). For temperature, the highest values of variable importance were recorded in the previous autumn (IncMSE: 43%) and in the winter season (39%). For previous autumn temperatures, a clear ordination of variable importance according to elevation was observed. Our results did not show differences in variable importance according to age classes.

To address the third research question (Q3), we analyzed the non-linearity in the response of spruce to climate in relation to elevation (Fig. 7.2). The random forest analysis highlighted linear and non-linear patterns of the spruce growth and climate relationship. A relatively linear dependence of RWI was observed with previous growing season temperature (negative dependence), except at low elevations (Fig. 7.2E). Similarly, a linear dependence was reported for winter temperatures, with a slight decrease for positive mean temperature at elevations < 800 m (Fig. 7.2G). A bell-shaped dependence of RWI to previous autumn and current growing season temperatures was observed (Fig. 7.2F and 7.2H). In the case of the previous autumn temperatures, we observed low RWI values for mean temperatures below 3 °C for high elevations and below 5 °C for elevations < 1100 m. Moreover, the RWI decreased for previous autumn temperatures above 7 °C at elevations higher than 1100 m and between 9–10 °C at lower elevations. In the current growing season, for elevations below 1400 m, we identified clear thresholds after which growth was negatively influenced by higher temperatures. For elevations above 1400 m, an increase in mean temperature up to 9 °C favored radial growth, while no influence was observed after this point. Also, for this season, our results highlighted a shift to high values of the temperature dependence curve as elevation increased.

The climate–growth relationship models' non-linearity was evident in the case of drought index (SPEI) (Fig. 7.2 SPEI panel). The growth dependence of the water deficit had a stepwise pattern, with important thresholds except for winter SPEI, where a bell-shaped dependence was reported (Fig. 7.2C). In the previous year of ring formation, SPEI values < -1 had a clear negative impact on spruce growth. Moreover, spruce at low elevations exhibited a more pronounced negative impact from low water availability in the previous autumn (SPEI < -1) compared to other elevation classes. Winter SPEI, as an index for snow importance, had a clear impact on spruce growth. At high elevations, lack of snow (SPEI < -1.5) negatively impacted tree growth, while at low elevations, excessive snow had a negative effect. During the growing season, RWI decreased due to low SPEI (<-1) at all elevations; however, the strongest reduction was observed at elevations < 800 m. Regarding age, younger trees benefited more from SPEI values > 1 during the previous autumn. On the other hand, winter SPEI—snow quantity—was more important for older trees, especially at elevations above 800m.

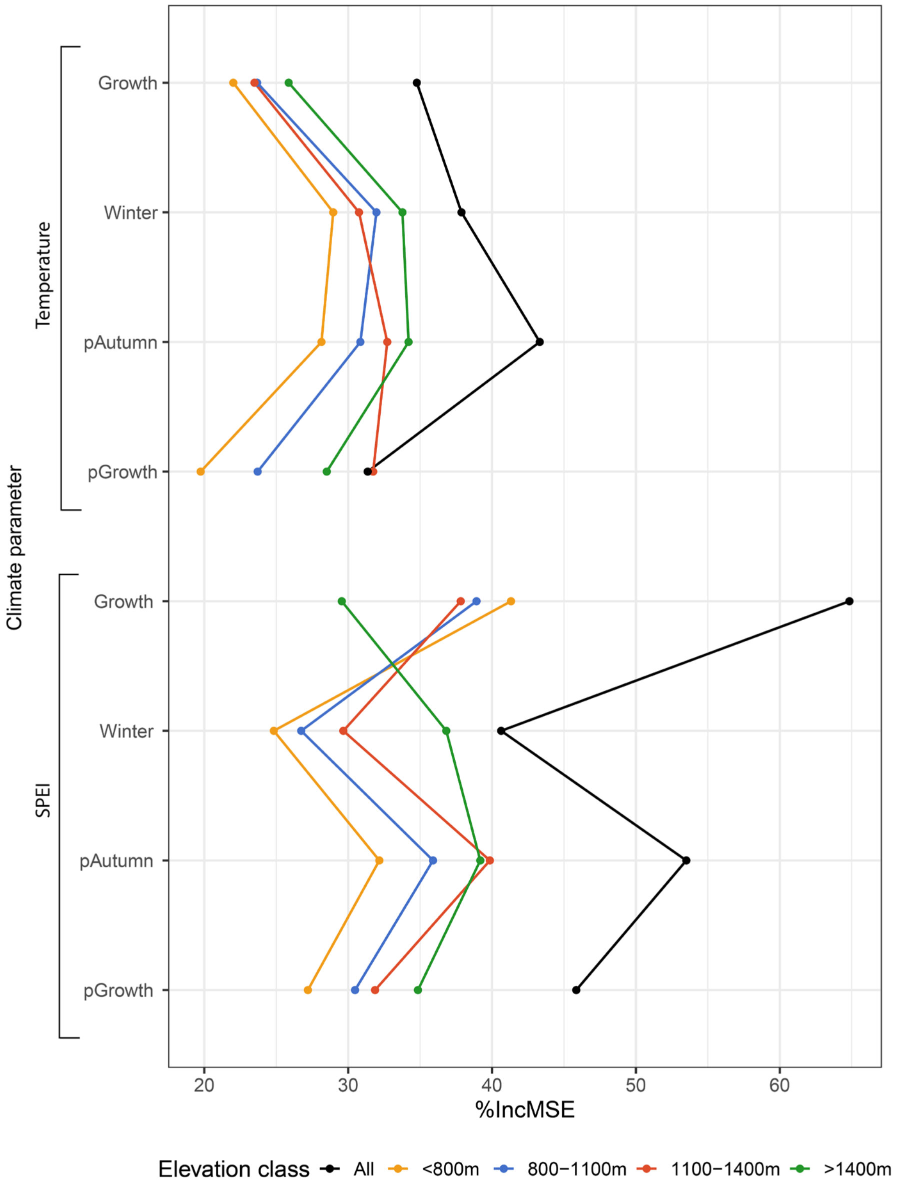

Figure 7.1 Importance of climatic variables (Temperature and Standardized Precipitation-Evapotranspiration Index: SPEI) on spruce growth in the period 1950–2020 from random forest analysis (RFA) in relation to elevation class;

7.4 Discussion

The results provided comprehensive answers to our initial research questions: (Q1) In relation to elevation, we found that spruce growth at low elevations is mainly limited by water availability, while winter temperatures are likely to have a slight influence along the entire elevational gradient; (Q2) we found that, in general, there were slight differences in spruce sensitivity to water availability and temperature in relation to age along the elevational gradient; and (Q3) our models showed that non-linearity in the response of spruce to climate variables is season-specific—namely, temperatures from the previous autumn and current growing season along with water availability during winter induce a bell-shaped response. In the following, we conduct an in-depth discussion of each of these findings.

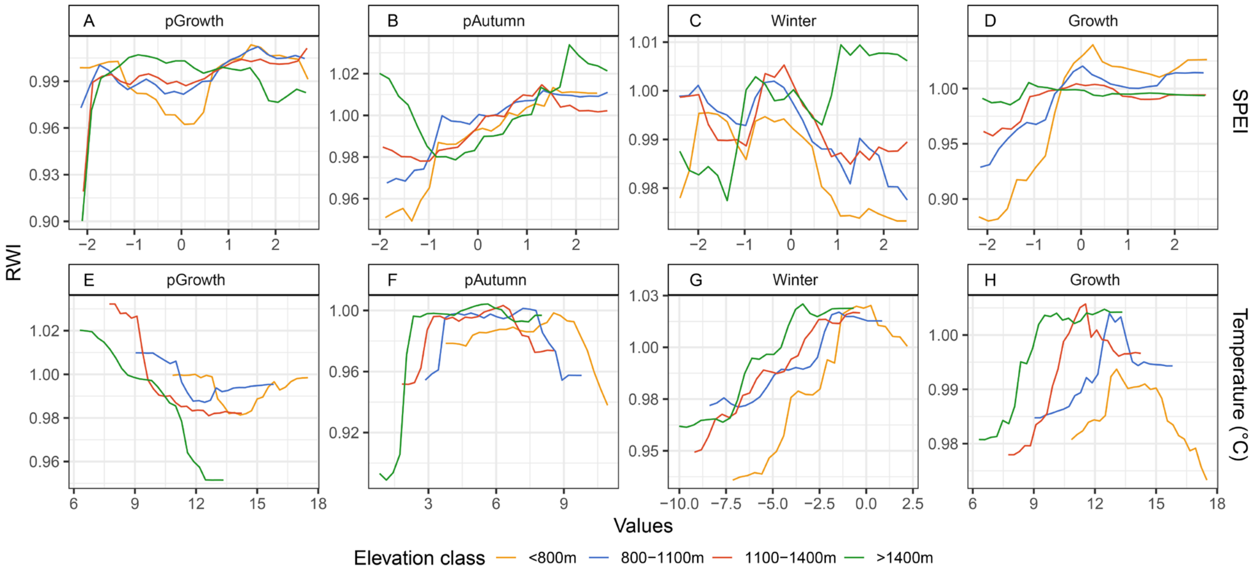

Figure 7.2 Partial dependence plots of spruce growth on seasonal climate variables (A-D) Standardized Precipitation-Evapotranspiration Index (SPEI) and (E-H) temperature (°C) in relation to elevation class

7.4.1 Non-linear pattern in the response of spruce to climate is season-specific

Physiological processes are complex phenomena and represent the sum of different interactions between environmental, climatic, and genetic factors. Photosynthetic activity is enhanced with the increase of temperature, followed by saturation and then inhibition states. Tree growth, as a result of assimilation processes, is usually limited by most constraint factors; however, these limitations are not linear but follow a bell-shaped form (Wilmking et al., 2020). In the first part of the curve, there is a strong limitation, followed by a gradual reduction until the optimal conditions are acquired. After certain thresholds at which saturation occurs, the limiting factor becomes an inhibiting one (see Box 2 in Wilmking et al., 2020). This clear non-linear response of spruce growth to climate was observed in our RFA models for specific seasons.

One of the clearest bell-shaped patterns was that depicting the influence of previous autumn temperatures on spruce growth (Fig. 7.2F). At high elevations, we could observe an increase in RWI with the increase of temperatures up to 3°C, after which higher temperatures reached the optimal threshold. We did not identify any inhibition effect, which led to the conclusion that even in the context of actual global warming, for spruce at elevations > 1400m, the temperature would not result in a saturation state. However, at middle elevations (800–1400m), we could observe all three parts of the bell-shaped form—namely the limiting, the saturation, and the inhibition phases—suggesting that spruce was in the optimal range at these elevations. Interestingly, at lower elevations, we could observe just the saturation phase and the inhibition phase. This fact mirrors stressful conditions for spruce that may lead to spruce decline, as has occurred in other parts of Europe due to extreme heatwaves and droughts.

For the current growing season, we found differences in the threshold at which temperature limited or inhibited spruce growth, as a result of elevational influences on temperatures (temperatures usually decrease by 0.6°C for every 100-m difference in elevation (Barry, 1992)). This different threshold of temperatures in the growing season is likely directly related to the cambial activity, the yearly onset of which varies along the elevational gradient (Treml et al., 2015). Similarly, at high elevations, as in previous autumn temperatures, we did not observe an inhibition phase of the current growth season temperature. At elevations < 1400m, there was a clear bell-shaped dependence of spruce growth on current growing season temperature. An important insight could be observed at low elevations: regardless of temperature thresholds, all dependence of RWI was below 1. These results show that spruce faces important constraints at low elevations due to high temperatures. These results may be associated with a severe growth reduction (up to 30% in basal area increment) within this elevation range in the last two decades (Popa et al., 2024a).

The non-linearity did not present a clear bell-shaped pattern in relation to water availability based on SPEI, with the exception of the winter season, where precipitation occurs in solid form (i.e., snow). At high elevations (>1400m), the lower snow depth negatively influenced the RWI, while above-average quantities of snow (SPEI > 1) favored RWI. During winter, snow plays an important role in forest ecosystems by providing a protective cover for tree roots from freezing. At the same time, snow may limit the freezing depth of soil, which can lead to a faster initiation of water transport by roots in the spring. Moreover, snow in mountainous areas has been reported to act as a valuable water reserve for shallow soils (Beniston et al., 2003). The negative effect of lack of snow (SPEI < -2) declines with decreasing elevation, thus confirming our hypothesis related to the protective cover of snow. At low elevations, the probability of occurrence of extremely low temperatures is lower compared with high elevations in mountainous areas. On the other hand, the positive influence of snow at high elevations changes and has an inhibiting effect at lower elevations. A possible explanation of this may be related to the fact that excessive snow at the end of the winter may delay xylogenesis.

7.5 Conclusions

Norway spruce is the most common coniferous species in Europe. In the context of climate change, this species faces major problems in Central Europe. At the moment, spruce decline in the eastern part of Europe occurs at lower rates compared to other parts of Europe; therefore, to better understand the future of this species, our study provides new insights into the influence of climate on spruce growth. Our results show that spruce is more limited by seasonal water availability (SPEI) compared to seasonal temperatures. Moreover, non-linearity in climate–growth relationships is season-specific; that is, temperatures from the previous autumn and current growing season, along with water availability during winter, induce a bell-shaped response.

8. ASSESSING CLIMATE-GROWTH RELATIONSHIPS BASED ON DIFFERENT TREE-RING PARAMETER

Andrei Popa, Ionel Popa, Cătălin-Constantin Roibu, Ovidiu Nicolae Badea, 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, 18: 2428. https://doi.org/10.3390/plants11182428, Q1; IF = 4.5

8.1 Introduction

Dendrochronological studies analyzing how trees are influenced by climate and how tree species adapt to new climate conditions also provide a record of the past climate (Fritts, 1976). Tree rings can be used as an important proxy to highlight annual climate variations (Jones et al., 2009). The main tree-ring proxy used in dendrochronology is tree-ring width (TRW). However, in some cases, TRW does not provide a strong and robust climate signal compared to other tree-ring parameters such as maximum latewood density (MXD) or stable isotopes (Nagavciuc et al., 2019). Usually, to ascertain MXD, expensive equipment is required, and there are logistical limitations. A relatively new parameter (image-based blue reflectance—blue intensity, BI) has been developed to respond to these limitations (Rydval et al., 2014). BI is a proxy that represents measured reflected light in specific wavelengths of the color spectrum. Studies have shown a strong correlation (over $r = 0.95$, $p < 0.05$) between BI and MXD (Wilson et al., 2014). BI has a stronger climate signal in temperature-limited ecosystems compared to TRW and is less sensitive to disturbances (Björklund et al., 2013; Wilson et al., 2014). Based on these findings, there is potential for BI to be used as a substitute for MXD. However, the basal area increment (BAI) represents a two-dimensional measurement, specifically on the surface of the tree ring. The basal area increment is more related to the biomass increment of the tree and stand productivity. Moreover, BAI is a suitable proxy that can preserve low- and medium-frequency growth variability (Biondi and Qeadan, 2008; Han et al., 2022).

In this study, we aimed to determine the climate signals captured in three tree proxies (TRW, BAI, and BI) of Norway spruce in an intramountain valley in the Eastern Carpathians along an altitudinal gradient. The specific research questions were:

- How does air temperature modulate Norway spruce growth in an intramountain valley of the Carpathians?
- Is the correlation between temperature and the investigated tree-ring parameters stable through time?

8.2 Material and Methods

8.2.1 Study area

The study was carried out in Gheorgheni region, a large intramountain valley in the center of the Eastern Carpathians (Romania). The altitude in the study region ranges from 700 m a.s.l. to 1770 m a.s.l. The study area is located between 46°37′N, 25°25′E and 46°50′N, 25°36'E. The general geology of the study area is represented by a volcanogenic–sedimentary complex.

8.2.2 Sample collection and data processing

To investigate the effect of altitude on the Norway spruce, climate response increment cores from 12 locations were collected: five locations at low elevation (altitude varied from 880m a.s.l. to 1020m a.s.l.) and seven locations at high elevation (altitude varied from 1510m a.s.l. to 1630m a.s.l.). In each plot, 15 to 20 dominant and healthy trees were selected to extract increment cores. By sampling strategy applied, we selected mature trees, and the limitation of the analysis period to available temperature data ensured the exclusion of the juvenile growth part from the climate–growth relationship analysis. One core per tree was extracted using a 5-mm-diameter Pressler borer at breast height (i.e., 1.3 m). For each sampled tree, 2 perpendicular breast-height diameters (DBH) were measured with a forest caliper. The mean of these two diameters was used to compute the BAI. All three tree-ring proxies (TRW, BAI, and BI) were measured/calculated for the same cores. A subset of 50 cores for each altitude level (high and low elevations), were selected for measurements and analysis. In order to obtain reliable BI measurements, we selected only cores with no discoloration due to fungi, no gaps due to broken cores, and with parallel rings, as well as from cores containing pith or those that allowed easy determination of any missing rings.

Norway spruce is a coniferous species with no visible differences between heartwood and sapwood. Based on this characteristic of spruce wood, it is possible to measure latewood blue reflectance without any chemical treatments (Björklund et al., 2015). To measure latewood blue reflectance, the standard protocol was followed (Campbell et al., 2011; Rydval et al., 2014). Window parameter settings were adjusted according to (Rydval et al., 2014). The tree-ring measurements (TRW and BI) were computed using CooRecorder software on scanned images (Maxwell and Larsson, 2021). No missing or false rings were observed. The BAI was reconstructed for each ring individually and adjusted according to the mean DBH of each tree.

For each analyzed tree-ring parameter, 2 chronologies were developed, one for low elevation and the second for high elevation. Indices were computed as the ratio between raw measurements and fitted values. In order to eliminate the autocorrelation that was still present in the standard index series, an autoregressive model was applied. In the analyses, we used the residual index chronologies obtained by bi-weight mean without variance stabilization. The carry-over effect of the previous year's climate condition on the current year's growth can be assessed by first-order autocorrelation (Fritts, 1976; Speer, 2010). The detrending, chronology development, and statistical parameters were computed using the dplR package on R software (Bunn, 2008).

8.2.3 Climatic dataset

Two local weather stations, Joseni (750 m a.s.l.)—valley weather station, and Bucin (1282 m a.s.l.)—up-hill weather station, provided the climatic data (daily mean temperature). Climatic data are available from 1963 at the Joseni weather station and from 1978 for the Bucin weather station. Therefore, the analyzed interval was limited to the common period, 1978-2019.

8.2.4 Climate–growth relationship assessment

The availability of local daily air temperature data in the study area allowed us to analyze the climate–growth relationship on a cumulative daily scale (Jevšenak, 2019). The daily temperatures were aggregated in moving time windows of 21 days to 120 days starting from June in the previous year of growth to October current growing season. The correlation between residual index chronologies and cumulative daily temperatures and time stability were computed using the dendroTools package in R (Jevšenak and Levanič, 2018).

8.3 Results and Discussion

8.3.1 Climate–growth relationships for three tree-ring parameters

The TRW residual index chronologies correlate positively with winter temperatures (cumulative windows width starting from 21 to 120 days) (Fig. 8.1). The correlation coefficient between high-elevation TRW index chronology and mean temperature from the up-hill weather station (Bucin) has the highest value (r = 0.494, $p < 0.05$, n=41) with the 3 December–18 January period. The low-elevation TRW index chronology has the highest correlation (r = 0.485, $p < 0.05$, n=41) with 1 November–12 February mean temperature from the up-hill weather station. Regarding the correlation between the TRW residuals index and the winter air temperature from the valley weather station, the maximum correlations were lower (r = 0.442, $p < 0.05$, n=41 – high-elevation chronology and r = 0.435, $p < 0.05$, n=41 – low-elevation chronology).

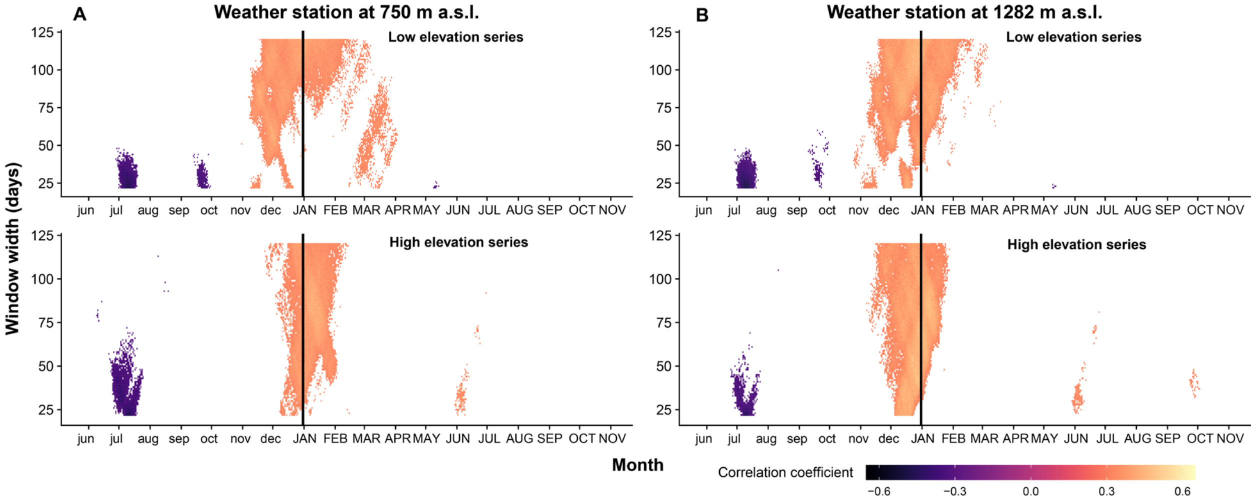

Figure 8.1 Correlation between TRW residual index chronologies and cumulative daily temperature from valley weather station (Joseni) (left) and from up-hill weather station (Bucin) (right) (vertical black line represents the limit between previous (with lowercase) and current (with uppercase) year)

Moreover, the TRW residual index chronology from low-elevation sites shows a positive and significant correlation with spring temperature (recorded in the valley) from March to April (r = 0.374, $p < 0.05$, n=41). For both chronologies, low and high elevation, a negative correlation between TRW residual index and mean temperatures is present in the previous vegetation season, in July. The maximum negative correlation between TRW residual index chronologies and previous summer temperature varies from $r = -0.502$ ($p < 0.05$, n=41) for low-elevation series (temperature from the up-hill weather station) to $r = -0.462$ ($p < 0.05$, n=41) for high-elevation series (temperature from the up-hill weather station). A significant negative correlation between TRW index chronology and temperature in the previous autumn is present only at low-elevation sites, regardless of the weather station.

A positive correlation between the TRW index and December temperatures has also been reported for other forests in the Eastern Carpathians (Sidor et al., 2015). In mountainous regions, and mainly at high elevation, the growth of Norway spruce is usually positively correlated with summer temperatures (Bouriaud and Popa, 2009; Leonelli and Pelfini, 2008; Levanič et al., 2009; Ponocná et al., 2016; Savva et al., 2006; Sidor et al., 2015). The positive correlation between TRW index chronologies and winter temperatures at an elevation above 1500 m a.s.l. is not a common dendroclimatic pattern for Norway spruce. The possible explanation for this climate–growth relationship could be related to temperature inversion with a high frequency during winter.

The BAI residual index chronology correlation pattern differs depending on elevation (Fig. 8.2). The correlation between high-elevation BAI index chronology and winter temperatures recorded at the up-hill weather station is significant and has a higher value for the period of 26 November to 18 February. Interestingly, the positive correlation between winter–spring temperatures and the BAI index chronology from a low elevation is no longer significant when the temperatures are considered from the up-hill weather station. Regarding the high-elevation BAI index chronology, the correlation patterns in respect of mean temperatures from both weather stations are similar. In the case of the winter period, the correlation with temperatures from the valley weather station is significant for longer cumulative window lengths.

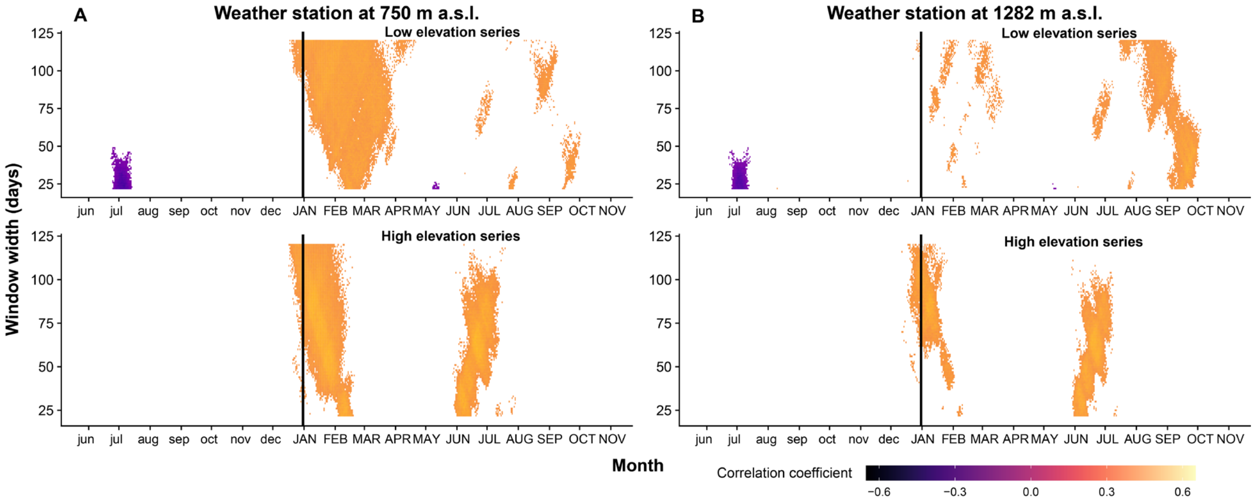

Figure 8.2 Correlation between BAI residual index chronologies and cumulative daily temperature from valley weather station (Joseni) (left) and from up-hill weather station (Bucin) (right) (vertical black line represents the limit between previous (with lowercase) and current (with uppercase) year)

Compared to the dendroclimatic pattern of TRW, a positive relationship with summer temperature was observed for BAI. The highest correlation was recorded between the BAI chronology from the high elevation and cumulative temperatures from the valley weather station from 17 May to 22 July ($r = 0.468$, $p < 0.05$, n=41). A positive correlation with summer temperature on the current year's wood accumulation is logical for high-altitude chronology, since temperature is a limiting factor for these habitats (Levanič et al., 2009). A negative correlation ($r = -0.507$, $p < 0.05$, n=41) between BAI residual chronology from lower sites and previous summer temperatures is significant for cumulative periods of 29 days (second half of June to the middle of July) for both weather stations. (Bouriaud and Popa, 2009) point out that higher temperatures during the summer can induce a high rate of respiration with negative effects on carbohydrate reserves used in the first phase of growth of the next year. The photosynthetic gain during the previous summer has a strong effect on current year ring width (Kozlowski and Pallardy, 1997; Selås et al., 2002).

A clear pattern of positive and significant correlation coefficient between temperature and BI chronologies was found only for the high-elevation chronology (Fig. 8.3). The highest correlation between the BI residual chronology from high-elevation series and summer/autumn from the up-hill station is 0.551, $p < 0.05$, n=41 for cumulative windows of 59 days (second half of August to the beginning of October). An unusual correlation was found between the BI index and winter temperature from the valley weather station. This may be a false-positive correlation because it is less likely that winter temperature has a strong influence on the wood density of latewood. The correlation between low-elevation BI chronology and mean temperature from the previous summer is negative and significant ($r = -0.481$, $p < 0.05$, n=41) for a cumulative window of 28 days; that is, 19 June–17 July. No significant correlation between BI index and previous year temperature was noted in the case of the high-elevation chronology.

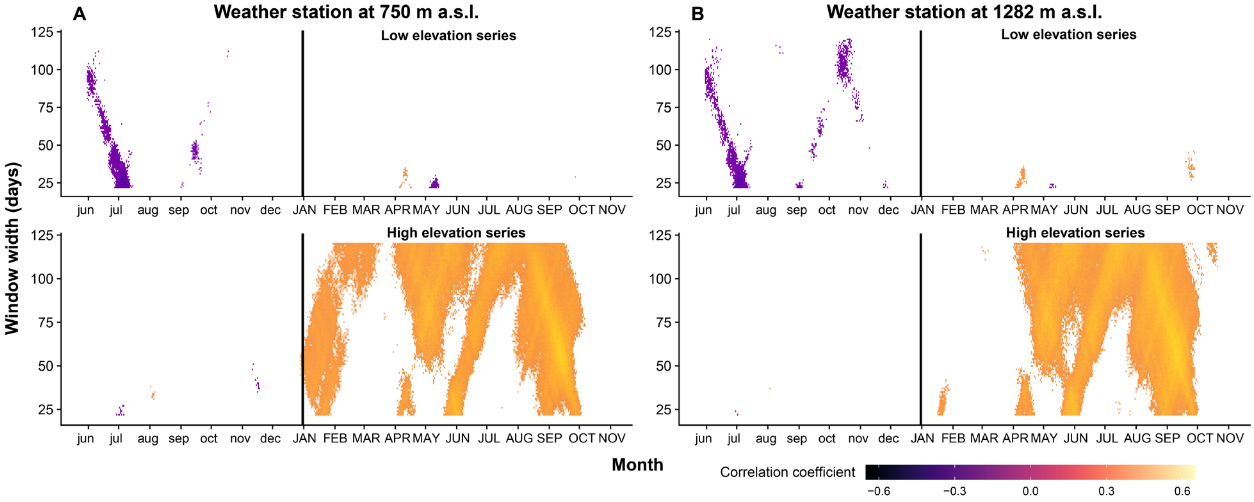

Figure 8.3 Correlation between BI residual index chronologies and cumulative daily temperature from valley weather station (Joseni) (left) and from up-hill weather station (Bucin) (right) (vertical black line represents the limit between previous (with lowercase) and current (with uppercase) year)

In contrast, at low elevation, the BI chronology shows almost no significant correlation with current year temperatures. This suggests that at elevations below 1000 m, in this intramountain valley, the late-summer temperature is not a limiting factor in the thickening and lignification of cell walls of Norway spruce. This can be linked to a longer growing season at lower-altitude sites and a higher stand productivity (Levanič et al., 2009). The highest correlation between tree-ring parameters and temperature has been reported for BI chronologies from the high elevation. These BI correlation patterns show that thickening of the secondary cellular wall and the lignification process at high altitude are driven by the late-summer temperature (Gindl et al., 2000). The negative relationship with the previous year's temperature can be explained by the trade-offs in the carbohydrate allocation for seed production, increment and formation of buds, with significant effects on nutrients reserves available for next year's growing start (Hacket-Pain et al., 2019; Matisons et al., 2021a). It has already been reported in the literature that BI chronologies, as surrogates for maximum latewood density, express a stronger relationship with climate compared to TRW at sites where the temperature is the most limiting factor (Nagavciuc et al., 2019; Știrbu et al., 2022).

Tree-ring width or basal area increment are tree-ring proxies containing aggregated information about the climate conditions throughout the whole growth season, and about disturbances. Meanwhile, the blue intensity contains information about the second part of the growing season. The combination of these three tree-ring proxies can offer an integrated perspective on the climate–growth relationship.

8.4 Conclusion

Our results show that each tree-ring proxy contains a different climate signal. In the studied intramountain valley in the Eastern Carpathians, the growth of Norway spruce is influenced by winter temperatures, and signals demonstrating this are present in both TRW and BAI chronologies. The presence of temperature inversions can explain the unusual correlation pattern. The TRW and winter temperature correlation is unstable through time for both elevations, with evident temporal shifts after 1996. The highest correlations for TRW were obtained for cumulative windows of 45 days at high elevation and for cumulative windows of 113 days for low elevation; both cumulative windows are centered at the beginning of January. The BAI at high elevation contains a strong temperature signal from the middle of the growing season. In the case of BI, a clear climatic signal was observed only for the high-elevation chronology for cumulative windows starting in the second half of August to the beginning of October. The preliminary results obtained in this study need to be replicated for other intramountain valleys in the Carpathians to confirm the change in the general dendroclimatic pattern (growth driven by summer temperature) due to specific local climate modulated by thermal inversions.

9. CONCLUSIONS, ORIGINAL CONTRIBUTIONS, DISSEMINATION OF RESULTS

9.1 Conclusions

In recent decades, climate change has become one of the main challenges faced by human society. Forests are among the ecosystems most vulnerable to environmental changes. At the same time, forests are instrumental in mitigating the negative effects of climate change. EU regulations (the European Green Deal and European Union Strategy on Adaptation to Climate Change) stipulate that all countries should achieve carbon neutrality by 2050. Based on these goals, it is crucial to understand how tree species react to global warming, how extreme events affect the resilience of trees, and what the adaptive capacities of forest ecosystems are.

In Europe, recent droughts have induced unprecedented dieback in forest ecosystems. These problems have posed significant challenges for the economic sector; at the same time, biodiversity and the provision of ecosystem services have been drastically affected. Consequently, major efforts have been made to understand the mechanisms behind this dieback. Due to the fact that changes in climatic conditions impact tree growth patterns, one of the most accurate methods of assessing past growth patterns is the use of tree rings.

One of the most widespread coniferous species in Europe, and simultaneously one of the top species affected by climate change, is the Norway spruce. In recent decades, spruce monocultures in Central Europe have experienced large-scale diebacks. Moreover, prediction models have shown that spruce is likely to be affected by bark beetle attacks as a secondary risk agent across Europe due to the continuous warming trend. These alarming signals have drawn the attention of both the research and production sectors. To be able to adapt current forest management practices and to implement climate-smart forestry, it is necessary to have updated information about spruce resilience, adaptive capacity, and response to climate change.

The Carpathians represent one of the largest and most continuous areas in which Norway spruce naturally occurs. Moreover, this mountain range forms the southeasternmost edge of its natural distribution in Europe. These factors corroborate the fact that in these regions, spruce dieback has been reported at lower scales in recent years, make the Eastern Carpathians the most suitable region in which to analyze the growth condition, resilience, and adaptive capacity of this challenged species.

The aim of this thesis was to evaluate the vitality and climate responses of managed even-aged spruce forest ecosystems in the Eastern Carpathians, thereby deriving updated information as a basis for developing sustainable forest management practices.

According to the identified knowledge gap and the proposed research objectives of this Ph.D. thesis, and based on its subsequent scientific results, the following conclusions can be formulated:

1. Regarding the growth dynamics of Norway spruce in the Eastern Carpathians in relation to elevation and age (Chapter 4 based on "Early warning signals indicate climate change-induced stress in Norway spruce in the Eastern Carpathians" Popa et al., 2024a)

Overall, the long-term growth of Norway spruce assessed based on the basal area increment (BAI) showed negative trends in 2002-2021 (defined as the late-warming period), highlighting a growth decline compared with the periods 1962-1981 (defined as the pre-warming period) and 1982-2001 (defined as the early-warming period). These negative trends were more pronounced at lower elevations. Moreover, younger stands were found to be more affected. These findings may be related to the dynamics of the BAI series but also to the historical management of spruce monocultures in Romanian forests.

Along with long-term growth trends during the same periods, the growth sensitivity (quantified by the first-order autocorrelation and standard deviation of BAI) showed that at elevations below 1400m a.s.l., first-order autocorrelation decreased in the late warming period, while this indicator increased at elevations above 1400m a.s.l. in the same period. Regarding the standard deviation of BAI, the highest values were found at lower elevations, indicating a more stressed condition of the spruce forest at these elevational bands.

Growth synchrony between trees, which indicates the climatic stress that forests face, has increased in recent decades. More specifically, in the last four decades, the highest growth synchrony was found at lower elevations (<800m a.s.l.), signifying an increased stress condition in the studied spruce forests. Interestingly, a continuous increase in growth synchrony in the last six decades was found at a high elevation (>1400m a.s.l.).

Overall, these findings suggest an intensification of the stress conditions that spruce forests face in the Eastern Carpathians. Even if the Norway spruce forests in the Eastern Carpathians look healthy and productive, our results indicate an increased vulnerability of this species.

2. Regarding resilience components of spruce in drought years along elevational and age gradients (Chapter 5 based on "Spruce suffers most from drought at low elevations in the Carpathians, though shows high resilience" – paper under review in Forest Ecology and Management journl)

In the context of increased drought frequency in Europe, the most severe drought years in the Eastern Carpathians were identified as 2012, 1987, and 2015. For these dry years, the spruce response to drought was quantified through resilience components: resistance, recovery, resilience, and recovery period.

Spruce resilience was shown to differ significantly in relation to the elevational gradient. Specifically, Norway spruce at low elevations (<800m a.s.l.) was characterized by the lowest resistance to drought, though it had a high recovery rate, while at high elevations (>1400m a.s.l.), a higher resistance was associated with a low recovery rate. Regarding the age of trees, it was found that older trees needed the longest time to recover from drought events.

The linear mixed-effect models highlighted the influence of water availability before, during, and after a drought event on spruce's ability to maintain its growth levels or to recover them in the case of any growth loss. Specifically, results showed that the climatic water balance during the drought has a strong impact on spruce resistance and resilience but a lower influence on recovery rate. On the other hand, as expected, the CWB condition two years before the drought negatively influenced resilience components; specifically, if conditions were favorable in the years before the drought, the spruce's capacity to maintain its growth or to recover decreased.

The implementation of the concept of the "line of full resilience" allowed an integrative assessment of resilience components and an efficient comparison of the response of spruce to drought in different years and in different elevational and age classes. Significant deviations of the "fitted line of resilience" from the theoretical "line of full resilience" were obtained, highlighting the vulnerability of spruce in drought years. Moreover, different thresholds were identified for spruce resistance, below which full resilience was not achieved. These results represent a scientific basis for adaptative forest management in the context of climate change.

3. Regarding climate–growth relationships of Norway spruce and non-stationarity in the last century (Chapter 6 based on "In pursuit of change: Divergent temporal shifts in climate sensitivity of Norway spruce along an elevational and continentality gradient in the Carpathians" – paper under review in Agricultural and Forest Meteorology Journal)

The temporal shifts of climate sensitivity (TSCS), mathematically defined as the slope parameter of the regression of climate sensitivity (the correlation coefficient) over time, allowed a comprehensive assessment of the degree of non-stationarity in the climate–growth relationships of spruce in the Carpathians. Specifically, differences in the radial tree growth of spruce were largely explained by the elevational gradient. In terms of climate–growth relationships, a significant summer temperature signal was observed in the two upper elevational belts in the early period, which largely disappeared in the late period. At low elevations (<800m a.s.l.), the signal of positive summer SPEI correlation became more frequent among sites toward 2021, while the strength of the positive winter SPEI correlation from the previous growing season weakened.

TSCS values were found to vary across different elevations, with some elevations showing an increase in sensitivity to temperature changes while others showed a decrease. Specifically, during late winter, high elevations exhibited a positive TSCS trend, whereas low elevations showed a decreasing trend that was partly negative. This indicates that high elevations are more sensitive to winter temperatures, while low elevations are less sensitive. Conversely, the opposite relationship was found for summer temperatures. Regarding the longitudinal gradient, TSCS was again observed to diverge from west to east.

Overall, these empirical results indicate that Norway spruce is increasingly being affected by climate change. In continuous warming scenarios, an increased water limitation is expected, by which this species is likely to be affected.

4. Regarding non-linearity in climate response of spruce (Chapter 7 based on "Non-linear response of Norway spruce to climate variation along elevational and age gradients in the Carpathians" – Popa et al., 2024)

Performing a Random Forest Analysis (RFA) as a multivariate non-parametric regression method of exploring the non-linearity of the relationship between RWI and seasonal climate (temperature and SPEI) enabled the visualization of the nature of the relationship between RWI and one climate variable while accounting for the average effect of the other predictors of the model. For the entire TRW network, the most important predictor in the RFA was the water availability index (SPEI). Moreover, the RFA revealed linear and non-linear patterns of the spruce growth and climate relationship. A relatively linear dependence of RWI was observed with previous growing season temperature (negative dependence), except at low elevations. Similarly, a linear dependence was reported for winter temperatures, with a slight decrease for the positive mean temperature at elevations <800m a.s.l. A bell-shaped dependence of RWI to previous autumn and current growing season temperatures was observed.

Overall, the analysis showed that non-linearity in climate–growth relationships was season-specific; that is, temperatures from the previous autumn and current growing seasons, along with water availability during winter, induced a bell-shaped response. Therefore, these results shed new light on the response of Norway spruce to climate in the Carpathians, which may aid in management decisions.

5. Regarding assessing climate–growth relationships based on different tree-ring parameters (Chapter 8 based on "Do Different Tree-Ring Proxies Contain Different Temperature Signals? A Case Study of Norway Spruce (Picea abies (L.) Karst) in the Eastern Carpathians" Popa et al., 2022)

Using the climatic data (temperatures) from two local weather stations located close to the study area provided better results than gridded climatic data. The comparison of climate–growth relationships based on daily climatic data and different tree-ring parameters allowed the identification of seasons in which spruce growth was most sensitive to temperatures. Specifically, the correlation coefficient between TRW chronology and the mean temperature had the highest value (r = 0.494) for the 3 December to 18 January period. The highest correlation between BAI chronology and cumulative temperatures was recorded for the period 17 May to 22 July (r = 0.468), while the highest correlation between BI residual chronology and summer/autumn temperature was 0.551 for cumulative windows of 59 days (second week of August to the beginning of October).

It was therefore established that different tree ring proxies capture different climatic signals. Consequently, different tree-ring parameters could be developed depending on specific research questions or study objectives. In recent years, much attention has been dedicated to developing BI chronologies worldwide since this parameter shows a stronger and more stable correlation with summer temperatures. The present research offers valuable information about Norway spruce growth and lignification processes in the Carpathians.

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In summary, through the research conducted in this Ph.D. thesis, updated information was obtained relating to Norway spruce's growth dynamics, its ability to resist—or recover after—drought events, as well as how its growth is influenced by climate. Importantly, it was shown how the relationship between the spruce growth process and climatic factors has evolved over time. Overall, the key finding is the indication that spruce-based forests in the Carpathian are already in a stressed condition due to climate change and continuous warming trends. In particular, the most stressful conditions were observed at lower elevations, with a gradual decrease of stress along elevational gradients. Under current climatic scenarios, urgent management practices are required to ensure a sustainable future for spruce forests.

9.2 Original contributions

Based on the research carried out in the Ph.D. thesis and on the conclusions obtained, the following original contributions are highlighted:

a) Development of one of the largest tree ring networks—with more than 3000 trees—for Norway spruce in managed forests in the Carpathians (Romania);
b) Evaluation of the application of the Early-Warning Signals (EWS) concept in identifying the potential decline of Norway spruce in managed forests along elevational and age gradients;
c) Application of a variance-covariance model for identifying the growth synchrony of trees in the context of increased stress caused by climate change;
d) Quantification of the variability of spruce resilience components along elevational and age gradients;
e) Calibration of linear mixed-effect models (LMMs) to identify the influence of water availability on spruce's ability to recover after drought events and predict how resilience components vary in relation to climatic water balance;
f) The use of the "line of full resilience" concept for an integrative assessment of Norway spruce resilience;
g) Development of a new method of assessing the temporal shifts of climate sensitivity (TSCS) of spruce, which can be replicated for other species to quantify the non-stationarity of climate–growth relationships;
h) A comprehensive assessment of climate–growth relationships of Norway spruce from managed forests along an elevational gradient based on climatic data (temperature, precipitation, and Standardized Precipitation-Evapotranspiration Index – SPEI) on a daily level;
i) The first evaluation in Romania of the non-linearity of climate–growth relationships of spruce using machine learning techniques;
j) Development of the TRW, BAI, and BI chronologies on the same cores for Norway spruce in the Eastern Carpathians;

k) Demonstration of the potential of BI chronologies for assessing the influence of late-summer temperatures on Norway spruce growth.

9.3 Dissemination of results

The results of the research carried out in this Ph.D. thesis were disseminated into seven scientific articles (3 published in peer-reviewed ISI-indexed journals in Q1, 2 published in BDI-indexed journals, and 2 under review at the time of submitting the thesis manuscript) and 10 international conferences, of which 6 were oral presentations, and 4 were poster presentations.

Scientific articles published based on the material of the thesis:

1. Andrei Popa, Ionel Popa, Cătălin-Constantin Roibu, Ovidiu Nicolae Badea, 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, 2022, no. 18: 2428. https://doi.org/10.3390/plants11182428, IF = 4.5

2. Andrei Popa, Ernst van der Maaten, Ionel Popa, Marieke van der Maaten-Theunissen, Early warning signals indicate climate change-induced stress in Norway spruce in the Eastern Carpathians, Science of The Total Environment, Volume 912, 2024, 169167, ISSN 0048-9697, https://doi.org/10.1016/j.scitotenv.2023.169167, IF=8.2

3. Andrei Popa, Ionel Popa, Ovidiu Badea, Michal Bosela, Non-linear response of Norway spruce to climate variation along elevational and age gradients in the Carpathians, Environmental Research, 2024, 119073, ISSN 0013-9351, https://doi.org/10.1016/j.envres.2024.119073, IF=7.7

4. I. Popa, A. Popa, A. Horvath, I. Ștețco, A. Korpos, Regional model for estimating the breast height diameter of Norway spruce as a function of stump diameter. Bucovina Forestieră 21(2):157-164, 2021, DOI: 10.4316/bf.2021.016, BDI indexed

5. Ionel Popa, Andrei Popa, Mihai Balabașciuc, Reziliența principalelor specii forestiere din Carpații Orientali la seceta din anul 2003, Revisat de Silvicultură și Cinegetică, 53, 2023, 5-11 BDI indexed

Scientific articles under review at the moment of thesis submission, based on the material of the thesis:

1. Andrei Popa, Marieke van der Maaten-Theunissen, Ionel Popa, Ovidiu Badea, Ernst van der Maaten, Spruce suffers most from drought at low elevations in the Carpathians, though shows high resilience, (Forest Ecology and Management, Q1, IF=3.7, under review)

2. Andrei Popa, Jernej Jevšenak, Ionel Popa, Ovidiu Badea, Allan Buras, In pursuit of change: Divergent temporal shifts in climate sensitivity of Norway spruce along an elevational and continentality gradient in the Carpathians, (Agricultural and Forest Meteorology, Q1, IF=5.6, under review)

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