Czech University of Life Sciences Prague

Faculty of Forestry and Wood Sciences

Spatiotemporal analysis of growth dynamics under climate change across European unmanaged forests

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Ph.D. THESIS ASSIGNMENT

Ing. Krešimir Begovič

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Spatiotemporal analysis of growth dynamics under climate change across European unmanaged forests

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Objectives of thesis

Primary montane forests and forests with high naturalness are an invaluable source of ecological data for studying the continuous impacts of global climate change on present-day forest landscapes. Understanding the effects of endogenous and exogenous drivers of tree growth is essential for projecting future forest dynamics and ecosystem functioning under shifting climatic constraints. Using extensive tree-ring datasets from a network of over 200 permanent study plots from primary mountain forest landscapes and nature forest reserves across Central-Eastern and Southeastern Europe, this Thesis aims to identify the intrinsic and extrinsic factors affecting tree growth at different spatiotemporal scales, with the overarching goal to extrapolate the significance of tree-level tradeoffs on contemporary forest dynamics, and disentangle the complex interactions between environmental controls and disturbance dynamics shaping contemporary forest ecosystem structure and processes. Specific objectives of the Thesis are:

1) Identify the general growth-climate associations using multiple tree-ring parameters, and analyze the climatic sensitivities, uncertainties, and growth patterns along an environmental gradient,

2) Explore the relationship between internal physiological tradeoffs (*i.e.*, growth-longevity tradeoff) and external mortality agents (*i.e.*, natural forest dynamics and climatic factors) shaping spatial forest structure and driving biomass accumulation under shifting climatic constraints,

3) Assess the species-specific responses to severe droughts and evaluate the significance of legacy effects on tree resilience and ecosystem dynamics along an altitudinal and latitudinal gradient.

Methodology

Each individual objective will have a distinct spatial and temporal scope. Sample plots will be selected from a network of permanent research plots established in primary forests in the Carpathian and Dinaric Mountains, as well as nature reserves across Czechia and Slovakia, using a stratified random sampling design. Field data collection will include recording of physiographic site and forest structural attributes, individual tree characteristics and extracting increment cores. Cores will be processed according to the established standard dendrochronological techniques, and ring widths will be accurately measured and dated. Tree-ring data will then be used to calculate disturbance parameters, life-history traits, reconstruct growth patterns and identify extreme climatic events. Statistical analysis will include correlation response analysis (linear and nonlinear methods), mixed-modelling techniques and nonparametric statistical tests.

The proposed extent of the thesis

150 pages

Keywords

dendrochronology, natural disturbance dynamics, primary forests, nature forest reserves, climate-growth relationships, growth-longevity tradeoffs, growth trends, drought legacy effects

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Recommended information sources:

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Prague on 04. 01. 2023

DECLARATION OF INDEPENDENCE

I hereby declare that this Ph.D. Thesis, titled “Spatiotemporal analysis of growth dynamics under climate change across European unmanaged forests”, was created independently and in an ethical manner. I declare all the information sources and literature have been indicated accordingly, and the Thesis was produced under direct supervision of my supervisor.

I agree with the disclosure of this Ph.D. Thesis according with Czech Law (Act No. 111/1998 Coll. Sb.) regardless of the Defense of Thesis results.

December 15th, 2022, Prague

SUMMARY

The past century has witnessed a global rise in greenhouse gas emissions and air temperatures, shifting hydroclimatic patterns, and increasing occurrence of climatic extremes. Disturbance regimes, as a key component shaping natural forest structure and driving individual tree growth dynamics, are concurrently changing rapidly with potentially dire consequences for forest ecosystem functioning and services, at the detriment of our socio-ecological systems.

This Thesis aimed to disentangle the complex interactions between the intrinsic (*i.e.*, physiological) and extrinsic (*i.e.*, environmental) drivers of tree growth in order to explore contemporary forest dynamics and landscape structure in Central-Eastern and Southeastern European unmanaged forests under changing environmental conditions. Using an extensive dendrochronological database from a network of over 200 permanent study plots, robust information about individual tree growth dynamics and growth response to shifting climatic constraints was derived in order to assess the impact of environmental changes on secondary wood formation, spatiotemporal variability in climate-growth sensitivity, contemporary forest structure and landscape dynamics, and ecosystem functioning.

At first, I examined the general climate-growth relationships of Norway spruce and silver fir in order to broaden the existing knowledge of growth-climate associations in mixed-species primary forests of the Dinaric Mountains (**Chapter 4.1**). Tree growth was mainly constrained by high temperatures and low precipitation and soil moisture during summer months in both species. I present strong evidence of the physiological weakening of Norway spruce trees under intensifying drought stress, that may lead to compositional shifts in favor of silver fir and carry major negative implications for the future development of the Dinaric primary mountain forests under increasing climatic and non-climatic perturbations.

Secondly, I analyzed the spatiotemporal variation in radial growth patterns from the Western Carpathian primary spruce forests to explore how growth-longevity tradeoffs, disturbance dynamics and recent global warming influence large old trees development and forest biomass accumulation (**Chapter 4.2**). I demonstrate that life-growth histories (*i.e.*, slow growth) and growth release events play an essential role for attaining multi-centennial lifespan in primary spruce forests and that, contrary to the general expectations, improving baseline conditions transcend age/size limitations for improved biomass accumulation, with significant implications for the future carbon sink role of primary mountain spruce forests.

Thirdly, I conducted a multi-parameter evaluation of drought impacts on Norway spruce and Scots pine growth across nature forest reserves in Czechia and Slovakia to infer conclusions about future resilience of Central European conifer forests under intensifying climatic constraints (**Chapter 4.3**). I show a clear dissociation of common growth patterns in temperature-limited Norway spruce mountain forests and increasingly moisture-limited Scots pine and Norway spruce montane and lowland sites, respectively, with a large site- and species-specific variability in growth sensitivity to shifting climatic constraints and response to extreme drought events, and pronounced legacy effects in wood formation during severe droughts.

Lastly, we systematically assessed the potential drivers of growth decoupling from climate (*i.e.*, non-stationarity), as well as its magnitude and extent, in Norway spruce and Scots pine temperate forests due to the unprecedented climate variability over recent decades (**Chapter 4.4**). We found that non-stationarity in growth-climate associations is a multifactorial phenomenon driven by the interaction of site climatic conditions, tree species, and methodological approaches to modelling climate-growth relationships. Future models should thus consider non-stationarity rather than stationarity as the baseline model of growth-climate associations in temperate forests.

The empirical findings from these studies are used to infer robust and concise conclusions about tree growth and forest ecosystem dynamics, and provide general recommendations for forest managers and conservationists for ecosystem-based management strategies that could ensure the preservation of forest ecosystem functioning, long-term carbon storage and biodiversity under global climate change.

Keywords: dendrochronology, natural disturbance dynamics, primary forests, nature forest reserves, climate-growth relationships, growth-longevity tradeoffs, growth trends, drought legacy effects

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This Thesis is a product of a six-year tumultuous journey at the Department of Forest Ecology at Czech University of Life Sciences Prague. From adventurous expeditions over valleys and mountain tops, long weekends exploring the nooks and crannies of sophisticated computer softwares, to the physical and psychological challenges of the sinuous and never-ending voyage towards academic and scientific maturity, this Thesis sums up my academic and personal explorations into the fundamental principles of ecological processes shaping one of the most complex and precious ecosystems on Earth – natural forests.

This journey has given me the opportunity to broaden my horizons and find inspiration through exchange of ideas and experiences during international conferences and collaborations with experts from around the world. It also allowed me to develop and hone the technical skills of wood processing that offers new avenues for systemic exploration of the impacts of environmental changes on tree growth and, consequently, forest ecosystems. Under the guidance and supervision of prof. Miroslav Svoboda, I found a scientific niche that fulfills my thirst for knowledge and allowed me to contribute to the global scientific community in improving the general understanding of intricate processes shaping natural forest ecosystems.

From colleagues and lab technicians to mentors and professors, it is impossible to acknowledge all the people who provided me with the much-needed support to be able to reach this moment, and so I say with utmost sincerity: “Thank you all!”.

Particularly, I say thank you to my family and to the love of my life, for accepting my virtues and flaws, tolerating my tantrums and doubts, and supporting me incessantly during these years with genuine honesty, constructive criticism and invaluable guidance.

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PREFACE

One felt as if there was an enormous well behind them, filled up with ages of memory and long, slow, steady thinking; but their surface was sparkling with the present: like sun shimmering on the outer leaves of a vast tree, or on the ripples of a very deep lake. I don't know, but it felt as if something that grew in the ground–asleep, you might say, or just feeling itself as something between root-tip and leaf-tip, between deep earth and sky–had suddenly waked up, and was considering you with the same slow care that it had given to its own inside affairs for endless years.

- JRR Tolkien, November 1954

INTRODUCTION

Rising temperatures and intensifying extreme climatic events, in part exacerbated by increasing anthropogenic CO_2 emissions over the last century, have caused pervasive shifts in global forest ecosystems over recent decades (IPCC, 2021; Steffen *et al.*, 2011). Forest ecosystems play a key role in the global carbon cycle due to their high carbon storage capacity (Pan *et al.*, 2011), and pertain the highest species diversity over many taxonomic groups (Lindenmayer *et al.*, 2006), but are now facing increasing risks due to intensifying disturbances triggered by extreme weather patterns, outbreaks of biotic agents and invasive species, and large-scale demographic shifts (*e.g.*, elevated mortality rates, species turnover, and/or physiological limits to growth). Furthermore, extreme climatic events exert disproportional effects on biogeophysical processes that directly facilitate forest ecosystem services and processes that contribute to human well-being, such as carbon uptake and biological variation of species (*i.e.*, biodiversity). Under rapidly changing climate, improved understanding of the diverse patterns and processes shaping forest landscape dynamics is needed before robust projections of global environmental impacts on future forest ecosystem functioning and development can be made.

Natural disturbances, defined as discrete events that disrupt the structure of entire populations, the developmental trajectories of an ecosystem, or change the resource availability in the physical environment, are fundamental components of forest structural development, biodiversity conservation and carbon dynamics (Franklin *et al.*, 2002; Nagel *et al.*, 2017; Turner, 2010; White & Pickett, 1985). However, rising frequency of severe and extreme climatic events have caused widespread tree mortality (Allen *et al.*, 2010; 2015; Phillips *et al.*, 2010; van Mantgem *et al.*, 2009), and led to progressive degradation of both managed and unmanaged forest landscapes in recent decades. Furthermore, contemporary trends in climate-change driven increase in drought frequency and severity could further reduce forested areas and compromise the role of forest ecosystems as the terrestrial carbon sink (Anderegg *et al.*, 2020; Ciais *et al.*, 2005). These global challenges necessitate identification and quantification of the underlying impacts of intensifying climate change on forest dynamics across biomes (Allen *et al.*, 2015; Latte *et al.*, 2015; Peltier *et al.*, 2016), in order to provide empirical information for policy-makers and implement adaptive management strategies that could mediate forest ecosystem carbon losses that would undermine the climate mitigation role of forest landscapes (Anderegg *et al.*, 2022; Lindenmayer *et al.*, 2017).

Forest preservation and sustainable land-use management have been highlighted as one the most viable climate mitigation strategies by the 2015 Paris Agreement (UNFCC, 2015). Primary forests and forests with high naturalness (*i.e.*, near-natural forests or unmanaged forests), characterized by a high degree of structural diversity and natural development of native species with no or negligible direct human impact, respectively (Mosseler *et al.*, 2003; 2011; White & Lloyd, 1994), have been widely recognized as areas of high ecological value. Due to a diverse offer of invaluable ecosystem functions and services, ranging from provisioning of mineral resources, oxygen, clean water, and critical habitats for a diversity of animal and plant species (Buotte *et al.*, 2019; Kulakowski *et al.*, 2017), to reductions of global greenhouse gas emissions and mitigating the impacts of rising CO_2, these forest ecosystems have been increasingly placed outside of intensive forest management practices (IUCN, 2020; Mikoláš *et al.*, 2019). Moreover, the absence of direct anthropogenic impacts on natural processes shaping forest structures make them an ideal reference for ecological research of global climate change impact on forest ecosystems.

Due to the complex interactions between various growth-influencing factors in unmanaged forests, quantifying growth-climate associations is challenging, yet insights into the regional growth responsiveness to intensifying climatic conditions will help predict how tree species and forest ecosystems adapt to the intensifying impacts of changing climate. A conceptual model put forward by Graybill (1982) and Cook (1985), termed the “linear aggregate model”, neatly summarizes the complexity of jointed interactions between intrinsic (endogenous) and extrinsic (exogenous) drivers of tree growth, highlighting climate as one of the integral components of tree growth variability. Furthermore, shifts in the impact of climatic drivers independently or synergistically (*i.e.*, by the interaction of multiple climatic and non-climatic factors) shape contemporary forest structure and alter forest dynamics (Seidl *et al.*, 2017). Therefore, abrupt changes in factors constraining tree growth could carry major implications for forest landscape functioning.

1.1. AIMS AND OBJECTIVES

This Thesis provides a composite of extensive studies of spatiotemporal variability in tree growth dynamics and forest ecosystem response to global climate change across Central-Eastern and Southeastern European unmanaged forests. Disentangling the relative contributions of endogenous and exogenous drivers on internal physiological processes driving tree growth is crucial before strong conclusions can be made regarding the ramifications of global climate change on emergent forest ecosystem properties. The results of the Thesis provide an outline for helping nature conservationists make realistic assessments of forest ecosystem resilience, and management practitioners to produce reliable predictions of future forest dynamics under projected climate scenarios.

Specific objectives of the Thesis were:

1) Identify the general growth-climate associations using multiple tree-ring parameters, and analyze the climatic sensitivities, uncertainties, and growth patterns along an environmental gradient,
2) Explore the relationship between internal physiological tradeoffs (*i.e.*, growth-longevity tradeoff) and external mortality agents (*i.e.*, natural forest dynamics and climatic factors) shaping spatial forest structure and driving biomass accumulation under shifting climatic constraints,
3) Assess the species-specific responses to severe droughts and evaluate the significance of legacy effects on tree resilience and ecosystem dynamics along an altitudinal and latitudinal gradient.

LITERATURE REVIEW

2.1 DENDROCHRONOLOGY – DISCIPLINE, A TOOL, AND ITS APPLICATION

Dendrochronology is one of the most important environmental recording techniques for a variety of natural environmental processes, and can be defined as a discipline focused on reconstruction of past events from the measurable impacts on tree growth and tree-ring structure (Douglass, 1946; Speer, 2010). Using tree-rings as a monitoring proxy, dendrochronology provides long-term records of internal and external processes affecting trees, both environmental and physiological in nature (Biondi, 2020). Knowledge of the principles and methods of tree-ring analysis have found utility across a range of topics and temporal scales, from reconstructions of past climate variability (*i.e.*, dendroclimatology; Hughes *et al.*, 2011), and chronological dating of archaeological structures and provenance tracing (*i.e.*, dendroarchaeology; Douglass, 1929), to recording natural ecological processes in forest ecosystems (*i.e.*, dendroecology; Fritts & Swetnam, 1989), and analysing past variability in biochemical composition in tree-rings to infer environmental fluctuations (*i.e.*, dendrochemistry; Cutter & Guyette, 1993).

One of the fundamental principles of dendrochronology is tree-ring cross dating, which is a technique of providing accurate calendar date to each individual tree-ring based on the variation of tree-ring widths within a population. To be able to extrapolate the information captured by tree-rings for analysis of environmental processes, dendrochronological dating is complemented by the concept of replication, *i.e.*, minimum number of samples supporting the designation of a calendar date to a tree-ring for a reliable production of a chronology (*i.e.*, site-representation of tree growth), and the principle of the limiting environmental factor of tree growth (based on Liebig’s law of the minimum; Speer, 2010). Furthermore, since tree-rings represent radial growth increase in stem size over time, they can also be used to reconstruct size development and growth rate trends over time (Husch *et al.*, 2003).

Tree growth is a product of assimilation of natural resources and complex physiological and chemical reaction sequences that propagate cell division and expansion in the meristematic cells, ultimately forming a tree-ring. In European temperate zone, tree-rings are produced annually, and most of tree-ring growth occurs from early spring to late summer/early autumn, indicating the inherent dependence of endogenous processes driving tree growth to environmental conditions (Fritts, 1976). The underlying principle of tree growth sensitivity to environmental variability, visible through the formation of anomalously narrow/wide tree-rings, is the basis for extracting dendrochronological information and extrapolating predictions of forest productivity and dynamics, carbon allocation, and growth response to environmental stress (Dobbertin, 2015; Hughes *et al.*, 2011). However, trees are individualistic biological entities that are driven by temporally variable intrinsic and extrinsic processes, which can obscure the interpretations of climatic or ecological processes recorded in annual tree-rings (Carrer, 2011; Meinzer *et al.*, 2011).

2.2 ON TREE GROWTH

Tree growth tends to be highly modular under temporally variable environmental conditions, and the physiological pathways under such nonlinear conditions are primarily determined by allometric patterns, phenotypic plasticity, and biomechanical constraints on tree growth (*i.e.*, maximum tree size; Koch *et al.*, 2004; Weiner & Thomas, 2001; Weiner *et al.*, 2004). When trees grow under favourable conditions, partitioning of resource allocation to growth versus survival leads to rapid growth rates due to ample resources access (Arendt, 1997; Coley *et al.*, 1985; Loehle, 1988), but at the cost of reduced investments into defensive compounds, mechanical and hydraulic tissues that favour stress tolerance (Bigler, 2016; Kleczewski *et al.*, 2010), resulting in long-term exposure to size-dependent risk factors, external mortality agents and, ultimately, shorter lifespan (Bugmann & Bigler, 2011; Ryan & Yoder, 1997). However, the plasticity in allocation patterns, *i.e.*, the extent to which trees that were previously acclimated to resource-limited growing conditions shift into rapid growth when growing constraints are alleviated, has rarely been tested in unmanaged forests (*e.g.*, Pretzsch, 2021).

Age is one of the fundamental variables used for modelling physiological pathways and individual tree growth dynamics, as well as predicting forest ecosystem structural changes and carbon dynamics. As trees age, they undergo complex physiological and morphological changes, mostly visible reduced photosynthetic and growth rates, leaf size reduction, and metabolic shifts due to changes in tree size and internal structural complexity (Ryan *et al.*, 1997; Stearns, 1992). However, the cambial meristem appears to be immune to the onset of senescence, defined as deterioration in tree performance based on the internal biological clock (Mencuccini *et al.*, 2014), indicating tree senescence and growth decline, and ultimately tree mortality, are a function of metabolic changes intrinsically connected with changing tree size and environmental stressors (Munné-Bosch, 2008; 2018). This carries major implications on the interpretation of tree longevity in natural forest landscapes, as well as for the predictions of forest structure and carbon dynamics under climate warming (Körner, 2017).

The growth-longevity tradeoff (*i.e.*, growth-mortality tradeoff), seen through the distinct negative association between age and size with growth, has been extensively described and suggests that intrinsically slow or suppressed growth leads to longer lifespan (Schulman, 1954). Furthermore, unfavorable environmental conditions (*e.g.*, low temperatures, poor site quality) have been considered a pre-requisite for achieving old age (Rotheli *et al.*, 2012; Suarez *et al.*, 2008). However, studies of the growth-longevity tradeoffs have generally focused on mean growth as an indicator of tree longevity (*e.g.*, Bigler & Veblen, 2009; Black *et al.*, 2008; Brienen *et al.*, 2020; Di Filippo *et al.*, 2012; Johnson & Abrams, 2009), yet tree growth is extensible under changing environmental conditions. Furthermore, studies of the growth-longevity tradeoffs in naturally developing forests are somewhat restricted due to the scarcity of large old trees or general inaccessibility (Frelich & Reich, 2003). In such ecosystems, drivers of forest dynamics, such as disturbances, directly shape the forest structural elements that alter the competitive interactions between trees over time, changing the growing conditions that influence attainability of old age (Landis *et al.*, 2005; Rohner *et al.*, 2013; Rozendaal *et al.*, 2010). However, additional regional drivers of tree growth have seldom been considered when assessing tree longevity or deriving the general implications of the growth-longevity tradeoff on the emergent forest properties such as productivity and carbon storage (*e.g.*, Di Filippo *et al.*, 2015).

Tree growth is inherently dependent on environmental variability in climate, soil, and atmospheric composition (Trouillier *et al.*, 2020). Over the last several decades, climate-warming induced increase in tree radial growth has been reported over various forest ecosystems across the European temperate zone (*e.g.*, Bošel'a *et al.*, 2018; Hofgaard *et al.*, 1999; Martinez-Vilalta *et al.*, 2008; Rolland *et al.* 1998; Shestaková *et al.*, 2016; Spiecker, 1996; Stephenson *et al.*, 2014; Voelker *et al.*, 2006; Schurman *et al.*, 2019). Phenological shifts and higher late spring/summer temperatures have extended the photosynthetically active period, thus increasing cell division and expansion, leading to enhanced wood formation and increased and prolonged tree growth. On the other hand, intensifying climate warming has increased the frequency and severity of heatwaves and recurrent droughts across the European temperate regions (Allen *et al.*, 2010; Ciais *et al.*, 2005; Jones *et al.*, 2001). Recurrent droughts alter xylem and sapwood characteristics and impart chronic growth declines several years after the alleviation of growth limiting factors (*i.e.*, drought legacy effects; Anderegg *et al.*, 2015).

Furthermore, resource allocation patterns under stressful growing conditions are coupled with trees' carbon status (Ogle & Pacala, 2009), indicating tree growth is additionally limited either by the amount of useable carbon within trees (*i.e.*, source limitation), or by the tree's capacity to actively utilize available carbon when under environmental stress (*i.e.*, sink limitation; Wiley & Helliker, 2012).

Thus, disentangling the effects of intrinsic (*e.g.*, size and age) and extrinsic (*e.g.*, climate) factors affecting tree growth has naturally become one of the key challenges in forest ecology (Coomes & Allen, 2007). The effects of the unprecedented 20th century global warming are generally species- and site-specific, but carry broad ramifications for future growth trajectories of individual trees and forest ecosystems. Moreover, understanding long-term growth trends under past environmental conditions is essential for robust predictions of future global carbon cycles, forest productivity and climate change impacts on ecosystem functioning. Due to the structural complexity of forest ecosystems (particularly unmanaged forests), as well as general growth-mortality tradeoffs, divergent forest dynamics and varying rates of environmental change from site- to landscape-level, ecological studies from extensive networks of permanent plots across different European temperate regions, and utilization of large multi-parameter tree-ring datasets, are indispensable for understanding the general patterns of global climate change and developing adaptive management strategies to mitigate the impacts of the intensifying environmental perturbations.

2.3 PRIMARY FORESTS AND NATURE FOREST RESERVES

Primary forests (*i.e.*, old-growth forests, virgin forests) represent forest communities that have been developing under complex natural disturbance dynamics without direct human activity (White & Lloyd, 1994), and exhibit unique ecological features and ecosystem services indicative of high naturalness (*e.g.*, heterogenous age and size distributions, abundance of snags and coarse woody debris, distribution of canopy gaps, etc.; Meigs *et al.*, 2017; Mosseler *et al.*, 2003; 2011; Nagel *et al.*, 2010). Mostly distributed in remote valleys and on steep mountain slopes across broad mountain ranges, primary forests are unique natural forest ecosystems containing substantial carbon storage and providing an invaluable refuge for biodiversity conservation through provision of micro- and macro-habitats for numerous European endemic and endangered species (Franklin, 2002; Mikoláš *et al.*, 2019; Pregitzer & Euskirchen, 2004). Furthermore, they carry an important role in mitigating the effects of changing climate by acting as a significant carbon sink (Gunn *et al.*, 2014; Pan *et al.*, 2011), either through the process of carbon sequestration or through preservation of natural structural features which in turn support biodiversity.

In Europe, forested areas cover around 40% of total land area (~190 million ha), making Europe one of the forest-richest regions in the world. However, European forest landscapes have historically been heavily influenced by intensive management practices and expansion of human-populated areas, at the expense of reduced connectivity between natural forest areas (Hansen *et al.*, 2013; Mackey *et al.*, 2014; Piovesan et. al, 2005; Veen *et al.*, 2010). With the loss and/or degradation of natural forests, ecosystem services such as carbon mitigation, as well as diversity of forest species, decline concurrently at high rates (Muller *et al.*, 2019; Nagel *et al.*, 2017). Additionally, forest biodiversity and carbon storage are significantly affected by the changing climate patterns (Dixon *et al.*, 1994), as disturbances that act as drivers of heterogenous structural variation within forest ecosystems gradually increased in frequency and severity (Allen *et al.*, 2015; Kulakowski *et al.*, 2017). Today, primary forests have been increasingly identified and mapped around Europe, but only a small portion remains formally protected (*e.g.*, UNESCO World Heritage Sites; Mikoláš *et al.*, 2019), with mostly lenient control measures of customary logging activities (Knorn *et al.*, 2013; Sabatini *et al.*, 2018).

Primary forests provide unique historical data that can be evoked through retrospective studies of tree-rings at larger spatiotemporal scales than from managed forest landscapes. However, they are disproportionately scarce and generally heavily fragmented over wide areas that were anthropogenically impacted but remained inaccessible due to harsh and unfavourable terrains.

An increasing number of nature forest reserves with high naturalness (*i.e.*, ecosystem state close to naturally expected state; Winter, 2012) have been increasingly identified and protected in recent years across generally managed landscapes. Although robust inventory data from forest reserves is usually spatiotemporally limited to shorter time periods (Pretzsch *et al.*, 2019), and the contemporary forest structure and composition are unambiguously affected by past management (Dorren *et al.*, 2004; Mathys *et al.*, 2021), nature reserves can help improve the general knowledge of present-day forest ecosystem responses to environmental changes in the decadal-to-centennial absence of human interventions. Thus, nature reserves as natural forest landscapes provide an „environmental laboratory“ from which the implications of the changing ecological processes and shifting chronic ecosystem drivers, as well as anthropogenic impacts, can be inferred for forecasting impacts of global climate forcing and improving future forest management strategies (Bauhus *et al.*, 2009; McDowell *et al.*, 2020).

The Carpathian Mountains envelop one of the largest remnants of primary temperate forests in Europe (Svoboda *et al.*, 2014), ranking them highly valuable among European regions (Mikoláš *et al.*, 2019; Sabatini *et al.*, 2020). On the other hand, the Dinaric Mountains are the largest mountain range in the central-southern part of Europe and are located on the intersection between the moderately temperate continental climate and the Mediterranean climate. Nature forest reserves in Czechia and Western Slovakian represent near-natural forests with probable occasional logging in the past, but capture the large tree-ring variability since the beginning of the 20th century. Overall, these forest landscapes represent a range of spatially heterogeneous geological and climatic conditions, thus offering an ideal opportunity for scientific research of contemporary impacts of global climate change on natural forest dynamics in Central-Eastern Europe.

2.4 DRIVERS OF NATURAL FOREST DYNAMICS

2.4.1 DISTURBANCES AND DISTURBANCE REGIMES

The nature of unmanaged forests' vertical and horizontal structural complexity, richness in micro- and macro-related habitats, and microclimatic conditions promoting heterogenous deadwood composition and high carbon sink potential, lies in the varying spatiotemporal extent of disturbances and disturbance regimes (Frelich, 2002; Čada *et al.*, 2016; Mikoláš *et al.*, 2017; Sommerfeld *et al.*, 2018; Trotsiuk *et al.*, 2014). Disturbances are discrete abiotic or biotic (or a combination of both) events that disrupt the structure of a population or an ecosystem, altering the physical environment and/or shifting its developmental trajectory (White & Pickett, 1985). In contrast to singular disturbance events, a disturbance regime refers to the spatial and temporal dynamics of disturbance events over longer time periods, and are spatially and temporally characterized by disturbance size, intensity and severity, and disturbance frequency, return interval and rotation period, respectively (Turner, 2010).

At a local scale (*i.e.*, population or a site), disturbance-related processes drive local resource availability through canopy openings and tree mortality, shifting the competitive interactions between trees, modifying canopy ascension strategies of understory trees, and shaping their life-growth histories (Canham *et al.*, 1990; Nagel *et al.*, 2014). At a landscape scale, the nature of region's disturbances regime dictates forest age and size structural heterogeneity (Fraver *et al.*, 2009; Meigs *et al.*, 2017, Nagel *et al.*, 2017; Svoboda *et al.*, 2014), drives annual tree mortality (Reilly & Spies, 2016) and biomass accumulation rates (Calfapietra *et al.*, 2015; Nabuurs *et al.*, 2016), and directly affects forest biodiversity and ecosystem functioning (Schelhaas *et al.*, 2003). Disturbance spatial patterns are strongly modulated by topographic complexity and climate, generating a mosaic of small patches and heterogeneous structures across the landscape, which could carry an advantageous role for the long-term preservation of carbon storage (Senf & Seidl, 2018).

Stand-replacing disturbances are generally rare in Central European temperate forests, occurring sporadically and episodically within a return interval of several centuries (Frelich *et al.*, 2002). Instead, natural forest ecosystems are generally shaped by small-scale disturbances, *i.e.*, continuous-cover dynamics (or canopy gap dynamics; Stokland *et al.*, 2012). In such ecosystems, mortality and growth rates are considered in an approximate pseudo-equilibrium, where natural dynamics driving spatiotemporal variation in background mortality rates, deadwood distribution and decomposition rates, and forest structure are progressively changing over time and space. In Central Europe, European bark beetle (*Ips typographus* L.) outbreaks following windfall have been considered key disturbance factors driving forest dynamics (Holekša *et al.*, 2017; Janda *et al.*, 2017, Schurman *et al.*, 2018). However, climate-related disturbances have intensified over recent decades (Allen *et al.*, 2010; Mezei *et al.*, 2014; Nikolov *et al.*, 2014; Rouault *et al.*, 2006), and widespread mortality events associated with the changing climate (*e.g.* extensive forest disturbances in the Bohemian Forest national parks in Bavaria and Šumava; Čada *et al.*, 2013; Lausch *et al.*, 2011) indicate an increasing interplay between mortality and disturbance regimes in reorganization of forest structural parameters (*e.g.*, reduction in stand densities, increase in canopy openness, and standing and lying dead wood; Dale *et al.*, 2001; Luo & Chen, 2013; Peng *et al.*, 2011; Seidl *et al.*, 2014; Trotsiuk *et al.*, 2014). Whereas disturbances shape forest structure and alter forest dynamics (Seidl *et al.*, 2017; Turner, 2010), climate exerts a temporally dynamic influence on post-disturbance patterns over various spatiotemporal scales (Schurman *et al.*, 2018).

Thus, understanding the effects of historical disturbance regimes in the sphere of contemporary forest dynamics and ongoing intensifying climatic pressures is essential for successful development of future management strategies that would sustain and utilize the invaluable ecosystem services, such as biodiversity conservation, carbon sequestration, soil and avalanche protection, water and nutrient cycling, and wood production (Bengtsson *et al.*, 2000; Jactel *et al.*, 2012; Peltzer *et al.*, 2009). Furthermore, considering disturbance legacies in the interpretation of the climate-growth-disturbance relationships in natural forest landscapes is necessary for improved understanding of contemporary forest dynamics (Pan *et al.*, 2011; Bond-Lamberty *et al.*, 2014; Schurman *et al.*, 2018).

2.4.2 CLIMATE-GROWTH RELATIONSHIPS

Tree-rings are a natural archive of climatic and non-climatic factors influencing tree growth that are recorded as intra- and inter-annual ring width variability. The climate-growth relationships are based on comparing temporally robust site-level representations of tree growth (*i.e.*, reference chronologies) with local/regional climate data. The validity and reliability of growth-climate associations is predicated on the ecological principles of the limiting factor, concept of ecological amplitude and site selection, and the principles of standardization (Speer, 2010).

The principle of the limiting factor is based on Liebig's law of minimum, which simplifies the axiom that the physiological response of tree growth to environmental forcing is based on the factor which is most limiting to growth at a certain time. However, local climatic conditions can vary and interchange in effect size magnitude over time, thus complicating the interpretation of environmental processes. The concept of ecological amplitude is based on the environmental gradient of climatic conditions that determine the species' optimal range of growing conditions. Selecting sampling sites that are closer to species or population's edge of ecological amplitude are more likely to produce higher tree growth sensitivity to a particular climatic factor. However, other non-climatic interactions (such as competition and/or biotic disturbances) or biological limitations may have, or still are, affecting tree growth. Overlapping (non) flexible curves over decadal or long-term trends in tree-rings (*i.e.*, standardizing or detrending) can minimize the potential non-climatic influences (*i.e.*, noise) and maximise the signal of interest, through production of dimensionless tree-ring indices. However, surrendering the complete control to the frequency-removing growth curves and generalised standardization parameters can unrealistically distort the true size- or age-corrected inter-annual growth signal and induce temporal coherency bias in the resulting chronologies (Klesse, 2021).

In response to the emerging uncertainties and occurring limitations, tree-ring parameters other than tree-ring width, such as tree-ring density or stable isotopes, have been utilized to study the climatic signals preserved in tree-rings. The thickening and lignification of cell walls is directly affected by climatic conditions, and this climatic information can be extracted using techniques such as x-ray densitometry (*i.e.*, MXD; Schweingruber *et al.*, 1978) or light reflectance analysis (McCarroll *et al.*, 2002; Sheppard *et al.*, 1996). The image-based blue reflectance (or blue intensity) parameter represents a measure of reflected light in the blue wavelengths of the colour spectrum, which is directly related to tree-ring density. Due to its relative affordability, enhanced sensitivity to climatic conditions (*i.e.*, stronger inter-annual climatic response compared to ring width) and decreased susceptibility to the influences of non-climatic factors (*e.g.*, disturbances), it is arising as an important new parameter in dendroclimatological research (*e.g.*, Björklund *et al.*, 2014; Campbell *et al.*; 2007; 2011; Fuentes *et al.*, 2016; Jiang *et al.*, 2022; Rydval *et al.*, 2014; 2017a; 2017b; 2018; Wilson *et al.*, 2014). However, there has been a general lack of utilization of the BI parameter, particularly from naturally developing forests across the environmental gradients (*e.g.*, drought-prone environments).

In Central-Eastern Europe, growth-climate associations have been well established over the last century, with a predominantly temperature-limited growth at high-elevation sites (*e.g.,* Hartl-Meier *et al.,* 2014; Kaczka *et al.*, 2017; Ponocná *et al.*, 2018; Pretzsch *et al.*, 2014; Rybníček *et al.*, 2012), and a predominantly moisture-limited growth at lower elevation sites (Babst *et al.*, 2013; Lebourgeois *et al.*, 2010; Ponocná *et al.*, 2016; Trnka *et al.*, 2017). However, rapidly shifting climatic constraints in recent decades have independently or synergistically (*i.e.*, by the interaction of multiple climatic and non-climatic factors) have disproportionately affected forest dynamics across forest biomes (Fyllas *et al.*, 2017; Kramer *et al.*, 2000; Lindner *et al.*, 2010), causing demographic changes and distributional shifts of forest communities (Franklin *et al.*, 2016; Taylor *et al.*, 2017). Furthermore, accelerating environmental changes have also altered the previously established climate-growth relationships on a global scale, leading to non-linear and temporarily unstable relationships between tree growth and climatic factors (*i.e.,* non-stationarity or “the divergence problem”; D’Arrigo *et al.*, 2008), and reducing the validity of linear climate-growth response functions (Wilmking *et al.*, 2020). Due to the complexity of interactions between various growth-influencing factors in natural forest landscapes, disentangling the climate-growth relationships remains a challenge, yet insights into species-specific growth responses from various environments, and improving the general understanding of the extent of environmental change impacts on growth-climate associations, may help to predict how individual tree species will respond and adapt to the projected impacts of changing climate.

One of the major effects of intensifying climatic constraints across forest biomes is the increase in climate-driven tree mortality (Allen *et al.* 2010; 2015; Anderegg *et al.*, 2015). Extreme droughts have pronounced effects on forest ecosystem processes, from offsetting carbon cycle feedbacks (Cook *et al.*, 2015; Dai, 2011), reducing forest productivity (Anderegg *et al.*, 2020), and exacerbating the combined effects of rising vapor-pressure deficits, to decreasing soil moisture on tree growth (Cook *et al.*, 2014; Park-Williams *et al.*, 2013; Zscheischler *et al.*, 2018). However, studies of the impact of rising temperatures and shifting hydroclimatic patterns on growth dynamics of natural temperate forests with various geomorphological characteristics are somewhat lacking (Shestaková *et al.*, 2016). As hotter droughts, *i.e.*, low water availability combined with simultaneous high air temperature, are projected to increase in frequency and severity across the temperate zone (IPCC, 2021), forest ecologists and policy makers face unprecedented challenges to develop strategies that would mitigate the impacts of climatic perturbations on forest ecosystem functioning.

CONCEPTS AND METHODOLOGY

This chapter aims to present the fundamental concepts of study design, data collection strategies and methods of statistical analysis in a concise manner, which is necessary for interpreting the Thesis results. The first section (**3.1**) will present the study area, the second section (**3.2**) will describe the design of study plots and data collection strategies, whereas the third section (**3.3**) will briefly characterize the data preparation and processing techniques. The final section (**3.4**) will outline the statistical methods employed according to each particular aim established in the Introduction of this Thesis. A more detailed descriptions of methods and analysis can be found in the methodological subsections of individual studies (*i.e.*, subsections **4.1**, **4.2**, **4.3**, and **4.4**).

This Thesis was realized within the network of permanent study plots established as part of the REMOTE project (REsearch on MOuntain TEmperate forests; REMOTE, 2021), and the network of study plots established in nature forest reserves as part of a collaboration with the Faculty of Science at Charles University in Prague. The REMOTE project is a long-term international collaboration with study plots distributed across primary montane forests of Central, Eastern and Southeastern Europe. Primary forests are defined here as forests without signs of direct human impact, and where natural disturbances are the primary driver of forest structure and composition. Nature forest reserves are defined as forests exempted from active management over the course of the 20th century, but with probable occasional logging in the past.

3.1 STUDY AREAS

The Dinaric Mountains (*i.e.*, Dinaric Alps, or Dinarides) are one of the most rugged and extensive mountainous areas of Southeastern Europe, extending approximately 645 kilometers along the Western Balkan Peninsula, from the Julian Alps in the northwest, to the Sharr and Korab Massif in the south. Velebit is the largest mountain range in Croatia, located along the Adriatic coast as part of the north-western Dinaric Alps. It covers an elevational range of 518–1757 m a.s.l., and an area of about 2200 km^2. It is located on the climatic border between the moderately temperate continental climate and the Mediterranean climate and is characterized by abundant annual rainfall (2000–3000 mm/year on average), long snow retention, and relatively low average annual temperature (2–6 °C). The research study was conducted in Smrčeve doline primary forest (see section 4.1.2; Fig. 1), located inside the Northern Velebit national park, within an area characterized by hydrologically highly permeable soils and exceptionally rich Dinaric karst features. Norway spruce and silver fir form forest communities with European beech in Norway spruce-dominated forests on more humid, colder, and shadier sites, in sinkholes, and European beech-dominated rockier sites with shallow soils.

The Western Carpathians envelop one of the largest remnants of subalpine primary spruce forests in Europe (Mikoláš *et al.*, 2019; Svoboda *et al.*, 2014; Sabatini *et al.*, 2020). The study area consisted of monospecific Norway spruce primary forest stands, determined by the national inventory of primary forests in Slovakia in 2009–2010 (www.pralesy.sk) and 2013 –2015 primary forest inventory (Mikoláš *et al.*, 2019; Svoboda *et al.*, 2014), and spanned across a latitudinal (from 48° 31′ 47″ N to 49° 31′ 24″ N and 19° 12′ 45″ E to 20° 11′ 53″ E) and altitudinal range (from 1200 m a.s.l. to the upper forest limit, *i.e.*, around 1600 m a.s.l.), capturing the wide gradient of Norway spruce forest natural distribution, and the wide range of geographical and geological variability, regarding physiographic (*i.e.*, slope, aspect, altitude) and structural (*i.e.*, regeneration density, canopy cover) attributes, thus encapsulating the landscape heterogeneity of the Western Carpathians. The average annual temperature ranges from 2.5 to 4.5 °C, while the annual precipitation ranges from 1000 mm/year at the southernmost locality in the Polana massif, to 2400 mm/year on the northern slopes of the Tatra Mts (Bošel’a, 2010; Holekša *et al.*, 2017). Bedrock and soils varied, with podzols and leptosols atop of granitoids and limestones being the predominant soil types (see section 4.2; Table 1).

A wide range of Norway spruce and Scots pine naturally distributed sites were selected for the study of drought legacies in Central Europe, spanning across a latitudinal (from 48° 56′ 4″ N – 50° 53′ 23″ N and 13° 06′ 47″ E – 20° 26′ 29″ E) and elevational range (from 460 m a.s.l. to 1450 m a.s.l.). Sites were selected as representative of near-natural forest reserves, based on the presence of mature canopy trees and limited impact of past forest management activities (Treml *et al.*, 2016). Study sites were categorized according to the expected predominant climatic limiting growth factor into moisture-limited low-elevation sites (*i.e.*, < 650 m a.s.l) and temperature-limited high elevation sites (*i.e.*, > 900 m a.s.l). Given the broad geographical and environmental range of the study area, mean annual temperature ranged from 0.5°C - 5.8°C and 5.5°C - 8.8 °C at high elevation and low elevation sites, respectively, while the annual precipitation ranged from 530 mm/year at the westernmost locality in the Rabštejn area, to 1530 mm/year on the southern slopes of the Low Tatra Mts (see section 4.3.2; Fig. 2). Additionally, collected data from the Central European nature forest reserves was extended with 63 Norway spruce and 62 Scots pine tree-ring chronologies spread across south-Eastern, Central and Northern Europe from the publicly available International Tree-Ring Data Bank (ITRDB; Zhao *et al.*, 2019) and REMOTE Forest database (Schurman *et al.*, 2019), in order to assess the impacts of climatic conditions, tree species, and modelling approaches on the level of non-stationarity of climate–growth responses.

3.2 SAMPLING DESIGN AND DATA COLLECTION STRATEGIES

Mixed-species and monospecific stands were pre-surveyed for indicators of naturalness (*e.g.*, coarse woody debris in various stages of decay, pit-and-mound topography, etc.), and all available historical information regarding land use were collected to avoid areas with evidence of past logging and/or grazing. A series of permanent sample plots were established by superimposing a 100×100m grid with 1- or 2-ha cell sizes over each stand, and randomly placing a single sample plot withing the interior of each cell using ArcView 9.3 Environment (ESRI ArcGIS, 2011). Each circular plot covered an area of 1000 m^2 (in the Western Carpathians) or 1500 m^2 (in the Dinarides). In each circular sample plot, site parameters (*i.e.*, geospatial location, species, altitude, slope, and aspect), composition and structure of live and standing dead trees with diameter at breast height (DBH) ≥10 cm, and canopy status were recorded.

In the Dinarides, each circular sampling plot consisted of three nested circular subplots of varying radius, which determined the minimal DBH of trees chosen for coring. In the inner circle, all trees with a DBH > 6 cm were cored, in the intermediate circle trees with a DBH between 10 cm and 20 cm were cored, and in the outermost circle only trees with a DBH > 20 cm were cored. In the Western Carpathians, increment cores were collected from randomly selected 15-25 living and standing dead trees per circular sample plot, with DBH ≥10 cm. In the Central European nature forest reserves, increment cores were collected from 40-60 dominant and co-dominant trees per stand. In all study areas, one core per tree was extracted 1 m above the ground perpendicularly to the slope to avoid wood compression, using a 5 mm Haglöf/ Pressler increment borer.

3.3 DATA PREPARATION AND PROCESSING

Laboratory analyses were based on dendrochronological dating techniques described by Stokes & Smiley (1996). Increment cores were air-dried, mounted on wooden boards, and sanded with different grit-level sanding papers until reaching clear visibility of annual growth rings. Annual tree-ring widths were measured using a stereomicroscope to an accuracy of 0.01 mm with a Lintab-TM traversing measuring stage in tandem with TSAP-WinTM software (www.rinntech.de). Cores were visually cross dated using the marker year approach (Yamaguchi, 1991), followed by statistical validation using COFECHA (Grissino-Mayer, 2001; Holmes, 1983) and CDendro software (Larsson, 2015). The number of missing rings was estimated by fitting a geometric pith locator to the innermost rings and converting the distance to the theoretical pith into a number of missing rings (Duncan, 1989). Cross dating of individual series was based on measures of GFK (Gleichläufigkeit; Schweingruber, 1988), T-test, and Pearson's correlation coefficient.

Measurements of the blue intensity (BI) values were carried out on subsets of Norway spruce and silver fir samples from the Dinarides, and Norway spruce and Scots pine samples from the Central European nature reserves. Following resin extraction in acetone for 24-72 hours, samples were surfaced with sanding paper up to 1200 grit grade and scanned using an Epson Expression 10000 XL scanner combined with SilverFast Ai (v.6.6 - Laser Soft Imaging AG, Kiel, Germany) scanning software at a resolution of 2400 dpi. Before scanning, calibration of the scanner was performed with the SilverFast IT8 calibration procedure using a Fujicolour Crystal Archive IT8.7/2 calibration target to allow for comparability of measurement data between different scanners and research facilities, and prevent drift of BI measurements (Campbell *et al.*, 2011; Rydval *et al.*, 2014). A resolution of 2400 dpi was used for scanning. During the scanning process, samples were covered with a black, non-reflective cloth to prevent biases due to potential influence of ambient light (Rydval *et al.*, 2014). Finally, early wood BI and late wood BI measurements were performed using the CooRecorder measurement software (Cybis, 2019).

Tree-ring width (TRW) chronologies were developed for each study, species, site, and tree-ring parameter using the program ARSTAN (AutoRegressive STANdardization; Cook & Holmes, 1986), and/or the *detrend* function from the *dplR* package (Bunn, 2008; Bunn *et al.*, 2013) in R software (v. 4.1.0, R Core Team, 2021). To remove the age/size biological trend and retain the inter-annual to multi-decadal growth fluctuations, individual TRW series were standardized by fitting a negative exponential function with adaptive power transformation (Cook, 1985; Cook

& Peters, 1997), and the standardized individual series were averaged by year using Tukey's robust mean to produce standard chronology (Mosteller & Tukey, 1977; Cook *et al.*, 1995). To retain only high-frequency variability without the influence of autocorrelation (or non-climatic trends), an autoregressive model was applied, and dimensionless ring width indices (RWI) were calculated as ratios between the observed TRW and modelled values. The detrended series were also averaged by Tukey’s robust mean to produce residual chronologies. Rbar-weighted stabilization was imposed to stabilize potential changes in variance related to decreasing sample depth over time (Osborn *et al.*, 1997), and measures of mean inter-series correlation (rbar) and expressed population signal (EPS) were used to evaluate the robustness of the chronologies (Cook & Krusic, 2005; Wigley *et al.*, 1984). Standardization and calculation of BI chronologies was performed similarly to TRW data, with the exception that age-related growth trends were removed either by using 67-year cubic smoothing splines with a 50% frequency cut-off (in the nature-reserves data) or using a negative sloping linear curve (in the Dinarides data), in accordance with the BI standardization procedures applied in previous studies (*e.g.,* McCarroll *et al.*, 2002, Wilson *et al.*, 2014).

Additionally, basal area increments (BAI) were derived from individual tree-ring series from the Western Carpathians to quantify annual biomass production and preserve the long-term growth trends (Rubino & McCarthy, 2000). Basal area (BA) was calculated for each tree using the tree radius and formula for circular cross-section, and BAI was calculated as the difference between current and previous year BA values. In order to evaluate growth differences across age groups, each tree was assigned to a 50-year age class based on tree age at sampling. Mean decadal growth values of individual BAI series were calculated and averaged within each age class for allowing inter-class comparisons. Additionally, the mixed-modelling approach was adopted following Shestaková *et al.* (2014) to estimate regional growth synchrony value (âc), calculated for successive 30-year periods lagged by 5-year increments (Alday *et al.*, 2018). RWI chronology versions (*i.e.*, standard and residual) were developed by standardizing individual TRW series by fitting a cubic smoothing spline with a 50% frequency response over 100-year periods (Cook, 1985), and averaged the same way as previously described.

3.4 DATA ANALYSIS

3.4.1 IDENTIFY THE GENERAL GROWTH-CLIMATE ASSOCIATIONS USING MULTIPLE TREE-RING PARAMETERS, AND ANALYZE THE CLIMATIC SENSITIVITIES, UNCERTAINTIES AND GROWTH PATTERNS ALONG AN ENVIRONMENTAL GRADIENT

Due to limited availability of instrumental climate data from local meteorological stations in the Dinarides and the Western Carpathians before the mid-1900s, CRU TS gridded 0.5° instrumental climate datasets (Climate Research Unit Time Series; https://climexp.knmi.nl/start.cgi) for the 1901–2014 (2018) period were obtained from KNMI Climate Explorer in order to assess climate-growth relationships (Harris *et al.*, 2014; Trouet & Van Oldenborgh, 2013). Temperature (average monthly temperature), precipitation (monthly totals) and self-calibrating Palmer Drought Severity Index (scPDSI; Wells *et al.*, 2004), which integrates available temperature and precipitation data to estimate relative drought, were obtained for the location of each study site. Climatic information for the assessment of climate-growth relationships in the Central-European nature reserves was obtained through geospatial interpolation (precipitation data) or orographic regression (temperature data) of available meteorological data from the nearest local weather stations for the period 1950-2018. The standardized precipitation evaporation index (SPEI) was computed using the Thornthwaite method following Vicente-Serrano *et al.* (2010). For the ITRDB database, station data were not publicly available, so the climatic data was acquired as daily resolved air temperature and precipitation data from the EOBS v22.0 gridded database with a resolution of 0.1° x 0.1° (Cornes *et al*., 2018).

Pearson's correlation coefficients were used to quantify the linear relationship between the RWI chronologies and temperature, precipitation, and moisture indices (*i.e.*, scPDSI in the Dinarides and Western Carpathian, and SPEI in the Central European nature forest reserves, respectively) within the previous and current year of growth, including summer seasonal windows which represent the mean values of climatic variables aggregated over summer months (June - September). Where available, the analysis was conducted for both the residual and standard chronology variants, as well as for BI chronologies. Temporal stability of the climate-growth associations was assessed over the studied periods by computing Pearson's correlation coefficients over 31-year moving window segments. Additionally, linear regression modelling and non-linear process-based models of wood formation (each at daily and monthly temporal resolution) were utilized to predict ring-width chronologies based on soil moisture, precipitation, and temperature. The temporal coherence (*i.e.*, stationarity) was then compared between models, climates, and species using bootstrapped transfer function stability tests (Buras *et al.*, 2017).

Climate-growth relationships were further investigated by assessing the influence of climatic extremes on tree growth through identification of pointer years (in the Dinarides data). Pointer years were detected using the dual-method approach: based on the threshold of +/- 2 standard deviations from the mean RWI value each year (Huber & Giertz-Siebenlist, 1969), and using the Cropper method (Cropper, 1979), which is based on the critical level threshold of 0.75 standard deviations and a 5-year indexation window. Pointer years were contextualized by overlapping against most responsive climatic variables from the climate-growth response analysis and referenced to the available historical data. More details on the quantification of the climate-growth relationships can be found in the subsections of the Results section (see sections 4.1.2, 4.2.2.4.2, 4.3.2 and 4.4.2).

3.4.2 EXPLORE THE RELATIONSHIP BETWEEN INTERNAL PHYSIOLOGICAL TRADEOFFS (*i.e.,* GROWTH-LONGEVITY TRADEOFF) AND EXTERNAL MORTALITY AGENTS (*i.e.,* NATURAL FOREST DYNAMICS AND CLIMATIC FACTORS) SHAPING SPATIAL FOREST STRUCTURE AND DRIVING BIOMASS ACCUMULATION UNDER SHIFTING CLIMATIC CONSTRAINTS

A series of linear regressions and mixed effect models were conducted to disentangle and quantify the effect sizes of drivers of tree age and growth in the Western Carpathians. Detailed descriptions of each individual predictor and its calculation can be found in the Results chapter (see section 4.2.3, subsection 4.2.3.4.1 Predictor variables).

At first, linear regression functions were fitted to the mean juvenile tree growth rates of all living and dead trees and compared against tree age and tree size (DBH), to identify the general tradeoff between productivity (*i.e.*, growth) and lifespan (*i.e.*, longevity). Additionally, the effects of age and time on early life mean decadal growth rates and age were tested using linear mixed-effect modelling with nested random effect structures to account for the hierarchical design of the study. Secondly, two separate generalized linear mixed-effects models (GLMM) were built to identify the most influential drivers of age (*i.e.*, "the longevity model") and recent growth trend of large old trees (*i.e.*, during the period of high regional temperature-growth synchrony; "the growth model").

The longevity model was fitted using a GLMM with a generalized Poisson distribution to account for data under dispersion, with age as the response variable and tree size (DBH), growth histories (*i.e.*, mean juvenile growth and relative suppression), competition index, disturbance factors (*i.e.*, disturbance severity and disturbance year), and site attributes (*i.e.*, slope and northness) as predictors. Only stand identity was considered as a random component of the model.

The growth model was fitted by a GLMM with Gaussian distribution and log-transformed annual BAI values of individual trees as a response variable. Tree age, tree size (*i.e.*, DBH), cumulative dynamic index, site attributes (*i.e.*, slope, aspect, and bedrock), and disturbance factors (*i.e.*, disturbance severity and disturbance year) were included as predictor variables, along with the monthly climate data of the most significant climatic drivers from the climate-growth response analysis (see section 4.2.4; Fig. 5). The random effect structure was identical to the linear mixed effects models of decadal growth (*i.e.*, trees nested in plots and plots nested in stands).

Individual predictor variables were sequentially excluded from the modelling analysis based on potential multicollinearity issues confirmed using the Spearman's correlation coefficients and variance inflation factors (Dormann *et al.*, 2013). Remaining predictors, based on the initial hypotheses and ecological interpretation, were fitted using maximum likelihood method (ML). Predictors were scaled (*i.e.*, *z*-score) prior to modelling to ensure comparability across effect sizes. Each predictor was individually dropped from the model to quantify their relative importance on the model fit based on differences in AIC and *p*-values (Chi-square test; Zuur *et al.*, 2009). The final models with remaining predictors were refitted using restricted maximum likelihood (*i.e.*, REML). Residuals were assessed for potential heteroscedasticity, zero inflation, and overdispersion by visual inspection of residual plots and graphical analysis (see Supplementary data S2, Fig. S8; Zuur *et al.*, 2009), as well as for temporal autocorrelation of residuals in the growth model using the Durbin–Watson test. Model performance was evaluated based on the proportion of variance accounted for by fixed effects only and fixed and random effects, following Nakagawa & Schielzeth (2013). Data analysis and model fitting were performed using R software (R Core Team, 2021) and the internal packages (see section 4.2.2, subsection 4.2.2.4.3 Linear regression modelling).

3.4.3 ASSESS THE SPECIES-SPECIFIC RESPONSES TO SEVERE DROUGHTS AND EVALUATE THE SIGNIFICANCE OF LEGACY EFFECTS ON TREE RESILIENCE AND ECOSYSTEM DYNAMICS ALONG AN ALTITUDINAL AND LATITUDINAL GRADIENT

Linear response analyses tend to underestimate the non-homogeneity (nonlinearity) in climate-growth relationships over time (D’Arrigo *et al.*, 2008), potentially leading to confounding interpretations of contemporary growth-climate associations. Thus, to improve the interpretation of the dominant climatic controls on inter-annual growth variability of Norway spruce and Scots pine, a process-based forward model was applied over the period 1940–2018 (*i.e.*, VS-lite model; Tolwinski-Ward *et al.*, 2011; 2013). VS-lite model is built around partial growth responses to temperature and moisture as growth drivers, in order to simulate annual tree growth rates at a monthly temporal resolution using nonlinear equations. The main parameters for temperature (T1, T2) and moisture (M1, M2) determine the climatic minima for cambial activation and maxima for optimal growth under the respective climatic driver (Rossi *et al.*, 2007; 2009). The interplay between temperature and moisture is further modulated by the third parameter, latitude (gE), theoretically representing the available sunlight for photosynthesis. The VS-Lite model was calibrated separately for each site by splitting the studied period into the calibration interval for parameter optimization (1940/1950–1979) and the verification period for prediction of site chronologies (*i.e.*, 1980-2018). Additionally, average partial monthly growth responses to temperature and moisture over a 20-year moving window period (*i.e.*,1940–1959, 1960–1979, 1980–1999, 2000-2018) were calculated to elucidate the impacts of shifting climatic constraints on tree growth. VS-lite modelling and model parametrization was done using the “*VS-Lite*” MATLAB scripts published by Tolwinski-Ward *et al.* (2011).

Climate-growth relationships in Central European nature reserves were additionally examined by investigating the influence of climatic extremes on tree growth through superposed epochal analysis (SEA). SEA is based on compositing and averaging matrices of high-frequency response signals to extreme events within a specified time window (D’Arrigo *et al.*, 1993). Mean epochal responses of RWI and BI chronologies were calculated for each species and site, and a 10-yr window was applied around the event year, covering the span of 5 years pre-drought and post-drought event. Extreme drought years were identified as severe deviations of the regional mean moisture index for the coordinates of the region.

RESULTS

The results of the Thesis are divided into four subsections composed from published studies or manuscripts currently under development. Each subchapter represents a separate individual study *in lieu* of the overarching aims of the Thesis. The published manuscripts are included in their originally published format:

Chapter 4.1: **Begović, K.**, Rydval, M., Mikac, S., Čupić, S., Svobodova, K., Mikoláš, M., Kozák, D., Kameniar, O., Frankovič, M., Pavlin, J., Langbehn, T., & Svoboda, M. (2020). Climate-growth relationships of Norway Spruce and silver fir in primary forests of the Croatian Dinaric mountains. *Agricultural and Forest Meteorology*, 288–289, 108000.

Chapter 4.2: **Begović, K**., Schurman, J. S., Svitok, M., Pavlin, J., Langbehn, T., Svobodová, K., Mikoláš, M., Janda, P., Synek, M., Marchand, W., Vitková, L., Kozák, D., Vostarek, O., Čada, V., Bače, R., & Svoboda, M. (2023). Large old trees increase growth under shifting climatic constraints: Aligning tree longevity and individual growth dynamics in primary mountain spruce forests. *Global Change Biology*, 29(2), 143 –164.

Chapter 4.3: **Begović, K.**, Rydval, M., Tumajer, J., Jumei, Y., Svobodova, K., Langbehn, T., Čada, V., Treml, V., & Svoboda, M. (*manuscript under development*). Spatiotemporal changes in drought sensitivity captured by multiple tree-ring parameters of Central European conifers.

Chapter 4.4: Tumajer, J., **Begović, K.**, Čada, V., Jenicek, M., Lange, J., Mašek, J., Kaczka, R.J., Rydval, M., Svoboda, M., Vlček, L., & Treml, V. (2023). Ecological and methodological drivers of non-stationarity in tree growth response to climate. *Global Change Biology*, 29(2), 462-476.

Manuscripts that are not included in this Thesis, yet contributed to the overarching story:

Jiang, Y., **Begović, K.**, Nogueira, J., Schurman, J.S., Svoboda, M., & Rydval, M. (2022) Impact of disturbance signatures on tree-ring width and blue intensity chronology structure and climatic signals in Carpathian Norway spruce. *Agricultural and Forest Meteorology*, 327, 109236.

4.1 CLIMATE-GROWTH RELATIONSHIPS OF NORWAY SPRUCE AND SILVER FIR IN PRIMARY FORESTS OF THE CROATIA DINARIC MOUNTAINS

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Abstract: The past century has witnessed a global trend of increasing greenhouse gas emissions, causing a rise in temperatures, changing hydroclimatic patterns and increasing occurrence of climatic extremes. Despite their importance for environmental conservation, scientific research and forest management, primary montane forests of the Dinaric Mts remain insufficiently studied.

In this study, we examined the relationship between climate and growth of Norway spruce (*Picea abies* (L.) H. Karst.*)* and silver fir (*Abies alba* Mill.) in the primary forests of Smrčeve doline, located in Northern Velebit National Park, Croatia. Using dendrochronological methods, the temporal relationships between tree-ring width (TRW) and blue intensity (BI) were assessed over the 1901-2014 interval, in relation to instrumental climatic data, including temperature, precipitation and self-calibrating Palmer Drought Severity Index (scPDSI).

TRW and earlywood BI (EWBI) chronologies of both species exhibited a clear negative response to summer temperatures, while also showing a positive relationship with summer precipitation and moisture, implying that tree growth in the region is water limited. Generally, correlation values of EWBI were stronger compared to the TRW chronologies. Although both species showed a degree of common growth response to climatic extremes, the strength of correlations with the most responsive climatic variables was temporally unstable and showed considerable variability in both tree-ring parameters. The observed differential response of the two species to climate indicates that the anticipated increase in dry conditions could potentially alter the future development and composition of these primary forests by shifting competitive pressures in favour of silver fir. Increasing drought stress around the Mediterranean could have major negative implications for these water-limited primary forests.

4.1.1 INTRODUCTION

Primary forests (*i.e.*, old-growth forests) represent forest communities that have attained high age through natural development, largely untainted by direct human activity over time, while still exhibiting unique ecological features and offering a diverse range of ecosystem services (White and Lloyd 1994, Mosseler *et al.* 2003, 2011; Kulakowski *et al.* 2017). They are characterized by a high degree of vertical and horizontal stand diversity, provide habitats for a diverse range of species, and generally contain a higher amount of accumulated biomass than managed forests, thereby playing an important role as a major global carbon sink (Gunn *et al.* 2014; Calfapietra *et al.* 2015; Nabuurs *et al.* 2016; Mikoláš *et al.* 2017). In recent decades, efforts have been made to quantify the impact of environmental change on forest stand dynamics (Black *et al.* 2008b; Bigler and Veblen 2009; Di Filippo *et al.* 2015) in order to differentiate the importance and strength of various growth-affecting factors, along with their interactions (Castagneri *et al.* 2011; Primicia *et al.* 2015; Latte *et al.* 2015). A conceptual model put forward by Graybill (1982) and Cook (1985), termed the 'linear aggregate model', neatly represents this complexity of interactions, and identifies climate, along with age, endogenous and exogenous disturbances, as one of the integral components contributing to tree growth variability. These components mutually interact, and while disturbances shape forest structure and alter forest dynamics (Turner 2010; Seidl *et al.* 2017), climate exerts a temporally dynamic influence on disturbance patterns over various spatial scales (Schurman *et al.* 2018).

Tree growth inherently responds to climatic conditions on a range of timescales (Fritts 1976; Speer 2010; Hartl–Meier *et al.* 2014; Parobekova *et al.* 2016), and therefore also to the effects of climate change, such as rising temperatures or increasing drought frequency and severity. Shifts in the impact of various climatic drivers independently or synergistically (*i.e.*, by the interaction of multiple climatic and non-climatic factors) directly influence mountain forest dynamics (Kramer *et al.* 2000; Lindner *et al.* 2010; Fyllas *et al.* 2017). In Mediterranean forests, changes in intensity, duration and frequency of drought events have significantly influenced tree growth and led to severe forest dieback (Peñuelas *et al.* 2001; Allen 2009; Granda *et al.* 2013). Climatic shifts have also been linked to fire regime alterations (Flannigan *et al.* 2000; Bowman *et al.* 2009), demographic changes of tree communities and distributional shifts at the range boundaries of some tree species in response to recent climate change (Franklin *et al.* 2016; Kolář *et al.* 2017; Taylor *et al.* 2017). Due to the complexity of interactions between various growth-influencing factors in mixed-species primary forests, quantifying and understanding climate-growth relationships remains a challenge, yet insights into species-specific growth responses may help predict how different tree species will respond and adapt to the expected impacts of climate change. The responses of autochthonous mixed-species forests to climate have been sparsely studied on the Balkan Peninsula, particularly in the Dinaric Mts, and as such remain poorly understood.

In paleoclimatic research, tree-rings are traditionally regarded as one of the most important proxy archives due to their ability to preserve annually resolved climate information (Jones *et al.* 2009). Increasingly, tree-ring parameters other than tree-ring width (hereafter 'TRW'), such as tree-ring density or stable isotopes, have also been utilized to study the climatic signals preserved in tree-rings. The thickening and lignification of cell walls is directly affected by climatic conditions and this climatic information can be extracted using techniques such as x-ray densitometry (*i.e.*, MXD; Schweingruber *et al.* 1978) or light reflectance analysis (Sheppard *et al.* 1996, McCarroll *et al.* 2002). The image-based blue reflectance (or blue intensity – hereafter 'BI') parameter represents a measure of reflected light in the blue wavelengths of the colour spectrum linked to lignin content, which is directly related to tree-ring density. Due to its relative affordability and sensitivity to climatic conditions, it is becoming an important new parameter in dendroclimatological research (*e.g.*, McCarroll *et al.* 2002; Campbell *et al.* 2007, 2011; Björklund *et al.* 2014; Rydval *et al.* 2014, 2017a, 2017b, 2018, Buckley *et al.* 2018). Previous studies have noted a stronger climatic response of the BI parameter in temperature-limited environments compared to TRW, particularly on inter-annual timescales, and that it is less prone to the influences of other site-specific and non-climatic factors such as disturbances (*e.g.*, Björklund *et al.* 2014; Fuentes *et al.* 2016; Wilson *et al.* 2014, 2017; Rydval *et al.* 2018). However, there has been a general lack of research into the relationship between moisture availability in drought-prone environments and BI. Although several studies have linked increased wood density (*e.g.*, Hoffmann *et al.* 2011; Xiao *et al.* 2014) and BI in tropical conifers (*e.g.*, Buckley *et al.* 2018) to drought, no prior study has investigated the drought response from the properties of the BI parameter in order to understand the reaction of temperate primary forests to drought stress.

In this study, our objective was to conduct a dendroclimatological analysis of Norway spruce (*Picea abies* (L.) H. Karst.) and silver fir (*Abies alba* Mill.) tree-ring samples from mixed primary forests of Smrčeve doline within the Northern Velebit national park in Croatia, in order to broaden existing knowledge of climate-growth relationships in this region. To this end, we applied a random sampling design to avoid potential sampling biases (Nehrbass-Alles *et al.* 2014; Rydval *et al.* 2018) and utilized standardization approaches intended to remove age-related trends, while allowing for the examination of both (multi-)decadal trends in tree-ring chronologies as well as short-term (interannual) relationships with climate (Tessier *et al.* 1997).

In order to assess the influence of climate on growth of these two co-occurring species, TRW, earlywood blue intensity (EWBI) and latewood blue intensity (LWBI) chronologies of both species were inter-compared and evaluated against climate variables (*i.e.*, temperature, precipitation and drought index) over the past century. To establish how the climate response of two co-occurring species differs in this water-limited forest ecosystem, pointer year analysis was also conducted to identify anomalous growth years and investigate their relationship with climatically extreme years.

4.1.2 MATERIALS AND METHODS

4.1.2.1 STUDY AREA

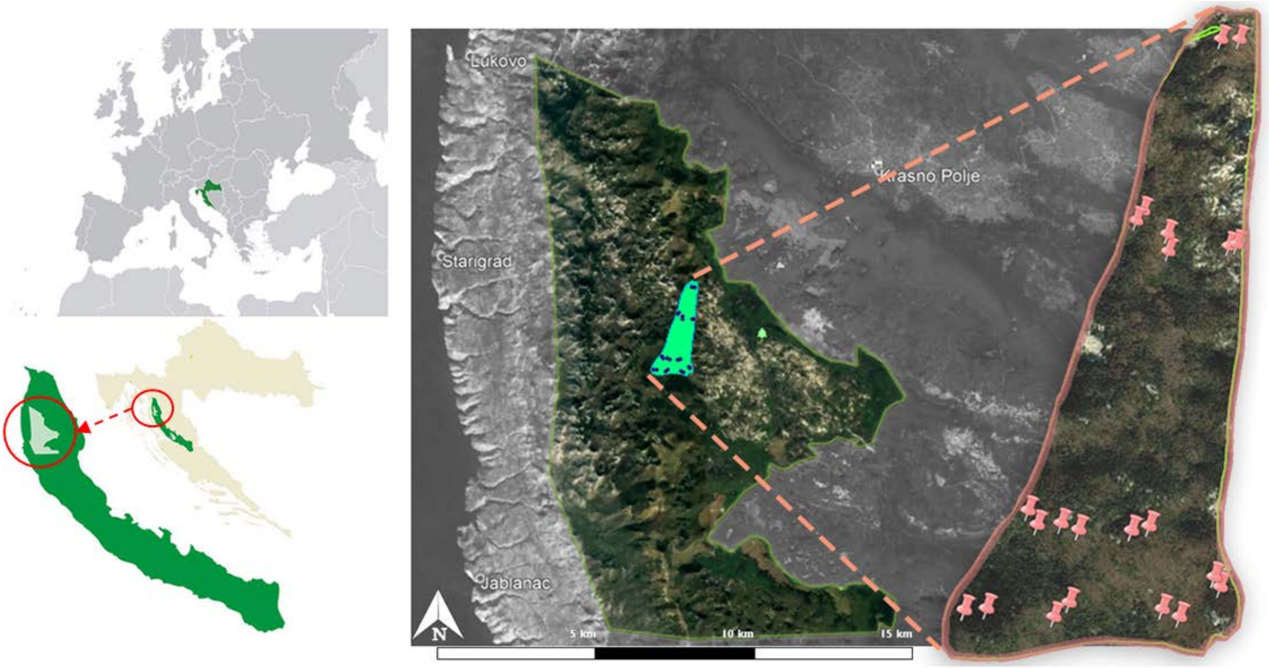

Fig. 1. Location of Northern Velebit national park and Smrčeve doline forest reserve.

Velebit is the largest mountain range in Croatia, located along the Adriatic coast as part of the NW Dinaric Alps. It extends over 145 km from north to south and over 30 km from east to west, with an elevational range of 518 to 1757 m a.s.l., and an area of about 2200 km^2. Velebit is located on the climatic border between the moderately temperate continental climate and the Mediterranean climate (Cf/Cs[1]) (NPSV Management Plan, 2007), with the mountain massif itself representing the boundary. Due to the considerable amount of water vapour transported by winds from the Adriatic Sea and condensing on Velebit's peaks, the area is characterized by abundant annual rainfall (2000-3000 mm/year on average) and relatively low average annual temperature (2-6 °C). Geographically, the Northern Velebit national park (NVNP) is located

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[1] Cf – temperate climate; Cs – Mediterranean climate (according to Köppen climate classification)

between 44° 41' 31" N and 44° 51' 17" N, and between 14°55 '27" E and 15° 2' 54" E (Fig. 1). Temperature inversions in depressions are a specific characteristic of the area, causing long snow retention (40 to 100 days of snow cover deeper than 30 cm; NPSV Management Plan, 2007).

In geomorphological terms, the area is characterized by an exceptionally rich Dinaric karst relief, where the parent material is made of resurfacing limestone breccias and limestone-dolomite blocks (Vukelić *et al.* 2011), forming a typical karst landscape. Erosion and the action of other climate-related transformations over time has produced a discontinuous terrain, and the entire mountain is composed of limestone and dolomitic bedrock with hydrologically highly permeable characteristics. Soil types vary spatially from lithosols and coluvial soils to limestone-dolomitic brown and slightly acidic soil (NPSV Management Plan 2007). At Velebit, Norway spruce and silver fir form forest communities with European beech in Norway spruce-dominated forests on more humid, colder, and shadier sites and in sinkholes with *Laserpitium krapfii* Crantz (*Laserpitio krapfii-Piceetum abietis* ass. nova Vukelić *et al.* 2010a). Norway spruce forests with *Hypericum richerii grisebachii* (*Hyperico grisebachii-Piceetum abietis* Bertović 1975; Vukelić *et al.* 2010a, 2011) are found on rockier sites with shallow soils. The sampled Smrčeve doline primary forest (Fig. 1) is representative of forests found on Velebit.

4.1.2.2 SAMPLE COLLECTION AND DATA PREPARATION

Mixed-species stands were pre-surveyed for indicators of naturalness (*e.g.* coarse woody debris in various stages of decay, pit-and-mound topography, etc.), and all available historical information regarding land use in these mountains was collected to avoid sampling stands with evidence of past logging and grazing. Selection of sampling plots was performed by superimposing a 100x100m grid over the stand, using ArcView 9.3 Environment (ESRI ArcGIS 2011). Within each grid cell, randomly selected points were used in order to establish the position of sampling plots (24 in total). Each circular plot covered an area of 1500 m^2 with an outer radius of 21.85 m and consisted of three nested circular subplots of varying radius (inner – 8 m; intermediate – 17.84 m; outer – 21.85 m), which determined the minimal DBH of trees chosen for coring. In the inner subplot, all trees with a DBH > 6 cm were cored, in the intermediate subplot trees with a DBH between 10 cm and 20 cm were cored, and in the outermost subplot only trees with a DBH > 20 cm were cored. One core per tree was extracted using Haglöf increment borer. In total, we collected 232 samples of Norway spruce and 122 samples of silver fir (Table 1).

By applying this type of coring strategy, we ensured an unbiased spatially representative sample of the studied area and a comprehensive and robust sample of various age and size groups. This methodological approach is consistent with the recent shift in dendro-sciences towards sampling trees representative of the entire forest, rather than size-mediated or treeline trees (*e.g.*, Sullivan and Csank 2016; Rydval *et al.* 2018; Schurman *et al.* 2019). This approach is applied in the Research of Mountain Temperate Forest network (REMOTE - www.remoteforests.org). Additional information along with a more detailed description of the coring strategy, sampling design and stand characteristics can be found in the Supplementary materials (Fig. S3, Table S1).

Laboratory analyses were based on dendrochronological dating techniques described by Stokes and Smiley (1996). Increment cores were dried, placed onto wooden mounts and sanded. Annual tree-ring widths were measured to an accuracy of 0.01 mm using a LintabTM traversing measuring stage and TSAP-WinTM computer software (www.rinntech.de). Cores were visually cross-dated using the marker year approach (Yamaguchi 1991) and crossdating was verified with COFECHA and CDendro (version 8.1) software (Holmes 1983; Grissino-Mayer 2001; Cybis 2019). The number of missing rings was estimated using the method of Duncan (1989). Crossdating of individual series was based on measures of GFK (Gleichläufigkeit) (Schweingruber 1988), TTest and Pearson’s correlation coefficient. Cores which could not be correctly cross dated, were excluded from further analysis.

4.1.2.3 BLUE INTENSITY (BI) ANALYSIS

Measurement of BI was carried out on 40 Norway spruce and silver fir samples. The subsets of tree cores were chosen randomly for the purpose of assessing latewood (LW) and earlywood (EW) measurements of the BI parameter. Following resin extraction in acetone for 72 hrs (Rydval *et al.* 2014), samples were surfaced with sanding paper up to 1200 grit grade, which is considered adequate for BI analysis (Babst *et al.* 2009). Cores were scanned using an Epson Expression 10000 XL scanner combined with SilverFast Ai (v.6.6 - Laser Soft Imaging AG, Kiel, Germany) scanning software prior to measurement and image analysis. Before scanning, calibration of the scanner was performed with the SilverFast IT8 calibration procedure using a Fujicolour Crystal Archive IT8.7/2 calibration target, in order to ensure comparability of data between different scanners and research facilities and prevent drift of BI measurements (Campbell *et al.* 2011; Rydval *et al.* 2014). A resolution of 2400 dpi was used for scanning. During the scanning process, samples were covered with a black, non-reflective cloth to prevent biases due to potential influence of ambient light (Rydval *et al.* 2014). CooRecorder measurement software was used to measure BI values from the scanned images (Cybis 2019). Since LWBI is inversely correlated with TRW, individual LWBI series were inverted according to Rydval *et al.* (2014), to express a positive relationship with TRW and instrumental data (no such inversion was necessary for EWBI) according to Eq. 1:

$$xn(adj) = 2.56 - xn*100 \qquad \text{(Eq. 1)}$$

where $x(n)$ is the raw BI value in year n, while the constant 2.56 is used to prevent $xn(adj)$ from becoming ≤ 0, considering all possible values of xn (0. . .255).

4.1.2.4 STANDARDIZATION PROCEDURE

Two chronology versions (standard and residual) were developed for each species and tree-ring parameter using the program ARSTAN (AutoRegressive STANdardization; Cook and Holmes 1986). To produce the standard (hereafter ’STD‘) chronology, a negative exponential function was used to remove age-related trends, while still preserving decadal to multi-decadal and higher frequency variance. This was achieved by subtracting values predicted by the negative exponential function from the observed individual tree-ring series using an adaptive power transformation to compensate for variance differences related to the local mean of the tree-ring indices (Cook and Peters 1997). These detrended series were averaged by year using Tukey's robust mean to reduce the influence of outliers on the tree-ring indices (Mosteller and Tukey 1977; Cook *et al.* 1995). Residual (hereafter ’RES‘) chronologies were developed to retain only high-frequency (interannual) variability without the influence of autocorrelation and any potential non-climatic trends (*e.g.* due to the impact of structural disturbances and competition). The RES chronologies were obtained by applying an autoregressive model to the individually detrended series and averaging the residual series by year. To construct the chronologies, Rbar-weighted stabilization was used to stabilize potential changes in variance related to differences in sample depth and rbar over time (Osborn *et al.* 1997). Mean interseries correlation (rbar) and expressed population signal (EPS) were used as the main statistical indicators in developing robust chronologies (Cook and Krusic 2005; Butler *et al.* 2013). R-bar represents the average correlation among tree-ring series for the common overlap period of those series, while EPS indicates the degree to which the chronology signal (expressed as a fraction of the hypothetical ideal population variance) represents the theoretical population signal when individual series are averaged (Briffa 1984; Wigley *et al.* 1984). The widely accepted value of EPS (= 0.85) is commonly used as the limit below which the observed chronology begins to lose a coherent collective signal and individual trees begin to dominate the overall signal (Cook and Kairiukstis

1990). Here this limit was slightly relaxed to 0.80, to maximise the useable chronology span of all parameters for climate response analysis, in line with other studies (*e.g.*, Fan *et al.* 2009; Matisons *et al.* 2015; Rydval *et al.* 2017a). Both the r-bar and EPS statistics were calculated using a 30-year moving window with a 29-year overlap.

Standardization of BI data was performed ditto, with the exception that age-related growth trends were removed using a negative sloping linear curve, in accordance with the BI standardization procedures applied in previous studies (*e.g.*, McCarroll *et al.* 2002; Campbell *et al.* 2007, 2011). BI chronologies were calculated and truncated (EPS > 0.80) in the same way as the TRW chronologies.

Subsequent analyses were performed on a truncated 277-year TRW chronology of Norway spruce (constructed from 174 samples) and a 267-year TRW chronology of silver fir (constructed from 95 samples). BI chronologies of Norway spruce (149 years) and silver fir (147 years) each consist of 40 samples (Table 1). Although beech trees were also widely present in the sampled locations, samples of beech were omitted from analysis in this study, as BI analysis is inapplicable to broadleaved species due to their wood structure.

Table 1. Descriptive statistics of the tree-ring chronologies from Smrčeve doline **(*** TRW – tree-ring width, EWBI – earlywood blue intensity, LWBI – latewood blue intensity**)**.

Number of studied plots	24 plots					
	Norway spruce			**Silver fir**		
Total number of collected cores	232			122		
Chronologies	TRW	EWBI	LWBI	TRW	EWBI	LWBI
Number of dated series	174	40		95	40	
Full chronology span	1655 - 2014	1687 – 2014		1614-2014	1622-2014	
Truncated chronology span (EPS>0.80)	1738-2014	1846-2014	1846-2014	1748-2014	1848-2014	1806-2014
Chronology overlap with instrumental data	1901 - 2014					
Mean inter-series correlation	.587	.342	.507	. 600	.346	.323
Average mean sensitivity	.207	.025	.035	.210	.023	.027

4.1.2.5 CLIMATE DATA

Due to limited availability of instrumental climate data from local meteorological stations before the 1950s, CRU TS 4.01 gridded 0.5º instrumental climate datasets for the 1901-2014 period were used to assess climate-growth relationships (Harris *et al.* 2014). Climatic variables, including temperature (average monthly temperature), precipitation (monthly totals) and self-calibrating Palmer Drought Severity Index (scPDSI; Wells *et al.* 2004), which integrates available temperature and precipitation data to estimate relative drought, were obtained from KNMI Climate Explorer (Trouet and Van Oldenborgh 2013), for the coordinates of the study location.

4.1.2.6 CLIMATE-GROWTH ANALYSIS

The climate response analysis was performed over a 114-year period (1901-2014), which represents the overlap of the CRU TS 4.01 (0.5°) instrumental data and tree-ring chronologies. Pearson's correlation coefficients were calculated to quantify the relationship between the chronologies and temperature, precipitation, and drought index (scPDSI) for 24 months (*i.e.*, the previous and current year of growth), as well as summer season windows, which represent the climatic variables averaged over summer months (June, July and August). The analysis was conducted for both the RES and STD chronology variants to evaluate short-term (interannual) and longer-term decadal / multi-decadal relationships, respectively. The temporal stability of climate-growth relationships was quantified using Pearson's correlation coefficients computed over 31-yr moving window segments, to investigate temporal changes in the climate-growth relationships. All climate response analyses were performed in R (R Development Core Team 2018) using the *bootRes* and *treeclim* packages.

4.1.2.7 POINTER YEAR ANALYSIS

Climate-growth relationships can additionally be examined by investigating the influence of climatic extremes on growth, which may shed further light on growth responses of individual trees and whole forest populations (Matisons *et al.* 2013). Climatically sensitive trees typically respond to extreme climatic events in the short-term with anomalous below- or above-average growth (Schweingruber *et al.* 1990), making these events detectable in tree-ring series. In this context, extremely narrow tree-rings are usually formed after negative temperature and/or precipitation anomalies (Kelly *et al.* 2002; Drobyshev *et al.* 2008; Rozas *et al.* 2009), while wide rings can form in years that are climatically particularly favorable for growth.

The identification of pointer years can be sensitive to the detection method used. Therefore, a dual-method approach was applied in this study to detect event years. In the first method, which follows the approach of Huber and Giertz-Siebenlist (1969), BI and TRW indices of residual (RES) chronologies that exceeded a threshold of +/- 2 standard deviations (σ) in a given year from the mean index value of the RES chronology were identified as event years. The second method detected pointer years using a 5-year indexation window with a critical level threshold of 0.75 standard deviations (Cropper 1979) using the „*pointRes*“ R package (van der Maaten-Theunissen *et al.* 2015). Years in which at least 75% of trees exceeded this specified threshold were defined as pointer years. Pointer years identified by both methods were also compared against climatic variables to which the RES chronologies were most responsive, in order to establish if the recorded annual growth extremes may have been of climatic origin. In addition to the comparisons with instrumental climate records, pointer years were interpreted with reference to available historical data from Croatia and Central-Southern Europe.

4.1.3 RESULTS

4.1.3.1 SAMPLE SIZE AND CHRONOLOGY METRICS

The full length of the Norway spruce (PIAB) and silver fir (ABAL) TRW chronologies spanned 360 and 401 years, respectively, while PIAB BI chronologies covered 328 years, and 393 years in the case of ABAL (Table 1, Fig. 2). The period of pronounced replication increase for both species coincides from about 1800 to 1900. Mean sensitivity (*ms*) was similar for chronologies of both species with respect to each parameter. However, TRW mean sensitivity (ms_{PIAB} = 0.207, ms_{ABAL} = 0.210) was about an order of magnitude higher compared to LWBI (ms_{PIAB} = 0.035, ms_{ABAL} = 0.027) and EWBI (ms_{PIAB} = 0.025, ms_{ABAL} = 0.023). In general, EPS decreased gradually back in time for all chronologies, reflecting a combination of changing replication and variable rbar over time. For both species (Fig. 2E, 2F), the average EPS values of STD TRW chronologies significantly exceeded the specified EPS boundary from around 1750 onwards, mainly reflecting high replication during that period. In contrast, the EWBI and LWBI STD chronologies generally showed weaker chronology EPS and the extent which exceeded the EPS threshold was shorter (Fig. 2E, 2F). The EWBI and LWBI PIAB chronologies reached the mid-19th century, with a similar extent of silver fir EWBI, while PIAB LWBI extended further back in time to about 1800. TRW chronologies generally exhibited the strongest r-bar, followed by the LWBI and finally the EWBI chronologies.

The STD and RES chronologies of TRW (fig. 3A, 3B) generally exhibit similar medium- and low- frequency growth patterns in most periods, except of the period around 1780, 1850 and 1960. This similarity (and the above-mentioned short-term periods of disagreement) is also apparent in the ‘raw’ chronologies of absolute growth rates of the two species (see supplementary Fig. S1), where most of the observed low-frequency trends can be attributed to a combination of age-related decline in TRW over time and a concentrated period of recruitment in the (early) 19th century. Residual chronologies of both species show a similar amount of high frequency variance and broad agreement ($r > 0.5$) over their replicated period of overlap with a few minor exceptions, most notably around the mid-19th century. Despite some minor deviations in the 20th century, both spruce and fir EWBI chronologies show similar trends in the mid- to low frequency (Fig. 3C) and high frequency (Fig. 3D) domains, with correlations generally above 0.5, although with some weaker periods (such as around 1880s and 1930s). Lower frequency trends of both ABAL and PIAB EWBI chronologies show a gradual increase until about 1900, followed by a sharp decline in the late 20th / early 21st century.

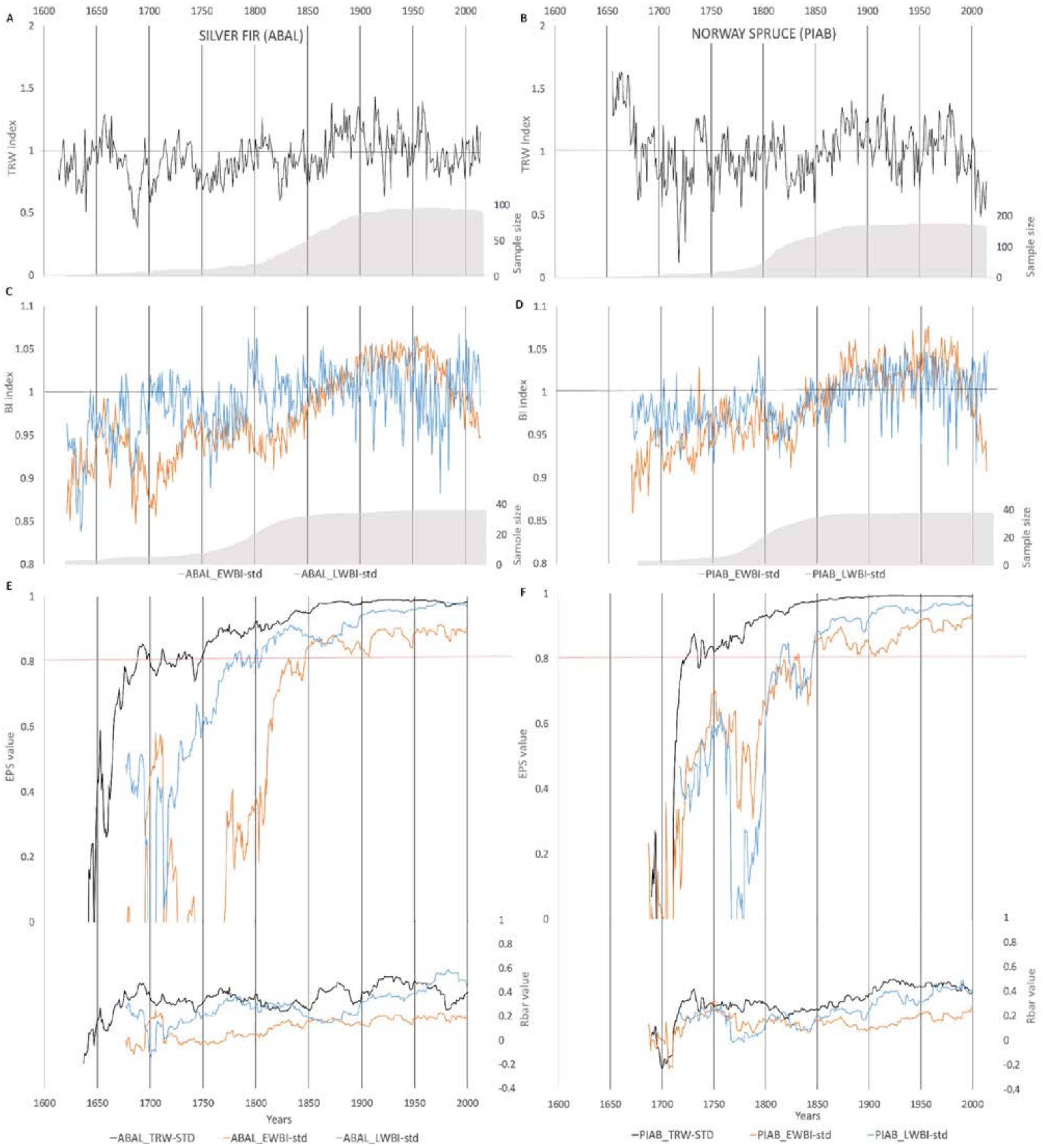

Fig. 2. Silver fir (ABAL) (left) and Norway spruce (PIAB) (right) standard (STD) chronologies and chronology metrics.

(A, B) TRW STD chronologies with replication, (C, D) EWBI (orange) and LWBI (blue) STD chronologies with replication, and (E, F) rbar and EPS for TRW (black), EWBI (orange) and LWBI (blue) STD chronologies. Red horizontal line marks EPS > 0.80.

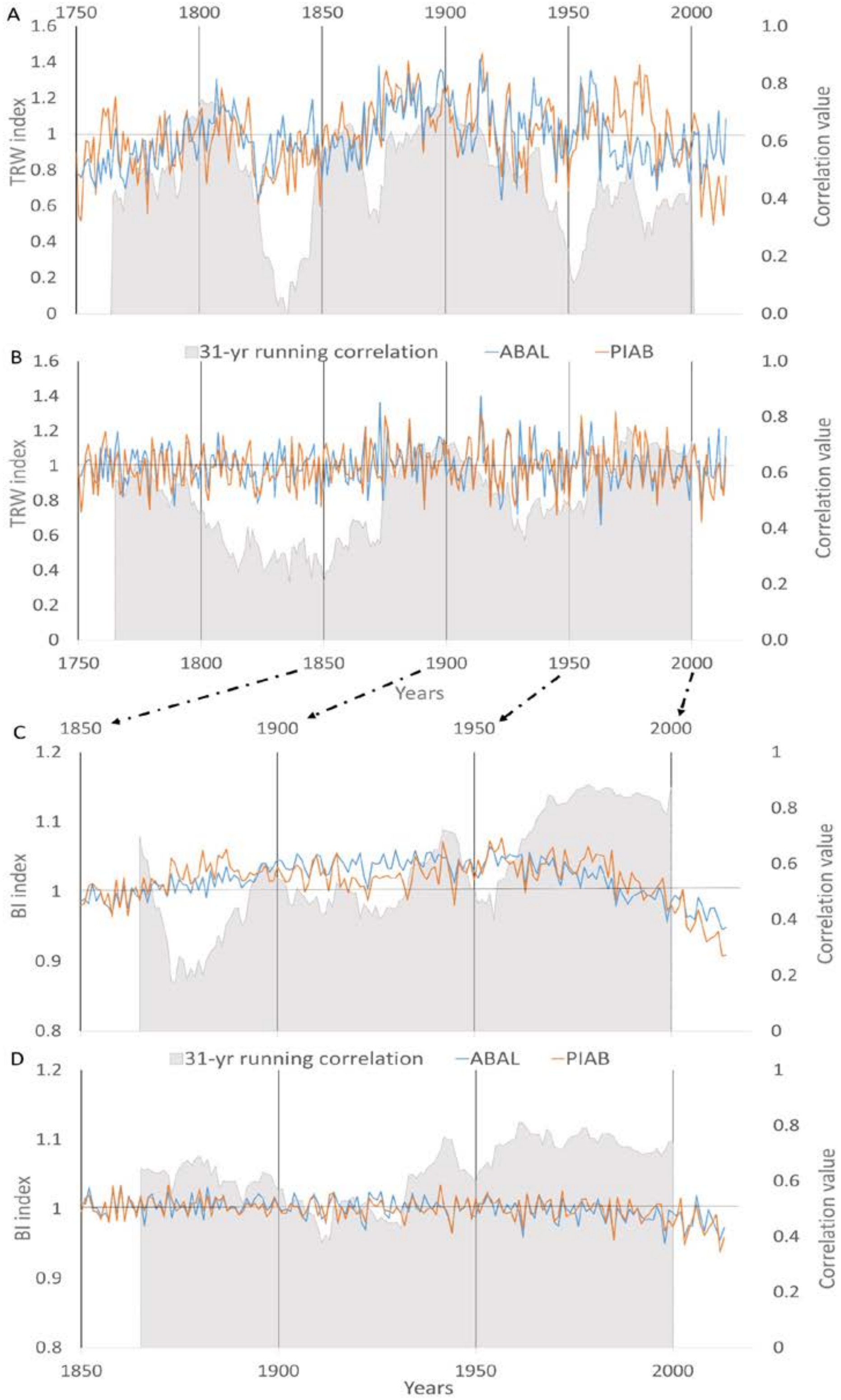

Fig. 3. Silver fir (ABAL) (blue) and Norway spruce (PIAB) (orange) TRW and BI chronologies with a 31-yr window running correlations between the species (shaded grey area).

(A) STD TRW chronologies of ABAL and PIAB, (B) RES TRW chronologies of ABAL and PIAB, (C) STD EWBI chronologies of ABAL and PIAB, (D) RES EWBI chronologies of ABAL and PIAB. Chronologies are shown for the periods where EPS > 0.80.

4.1.3.2 CLIMATIC RESPONSE OF NORWAY SPRUCE AND SILVER FIR

The correlation analysis of standard chronologies (Fig. 4A) revealed that both species showed a statistically significant positive relationship with total precipitation during July of the previous and current year of growth, while silver fir (ABAL) exhibited a positive response in August. The residual chronology results (Fig. 4B) also indicated a relationship of both species with current year July total precipitation, which appeared stronger in Norway spruce (PIAB), but only ABAL showed a significant prior year relationship with August total precipitation.

Correlations of STD and RES chronologies with monthly average scPDSI (Fig. 4C, 4D) showed a somewhat broader and stronger prior year relationship compared to precipitation totals, but a weaker current year response. While the STD chronologies showed a significant relationship with scPDSI throughout most of the previous year growing season (April to September) in both species (r = ~0.35), only a weak relationship of PIAB STD was observed in late winter months of the current year. In contrast, RES chronologies of both species exhibited a weaker (r = ~0.27) growth response to moisture in the previous year, although only PIAB RES showed a significant, though weak (r = 0.28), relationship with current year summer PDSI.

Statistically significant negative correlations between PIAB STD chronologies and average monthly temperature (Fig. 4E) were apparent during the whole growing season (April – September) in the previous year of growth, as well as in the spring and summer months (April, May, July and August) of the current growth year. ABAL only showed a weaker (r = -0.33) significant negative relationship with August temperature of the previous year. The RES chronologies showed a similar negative relationship with average temperature (Fig. 4F), which was somewhat weaker (r = -0.42) and temporally more restricted (previous and current year July-August) with respect to PIAB, while ABAL also displayed a positive response to current year February temperature in addition to the negative relationship with previous August temperature.

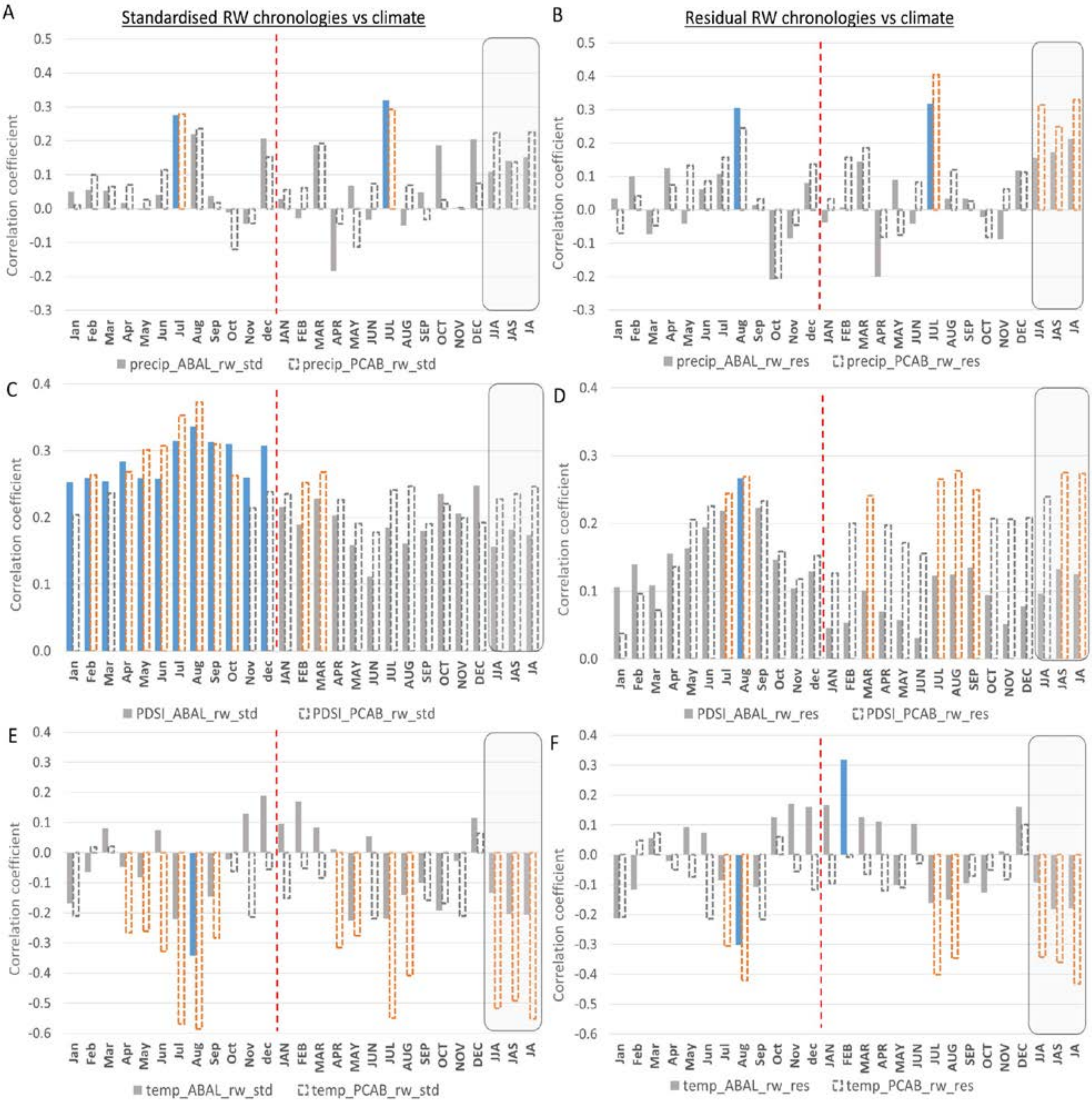

Fig. 4. Correlation response of silver fir (ABAL, filled bars) and Norway spruce (PIAB, empty bars) TRW chronologies in relation to monthly climatic variables (average temperature, total precipitation and average scPDSI) for the current and prior year relative to the year of growth, and with summer months (grey shaded rectangle).

Plots (A, C, E) show relationships with standard (STD) chronologies, whereas (B, D, F) show relationships with residual (RES) chronologies. Relationships with (A, B) precipitation, (C, D) PDSI and (E, F) temperature are shown. Blue (ABAL) and orange (PIAB) coloured bars indicate statistically significant correlations ($p < 0.05$). Red vertical dashed line separates results of prior and current year of tree-ring formation.

With regards to the blue intensity results, climate variables displayed significant relationships only with EWBI STD and RES chronologies. Therefore, LWBI results were omitted from all subsequent analyses and results are only shown for EWBI. However, a full overview of TRW and BI (including LWBI) STD and RES chronology correlations with climate is provided as supplementary data (Table S2).

The correlation analysis of EWBI STD chronologies (Fig. 5A) with precipitation monthly totals indicated the strongest relationship of both species with the current year June-August season (around $r = 0.25$). Considerably stronger responses were observed with RES chronologies (Fig. 5B) for the same summer season, with silver fir (ABAL; $r = 0.5$) showing a stronger relationship than Norway spruce (PIAB; $r = 0.4$).

STD EWBI chronologies showed a range of significant, though weaker ($r \leq 0.3$) relationships with monthly scPDSI (Fig. 5C), including previous year July-August and current year August for PIAB and prior year autumn / winter and current year summer / autumn for ABAL. In contrast to the STD results, residual EWBI chronologies of both species did not express any significant prior year relationships with scPDSI (Fig. 5D) and instead exhibited a clear (mainly July-August) summer response.

Both species exhibited strong negative correlations with average monthly temperature (Fig. 5E) throughout most of the growing period and particularly over the current year June-August season ($r = 0.60$), and showed strong monthly relationships, reaching $r = -0.50$ for PIAB and $r = -0.45$ for ABAL during August of the previous year. RES chronologies showed somewhat weaker negative correlations (Fig. 5F) with temperature in August of the current and previous year and in September of the previous year compared to correlations obtained when using STD chronologies (Fig. 5E).

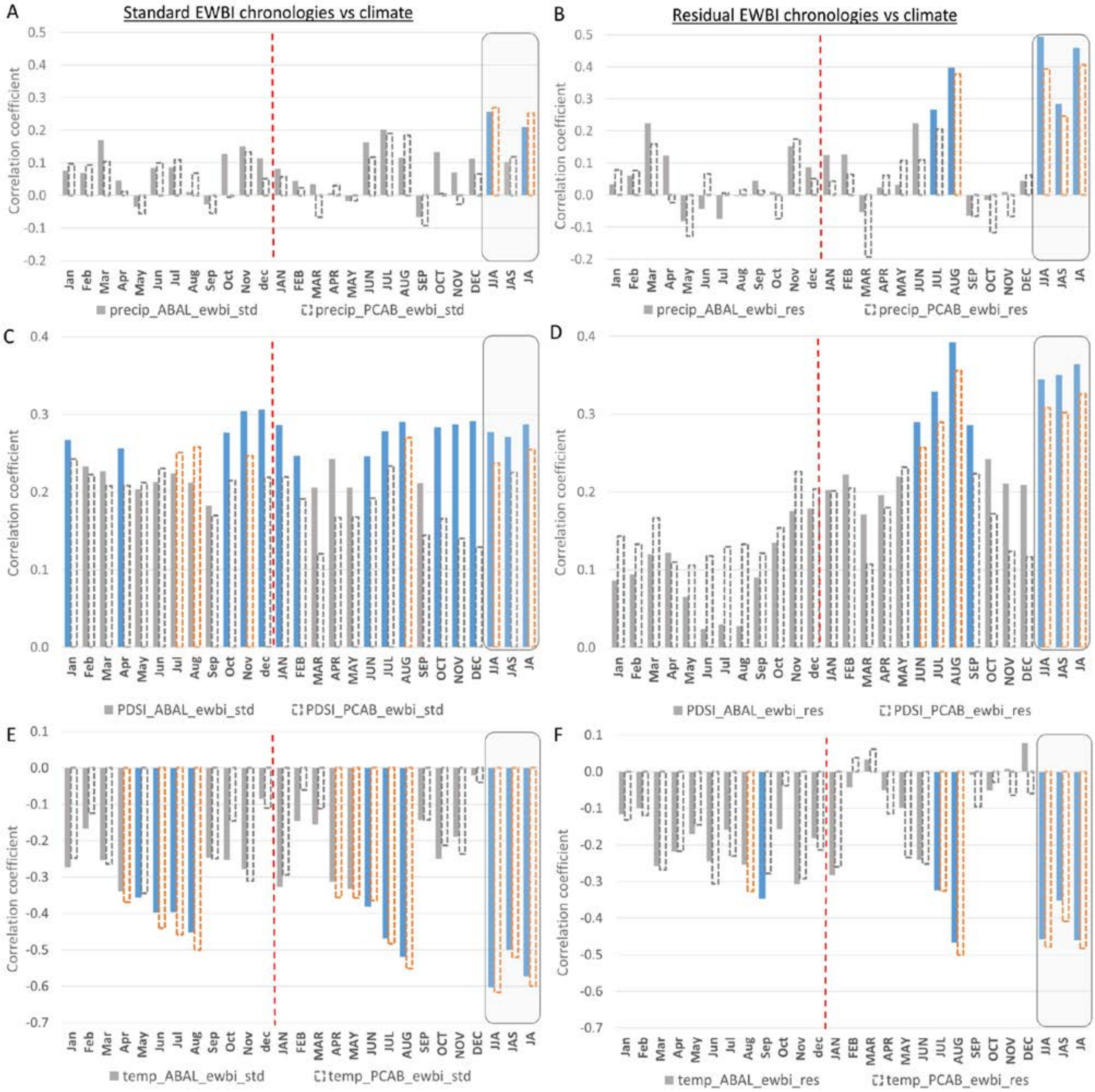

Fig. 5. Correlation response of silver fir (ABAL, filled bars) and Norway spruce (PIAB, empty bars) EWBI chronologies in relation to monthly climatic variables (average temperature, total precipitation and average scPDSI) for the current and prior year relative to the year of growth, and with summer months (grey shaded rectangle).

Plots (A, C, E) show relationships with standard (STD) chronologies, whereas (B, D, F) show relationships with residual (RES) chronologies. Relationships with (A, B) precipitation totals, (C, D) average scPDSI and (E, F) average temperature are shown. Blue (ABAL) and orange (PIAB) coloured bars indicate statistically significant correlations ($p < 0.05$). Red vertical dashed line separates results of prior and current year of tree-ring formation.

Fig. 6 shows the temporal variability in the relationship between STD chronologies and the most significant variables identified by the climate response analysis in Fig. 4 and 5. The correlation between silver fir (ABAL) TRW and July precipitation appeared to be decreasing from around r = 0.60 at the start of the 20th century, to almost no relationship in the 1950s, followed by a slow increase towards the beginning of the 21st century. The relationship with July-August temperature (shown inverted in Fig. 6 to facilitate visual interpretation) appeared weaker, yet more stable, over most of the 20th century, although disappearing in the most recent decades. The relationship between summer temperature and Norway spruce (PIAB) TRW showed a marked weakening trend over the 20th century and the correlation with July precipitation also generally decreased over time, although it remained a bit stronger compared to temperature in the most recent period (Fig. 6B).

The relationship of the ABAL EWBI chronology with both June-July-August (JJA) (inverted) temperatures and JJA precipitation (Fig. 6C) was quite temporally variable, although the correlation with precipitation was consistently higher until the late 20th century. With respect to PIAB EWBI chronologies, a positive relationship with JJA precipitation is mirrored by a negative relationship with JJA temperatures (Fig. 6D), showing a similar increasing trend in the strength of the relationship (inverted in the case of temperature) with both variables over the 20th century, contrasting with the generally decreasing relationship observed in the TRW chronology. The decreasing trend in EWBI chronologies of both species coincides with overall higher summer temperatures and considerably drier conditions at the end of the 20th and beginning of the 21st century.

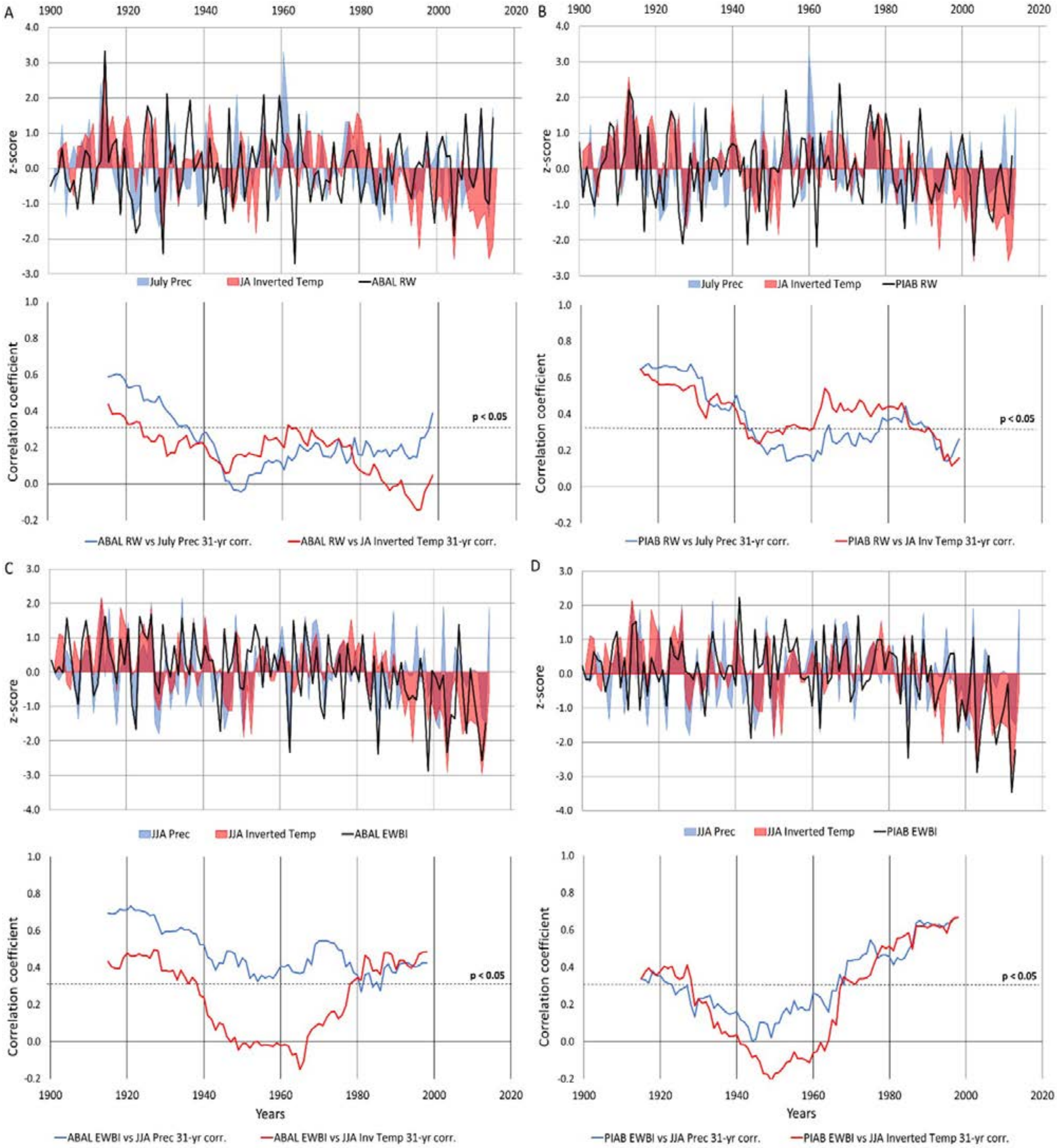

Fig. 6. Silver fir (ABAL) and Norway spruce (PIAB) STD TRW (A, B) and STD EWBI (C, D) chronologies together with the most responsive climatic variables and 31-year running correlations between the chronologies and climatic series underneath.

(A) ABAL STD TRW and (B) PIAB STD TRW with July precipitation and JA inverted temperature, (C) ABAL STD EWBI and (D) PIAB STD EWBI with JJA precipitation and JJA inverted temperature. All series are expressed as z-scores relative to the 1901-2014 period. Dashed horizontal lines present significance threshold ($p < 0.05$).

4.1.3.3 POINTER YEAR ANALYSIS

Pointer year analysis of silver fir (ABAL; Fig. 7A, 7C) and Norway spruce (PIAB; Fig. 7B, 7D) residual chronologies was performed in relation to the most significant climatic variables with respect to each species and tree-ring parameter. In the ABAL RES chronology (Fig. 7A), a total of 5 negative (1783, 1891, 1923, 1929, 1963) and 2 positive (1873 and 1914) pointer years were identified. A total of 10 negative (1751-1752, 1779, 1891, 1933, 1945, 1963, 1975, 1986 and 2004) and 1 positive (1914) pointer years were observed in the case of PIAB RES chronology (Fig. 7B). Cropper's method supported the identification of some of the previously identified pointers (*e.g.*, 1873, 1923, 1929, 1963 in ABAL RES; 1751, 1779, 1891, 1945, 1963, 1975 and 2004 in PIAB RES), but also detected additional event years (*e.g.*, 1999, 2011 in ABAL RES; 1918 in PIAB RES), adding to the overall reliability of pointer year detection. Chronologies of the two species contained the same pointer years in four cases (*i.e.*, 1779, 1891, 1914 and 1963), indicating a limited degree of common growth response to extreme conditions.

Both species were strongly negatively impacted by summer temperatures, resulting in common pointers related to low (*e.g.*, 1914) or high (*e.g.*, 2004) summer temperatures. Summer months humidity was identified as another important climatic parameter (Fig. 4); therefore, TRW chronologies were also compared against the moisture parameter exhibiting the strongest growth response (July precipitation). Summer rainfall appeared to have a considerable impact on the occurrence of TRW pointers, whether solely by itself (*e.g.*, cumulative below-average rainfall producing a negative pointer in ABAL TRW in 1923) or combined with the impact of lower (*e.g.*, 1914) or higher (*e.g.*, 2004) summer temperatures. Some pointer years may be showing a one-year response delay in relation to hydroclimatic conditions of the previous year, including positive response to very wet summers (*e.g.*, 1914 in both species) or negative growth response to extreme drought conditions (1923, 1929 in ABAL; 2004 in PIAB).

With regards to the residual BI chronologies, 4 negative pointer years (1923, 1945, 1963 and 1999) were identified for ABAL (Fig. 7C), and 3 negative pointer years in relation to PIAB (1945, 1963 and 1986). Cropper's method supported the identification of event years in ABAL BI, but did not detect any pointer years in the PIAB BI chronology. Both species shared several pointer years (*e.g.*, 1945 and 1963), indicating pointer year agreement between the two species in both EWBI and TRW. Some pointer years also coincided with climatic extremes (*e.g.*, the 1945 pointer year identified in both ABAL and PIAB EWBI coincided with drier summer conditions).

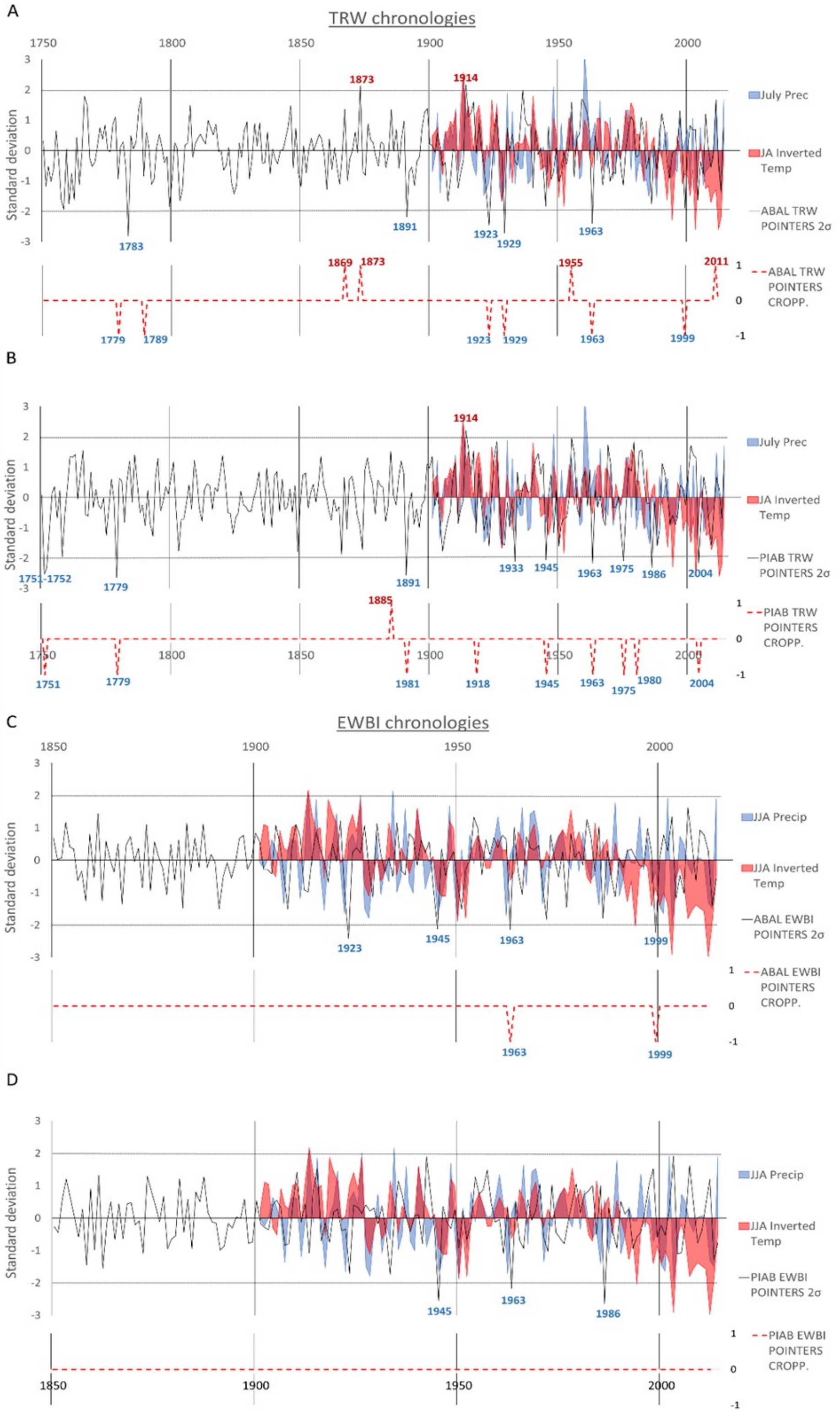

Fig. 7. Pointer year analysis based on residual chronologies of (A) Silver fir (ABAL) TRW (B) Norway spruce (PIAB) TRW, (C) ABAL EWBI and (D) PIAB EWBI together with the most responsive climatic variables for each tree-ring parameter.

All series are expressed as z-scores relative to the 1901-2014 period and chronologies are shown for the period where EPS > 0.80. Black horizontal lines indicate 2 standard deviation (2σ) thresholds. Red dashed line (CROPP.) shows the occurrence of positive (+1) or negative (-1) pointer years according to the Cropper method.

4.1.4 DISCUSSION

4.1.4.1 CLIMATE-GROWTH RELATIONSHIPS OF NORTHERN VELEBIT FORESTS

4.1.4.1.1 CURRENT YEAR RELATIONSHIPS

In an overview of published climate reconstructions, Poljanšek and Levanič (2015) found two general types of response to climate on the Balkan Peninsula: one with a clear precipitation/drought signal from the continental areas, and a less pronounced drought signal from mountainous sites near the seacoast. At Smrčeve doline site, both Norway spruce and silver fir grow at the limit of their ecological niche in SE Europe. Climate-growth relationships are more conspicuous at these mountain sites, where individual trees exhibit a higher sensitivity to climate compared to other growth-influencing factors, making Smrčeve doline well suited for climate reconstructions.

Despite the relatively high elevation of the study site, growth of Norway spruce and silver fir trees in Smrčeve doline mainly appears to be driven by soil moisture availability, in contrast to temperature driven Norway spruce forests in more continental parts of Europe (*e.g.*, Savva *et al.* 2006; Büntgen *et al.* 2007; Lebourgeois 2007; Bijak 2010; Parobekova *et al.* 2016). Both species express a positive relationship with summer precipitation and a negative response to summer temperatures, making summer drought conditions the primary growth-limiting factor during hot and dry summers (Fig. 4, 5). June–July is the period of most intense cell enlargement, which is when the positive influence of precipitation on growth appears to have the strongest effect. Even though these forests receive abundant annual rainfall, orographic precipitation, high soil permeability and porose bedrock considerably limit groundwater retention during the growing season, while high summer temperatures further reduce water availability and increase evapotranspirative demands, ultimately limiting growth. This makes drought stress the logical primary climatic driver of tree growth in the Velebit Mt.

Even though trees in Smrčeve doline appeared to be drought-sensitive, the strongest relationship was observed between summer temperatures and all tree-ring parameters (Fig. 4E, 4F, 5E, 5F; $r > 0.50$), rather than the drought metrics (Fig. 4C, 4D, 5C, 5D; $r < 0.40$). These weaker relationships with scPDSI could, in part, be attributed to the limited ability of available climate data to accurately represent the actual microclimatic conditions at the site, due to the relatively coarse resolution of the gridded scPDSI data interpolated from a network of meteorological stations. Furthermore, the scPDSI drought parameter may not adequately reflect local soil conditions, such as the water holding capacity of the substrate and soil moisture content (van der Schrier *et al.* 2013), or account for hydrological dynamics (*e.g.*, runoff, snowpack, reservoir storage, etc.).

The only identified positive relationship with temperature was between the silver fir RES chronology and February mean temperature, which may indicate pronounced sensitivity of silver fir to winter conditions. This positive effect of February temperature on radial growth is in accordance with earlier findings from high-elevation mixed forests from the Dinaric Mountains (*e.g.*, Čavlović *et al.* 2015) and other silver fir temperate forest stands (*e.g.*, Pirenees/Iberian Peninsula, Macias *et al.* 2006; French Alps, Lebourgeois *et al.* 2010). Higher winter temperatures improve thermal soil properties and accelerate snowmelt, thus promoting an earlier onset of cambial reactivation and apical growth (Rossi *et al.* 2007, 2009), decreasing the risk of xylem embolism (Mayr *et al.* 2019) and protecting tree tissues (*i.e.*, buds and roots) from winter freezing (Miller-Rushing *et al.* 2008; Toromani *et al.* 2011). These factors offer a plausible explanation for the temperature-driven stimulation of earlywood formation in spring.

4.1.4.1.2 PREVIOUS YEAR (LAG) RELATIONSHIPS

Both species also show that prior year climate strongly affects tree-ring formation in the subsequent year. Understanding this relationship requires the interpretation of complex multi-factor interactions between climate and tree physiology, including the autocorrelation characteristics of some of the climatic variables.

The observed negative response to prior year conditions is a feature observed at a range of locations throughout the Mediterranean basin (*e.g.,* Macias *et al.* 2006; Tegel *et al.* 2014; Fyllas *et al.* 2017), south-eastern Europe (*e.g.,* Panayotov *et al.* 2010, Toromani *et al.* 2011) and Alpine mountain region (*e.g.*, Lebourgeois *et al.* 2007, 2010; Carrer *et al.* 2010). According to Fritts (1976), radial growth and climate in the year prior to ring formation greatly affect radial growth in the subsequent year. In conifers however, this is usually related to their physiology, *i.e.,* large amounts of carbohydrates stored in needles of different ages (Kozlowski 1992) and seasonal carbohydrate dynamics. Since the photosynthetic capacity of conifers largely depends on the number and size of annually formed buds, unfavourable climatic conditions during this period can impact tree-ring formation through a decrease in carbon assimilation in the following growing season (Lebourgeois *et al.* 2010). As the same generation of needles can be retained and remain active for several years, extreme conditions (*e.g.,* dry summer conditions as in 1962 and 1985; Fig. 7) can impact radial growth over a longer period of time. Impacts of severe climatic events, such as severe droughts, have also been known to impart a delayed response even in the second tree-ring formed after such an event (Rozas 2001; Piovesan *et al.* 2008).

Repeated episodes of carbon starvation could trigger conservative carbon allocation strategies on the expense of stem growth (Linares and Camarero 2012), building greater carbon reserves to be used for maintenance and plant protection in resource-limited conditions (Wiley and Helliker 2012). These species-specific physiological traits and adaptation strategies could potentially explain the lag effects observed in silver fir and Norway spruce.

The influence of climatic variables of the previous year on current year growth is observed not only in the STD chronologies (more so in the case of TRW which typically exhibits higher autocorrelation than BI; Buckley *et al.* 2018), but to a lesser degree also in the RES chronologies, where autocorrelation was removed. Therefore, this effect may be related to temporal autocorrelation of the actual climatic variables. Of the climatic variables examined, summer season temperatures showed a significant, though limited, degree of autocorrelation among consecutive years (see supplementary Fig. S4). It is therefore reasonable to expect that this ‘persistence’ in the climate system has at least partly contributed to the observed lag relationships in tree growth.

4.1.4.2 SPECIES- AND PARAMETER-SPECIFIC RESPONSES

The application of the earlywood blue intensity (EWBI) parameter to investigate climate-growth relationships complemented the TRW analysis and showed similar, yet stronger, seasonal climatic responses compared to its TRW counterpart (Fig. 5). To our knowledge, this study is the first in Europe to explore the EWBI tree-ring parameter in relation to drought and precipitation metrics and represents a considerable improvement in drought-signal strength over earlier work on moisture limitation in the Mediterreanean (*e.g.*, Martinez-Vilalta *et al.* 2011; Papadopoulos 2016; Hacket-Pain *et al.* 2017; Fyllas *et al.* 2017).

EWBI of silver fir exhibited stronger overall relationships with precipitation and PDSI than EWBI of Norway spruce, with summer season rainfall and water availability at the beginning of the growing season having a strong positive effect on earlywood formation. This relationship further underscores the importance of water availability on cell formation during the early part of the growing season and helps to explain the overall sensitivity of growth to climate. In contrast, the climatic response of latewood blue intensity (LWBI) was very weak, which is not surprising since LWBI is usually sensitive to late summer temperatures in temperature-limited environments, but this was not the predominant climatic limitation at our site.

Longer-term differences in climate–growth relationships between Norway spruce and silver fir may be related to distinct biological differences between the two species. Norway spruce is a semi-heliophilic species adapted to withstand harsh cold winter and early winter/late spring frosts (Idžojtić 2009). In contrast, silver fir is a sciophytic species, capable of growing for longer periods of time under supressed growth conditions beneath the canopy of neighbouring trees, but prefers deep, nutrient-rich soft acidic soils and a humid environment (Idžojtić 2009). Bearing in mind that the trees at the studied site grow on rather shallow soils atop porose limestone, soil drying is expected to have a strong impact on mortality of fine root biomass, resilience and biological adaptation of these species to climatic stress. Given that Norway spruce forms a shallow vertical rooting system, higher sensitivity to drought and temperature variability can be expected compared to silver fir, which forms a deep root system with a deep taproot (Idžojtić 2009). With the climate becoming increasingly warmer and drier, this morphological difference between the two species may reduce the competitiveness of Norway spruce compared to silver fir, and may thus lead to a shift in species composition in favor of silver fir. Bošela *et al.* (2016a) suggested that the greater genetic diversity of the Balkan populations helps silver fir to mitigate the effects of changing environmental conditions, while Gazol *et al.* (2016) showed how factors including higher genetic diversity and greater functional diversity of forest stands increase the capacity of silver fir to tolerate drought. A negative growth trend in the Norway spruce chronology is already visible in the last 20 years at the studied site (Fig. 3), and may represent an initial indication that the vitality and resilience of Norway spruce trees in these mountains is beginning to decline.

Both species displayed temporal instability with the investigated climatic parameters (Fig. 6). Unlike TRW chronologies of both species, which showed a sharp decline in the strength of the most important climate-growth relationships towards the end of the 20th century, EWBI chronologies showed a steady or increasing trend in the strength of the relationship over the same period (Fig. 6). This difference may partly be explained by the fact that the EWBI signal originates from wood formed at the beginning of the growing season (*i.e.* earlywood), while TRW is a proxy for tree growth over the whole growing season. Recent climate observations from Velebit (RegCM 2009; Zaninović *et al.* 2008) show a decrease of snow cover and a rise in spring temperatures, indicating more favourable conditions for an earlier start of the growing season. Although high-elevation conifer forests around Europe have generally shown an increase in radial growth in response to rising temperatures in recent decades (Rolland *et al.* 1998; Körner 2012; Pretzsch *et al.* 2014; Piovesan *et al.* 2019), the impact of major drought events on tree vitality may prove to be more severe than changes in temperature-related conditions (Fuhrer *et al.* 2006; Allen *et al.* 2010), praticularly in drought-prone areas such as Velebit. Considering the inconsistent and temporally variable growth sensitivity to the most dominant climatic drivers over time, it is possible that these primary forests will increasingly exhibit a nonlinear growth response to climate as environmental conditions continue to change.

4.1.4.3 POINTER YEAR RELATIONSHIPS

The pointer year analysis (Fig. 7) demonstrated how both species were responsive to stressful growing conditions related to climatic extremes in some years. Although not all pointer years could be reasonably explained, the examination of the most relevant climatic variables helped to plausibly interpret some of these extreme growth years as being climatically driven. Interestingly, while most pointers in the chronologies of both tree-ring parameters coincided with distinct climatic extremes, some pointers (*e.g.*, 1986, 2004) occurred the year following a climatically extreme event. This is in line with the observed prior year climate-growth relationships and further highlights the sensitivity of growth to climatic conditions in the year prior to ring formation (in addition to current year conditions), particularly in the case of TRW. In Table 2, we present possible explanations for the occurrence of some of the most notable pointer years identified in the chronologies presented in Fig. 7.

Table 2. Detailed description of events which may explain the occurrence of specific pointer years.

EVENT YEAR	CHRONOLOGIES	DESCRIPTION OF EVENT YEAR
1914 (+)	**ABAL TRW, PIAB TRW**	Higher minimum temperatures during the beginning of the vegetation period (April to June), and a prolonged 1913/1914 winter season with large amounts of snow (Larcher 1995; Rolland *et al.* 2000)
1929 (-)	**ABAL TRW**	The "winter of the century" was recorded throughout most of Croatia (CroMeteo 2013). Due to the abrupt penetration and extended duration of cold air over the Mediterranean with frequent and abundant amounts of snow precipitation, very low air temperatures and long-lasting snow cover prolonged unfavourable conditions for growth until mid-April.
1945 (-)	**PIAB TRW, ABAL BI, PIAB BI**	Growing season of 1945 was marked by fairly dry and warm conditions and has been noted around Central-Europe as an event year (Neuwirth *et al.* 2007).
1963 (-)	**ALL TRW AND BI**	Significant decrease in average annual temperature with the winter of 1962/1963 being marked as one of the coolest and longest winters in 20th century meteorological records. A relationship between 1963 temperatures and an increase of atmospheric aerosol concentrations attributed to an eruption of the Agung volcano in Indonesia in February 1963 has also previously been noted (Ammann *et al.* 2003; Fischer *et al.* 2007).
1986 (-)	**PIAB TRW AND PIAB BI**	Severe summer season drought throughout Southern Europe in 1985 (Spinoni *et al.* 2015), which could explain the negative pointer in 1986 (influence of previous year on growth in subsequent year).
1999 (-)	**ABAL TRW AND ABAL BI**	Occurrence of late spring frost. No other climatic parameters were unusually above or below average.
2004 (-)	**PIAB TRW**	An exceptional heat wave in 2003 recorded throughout Central-Eastern Europe, resulted in a mild winter and one of the hottest summers in recent centuries (Stott *et al.* 2004). With lower winter precipitation prior to the start of the growing season in 2004, severe drought may have led to substantially narrower ring development.
2011 (+)	**ABAL TRW**	Summer in Smrčeve doline was marked by above-average precipitation and temperature, creating favorable growing conditions.

4.1.4.4 POTENTIAL NON-CLIMATIC INTERACTIONS

In recent decades, tree growth may have in part become less sensitive to climate, because of the impact of non-climatic agents (*e.g.*, disturbance, competition, etc.). By applying the relatively inflexible negative exponential detrending curve in the development of the STD chronologies intended to retain decadal / multidecadal trends, this may have invariably led to the preservation of decadal growth trends that may be of non-climatic origin (Rydval *et al.* 2016). Trends related to disturbance could at least partly explain and account for some of the divergent growth trends apparent when comparing the TRW chronologies of the two species (*e.g.*, after 1970 in Fig. 3A), but do not appreciably affect the BI chronologies (Rydval *et al.* 2018).

Extreme climatic events may also lead to physiological weakening of trees and potential subsequent increases in pest populations, which may have detrimental impacts on the recovery and vitality of these old forests. For example, warmer temperatures have been shown to directly correspond with over-wintering potential of spruce bark beetle (*Ips typographus* L.), causing earlier seasonal appearance, prolonged periods of activity and increased reproduction (Jönsson *et al.* 2009, 2011; Hrašovec *et al.* 2011; Dworschak 2013), potentially causing rapid tree mortality. Spaić (1955) recorded a case of 600 ha of spruce forest dieback, caused by a bark beetle outbreak following a severe windstorm and fire disturbance event that occurred in 1940 in the Northern Velebit area.

Although not many fire disturbances were recorded in the Northern Velebit national park in the last 50 years, Zaninović *et al.* (2008) have shown an increase in the frequency of forest fires around the Velebit mountain range, further highlighting the vulnerability of Dinaric primary forests. As climate change gradually increases the likelihood of warmer and drier summers around the Mediterranean, specific disturbance events (incl. windstorms, fire events, bark beetle outbreaks) may increasingly threaten the future vitality of these valuable forest ecosystems.

4.1.4.5 FUTURE RESEARCH POTENTIAL

The Europe-wide net primary productivity reduction, observed after the extreme drought in the summer of 2003, showed how sensitive forest ecosystems are to climatic extremes (Ciais *et al.* 2005; van der Maaten-Theunissen *et al.* 2015). Changes in average climate conditions, and related changes in the response of various tree species to those climatic changes, will likely lead to significant shifts in forest composition. The influence of increasing temperatures and changing hydroclimatic patterns on growth dynamics of temperate forests in a range of geographic regions with various soil substrate types, remains inadequately researched

(Shestaková *et al.* 2016). There is also a risk that failure to consider disturbance legacies as a factor contributing to contemporary forest dynamics could potentially confound a broader understanding and interpretation of climate-growth-disturbance interactions in primary forests (Pan *et al.* 2011b; Bond-Lamberty *et al.* 2014; Schurman *et al.* 2018). Additional analysis extended by stratifying stand structural attributes and evaluating disturbance histories could be helpful in expanding our knowledge of the multi-factor interactions that may influence future climate sensitivity of these primary forests and help to explain more fully some of the chronology trends observed in this study.

4.1.5 CONCLUSION

Using dendrochronological methods, the growth response of Norway spruce and silver fir trees to climate in NP Northern Velebit showed similar climate responses to mountain forests in other parts of Europe, where high temperatures along with concurrent limited moisture availability inhibit growth during dry summer months. Using the novel earlywood blue intensity tree-ring parameter, earlywood formation of both species showed a dependency on water availability and associated sensitivity to the growth-inhibiting effect of high summer season temperatures. With the expected continuation of the global trend of rising atmospheric temperatures throughout the 21st century, along with increasing drought stress in southern Europe, increasingly stressful growing conditions for mixed-species primary forests in the Dinaric Mountains may lead to physiological weakening of trees and higher susceptibility to the impacts of both climatic and non-climatic perturbations in the future. Due to the unstable climatic signal of both Norway spruce and silver fir trees at Smrčeve doline, the future development of any potential climate reconstruction may be complicated by the complex interactions of growth dynamics and various growth-influencing factors, regardless of the type of tree-ring parameter examined. This study offers strong evidence for climate-induced growth changes that may have far-reaching implications for the health and future development of primary mountain forests of the Dinaric Mountain chain. These insights should inform the adaptation of future protection and management strategies, which could improve ecosystem functions provided by these forest communities and help mitigate some of the anticipated impacts of climate change.

DECLARATION OF COMPETING INTERESTS

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

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SUPPORTING INFORMATION

Supplementary material associated with this article can be found in the online version, or in the Supporting Information subsection (S1) of the Bibliography section at the end of this Thesis.

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4.2 LARGE OLD TREES INCREASE GROWTH UNDER SHIFTING CLIMATIC CONDITIONS: ALIGNING TREE LONGEVITY AND INDIVIDUAL GROWTH DYNAMICS IN PRIMARY MOUNTAIN SPRUCE FORESTS

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Abstract: In a world of accelerating changes in environmental conditions driving tree growth, tradeoffs between tree growth rate and longevity could curtail the abundance of large, old trees (LOTs), with potentially dire consequences for biodiversity and carbon storage. However, the influence of tree-level tradeoffs on forest structure at landscape scales will also depend on disturbances, which shape tree size and age distribution, and on whether LOTs can benefit from improved growing conditions due to climate warming. We analyzed temporal and spatial variation in radial growth patterns from ~ 5000 Norway spruce (*Picea abies* (L.) H. Karst) live and dead trees from the Western Carpathian primary spruce forest stands. We applied mixed-linear modelling to quantify the importance of LOT growth histories and stand dynamics (*i.e.*, competition and disturbance factors) on lifespan. Finally, we assessed regional synchronization in radial growth variability over the 20th century, and modelled the effects of stand dynamics and climate on LOTs recent growth trends.

Tree age varied considerably among forest stands, implying an important role of disturbance as an age constraint. Slow juvenile growth and longer period of suppressed growth prolonged tree lifespan, while increasing disturbance severity and shorter time since last disturbance decreased it. The highest age was not achieved only by trees with continuous slow growth, but those with slow juvenile growth followed by subsequent growth releases. Growth trend analysis demonstrated an increase in absolute growth rates in response to climate warming, with late summer temperatures driving the recent growth trend. Contrary to our expectation that LOTs would eventually exhibit declining growth rates, the oldest LOTs (> 400 years) continuously increase growth throughout their lives, indicating a high phenotypic plasticity of LOTs for increasing biomass, and a strong carbon sink role of primary spruce forests under rising temperatures, intensifying droughts, and increasing bark beetle outbreaks.

4.2.1 INTRODUCTION

Large old trees (hereafter "*LOTs*") are generally a rare feature in forest landscapes and global change forces are likely driving further declines (Lindenmayer, Laurance, & Franklin, 2012). Although limited in abundance, LOTs are keystone ecological components, providing habitat (Lindenmayer *et al.*, 2014, 2016), large carbon storage (Clark & Clark, 2000; Keith, Mackey, Berry, Lindenmayer, & Gibbons, 2010; Slik *et al.*, 2013; Mildrexler, Berner, Law, Birdsey, & Moomaw, 2020), and shaping micro- and meso-climates (Lindenmayer & Laurance, 2017). LOTs also serve as valuable indicators of historical ecosystem dynamics and forest naturalness (Di Filippo, Biondi, Piovesan, & Ziacco, 2017; Piovesan & Biondi, 2020), highlighting areas of high ecological value and placing them outside of intensive forest management practices (Mikoláš *et al.*, 2019). Subtle changes in factors constraining LOT growth and abundance therefore carry major implications for forest landscape functioning, but the inherent rareness of LOTs has impeded accurate assessments of their dynamics.

One important constraint on LOT abundance is the theorized tradeoff between tree growth rate and longevity (*e.g.*, Schulman, 1954; Abrams, 2007; Di Filippo, Biondi, Maugeri, Schirone, & Piovesan, 2012, Di Filippo *et al.*, 2015; Piovesan *et al.*, 2019), which recently found strong empirical support in a comprehensive tree-ring analysis of living and dead trees (Büntgen *et al.*, 2019). The growth-mortality tradeoff arises from a partitioning of resource allocation to growth versus survival when growing conditions are favorable, leading to rapid growth rates due to ample resources access (Loehle, 1988; Arendt, 1997), but at the cost of reduced investments into defensive compounds, mechanical and hydraulic tissues that favor stress tolerance (Kleczewski, Herms, & Bonello, 2010; Bigler, 2016), resulting in long-term exposure to size-dependent risk factors, external mortality agents and, ultimately, shorter lifespan (Ryan & Yoder, 1997; Bugmann & Bigler, 2011; Di Filippo *et al.*, 2015).

Studies of the growth-mortality tradeoff have generally focused on mean growth as an indicator of tree longevity (*e.g.* Black, Colbert, & Pederson, 2008; Johnson & Abrams, 2009; Bigler & Veblen, 2009; Di Filippo *et al.*, 2012; Brienen *et al.*, 2020), yet tree growth tends to be highly modular under temporally variable conditions, and the extent to which trees that were previously acclimated to resource-limited growing conditions shift into rapid growth when growing constraints are alleviated, has rarely been tested (*e.g.* Pretzsch, 2021). Furthermore, it is commonly assumed that growth rates of LOTs will eventually decouple from environmental variability, because if nothing else, tree growth is ultimately limited by biomechanical constraints on maximum tree size (Weiner & Thomas, 2001; Koch, Sillet, Jenings, & Davis, 2004). Yet, we rarely have precise data on LOT growth rates and their drivers, potentially leading to underestimation of the role of LOTs in contributing to increasing forest C sequestration (Luyssaert *et al.*, 2008; Stephenson *et al.*, 2014).

Although growth-mortality tradeoff is a well-conserved phenomenon (*e.g.*, Black *et al.*, 2008; Bigler & Veblen, 2009; Johnson & Abrams, 2009; Brienen, Gloor, & Ziv, 2016; Bošela *et al.*, 2018; Piovesan *et al.*, 2019), additional regional factors should be considered before strong conclusions are made regarding the implications of the growth-mortality tradeoff for emergent forest properties such as productivity, carbon storage and LOT abundance. The character of a region's natural disturbance regime plays an important role in dictating forest age structure (Fraver, White, & Seymour, 2009; Turner, 2010; Svoboda *et al.*, 2014; Meigs *et al.*, 2017; Pavlin *et al.*, 2021) and the competitive interactions between trees (Nagel, Svoboda, & Kobal, 2014). In closed-canopy forests, many trees will have recruited in shade and undergone repeated cycles of suppression and releases, whereas others will have recruited in canopy openings following a severe disturbance (Canham *et al.*, 1990), thus shaping the conservativeness of a tree’s growth history and, potentially, longevity. In an environment where trees rarely reach their maximum size or high age due to the frequency of disturbances, observing LOTs responding positively to the alleviation of growth-limiting factors could allow trees to attain larger sizes prior to disturbance, which would almost certainly benefit carbon sequestration. However, if accelerated tree growth rates under warmer conditions are paired with intensifying disturbances, decreased longevity and reduced LOT abundance, then the potential increases in forest biomass could be limited (Büntgen *et al.*, 2019), and carbon gains offset by rising mortality.

Warmer conditions and extended growing season have generally enhanced forest productivity in high-elevation Western Carpathian forests (Bošela *et al.*, 2018; Schurman *et al.*, 2019). However, intensifying drought-induced stress has increased vulnerability of spruce trees to bark beetle outbreaks in recent years (Mezei, Grodzki, Blaženec, & Jakuš, 2014), whereas past temporally synchronous disturbances have predisposed parts of the landscape to extensive and severe windstorm events in the region (Janda *et al.*, 2017; Schurman *et al.*, 2018), potentially modifying the climate-growth associations (Ponocná *et al.*, 2018; Lange *et al.*, 2018). These trends raise additional concerns for the survival of LOTs, as they show heightened physiological vulnerability to stochastic environmental changes (Phillips, Buckley, & Tissue, 2008; Primicia *et al.*, 2015; Bennett, McDowell, Allen, & Anderson-Teixeira, 2015). Whereas the general ability of individual trees to cope with stochastic events (*e.g.* an extreme drought) is predominantly determined by their phenotypic plasticity (Klein, Hoch, Yakir, & Körner, 2014) and C allocation strategies (Weber, Gessler, & Günter, 2018), macroclimatic variation can trigger synchronous growth patterns at broad spatiotemporal scales (Hughes *et al.*, 1982; Briffa *et al.*, 2008; Zhou, Fang, Zhang,, Dong, & Chen, 2016; Shestaková, Gutiérrez, Valeriano, Lapshina, & Voltas, 2019; Camarero, Colangelo, Gazol, & Azorin-Molina, 2021), which could indicate increasing vulnerability of forest ecosystems across environmental gradients. In this context, adequate identification of local and regional environmental drivers of tree growth, and quantification of the temporal trends in ring width synchrony, could provide a meaningful interpretation of regional growth patterns (Babst *et al.*, 2013; Shestaková *et al.*, 2019), and help predict potential ecological consequences of global climate change on LOTs abundance and, subsequently, the functioning, productivity and carbon sink strength of primary spruce forests.

We used an extensive tree-ring dataset from Western Carpathian primary Norway spruce (*Picea abies* (L.) H. Karst) forests in order to disentangle the importance of various spatial and temporal factors complicating the presupposition that the existence of the growth-mortality tradeoff could place an upper limit on forest biomass and LOT abundance under climate change. In this respect, we address the following research objectives:

1) Assess to what extent life-growth histories and longevity covary. We tested for the negative correlation between mean growth rate and age (for 4405 living trees), and mean growth and age at death (for 620 dead trees). Furthermore, we adopted a mixed model analysis of variance approach (ANOVA; Wigley, Briffa, & Jones, 1984) to examine the differences in juvenile growth patterns between living and dead trees and confirm the existence of the growth-mortality tradeoff.

2) Determine the relative contribution of internal physiological tradeoffs and external mortality agents for driving spatial variability in tree age. We used linear mixed modelling to compare the effects of tree' (*i.e.,* growth histories, tree-to-tree competition) and site (*i.e.,* bedrock, aspect, and slope) features vs disturbance histories as drivers of spatial variation in forest age structure.

3) Investigate the temporal variability in radial growth patterns. We adopted the tree-ring synchrony approach (*sensu* Shestaková *et al.*, 2016) as a diagnostic for the degree of macroclimatic control of tree growth over the 20th century. Furthermore, we incorporated the sigmoid growth curve as a theoretical representation of intra-annual growth variation juxtaposed to the observed regional growth patterns.

4) Disentangle the dominant drivers of LOTs recent growth trend. We used linear mixed modelling to infer whether growth patterns established early in life influence the growth sensitivity to limiting factors later in life, and whether LOTs can shift into rapid growth under recent climate warming, which could contribute to a net increase in forest biomass.

4.2.2 MATERIALS AND METHODS

4.2.2.1. STUDY AREA

The Western Carpathians envelop one of the largest remnants of subalpine primary spruce forests in Europe (Svoboda *et al.*, 2014), ranking them highly valuable among European regions (Mikoláš *et al.*, 2019; Sabatini *et al.*, 2020). The study area consisted of monospecific Norway spruce primary forest stands, determined by the national inventory of primary forests in Slovakia in 2009-2010 (www.pralesy.sk) and 2013-2015 primary forest inventory (Svoboda *et al.*, 2014; Mikoláš *et al.*, 2019). The study area spanned across a latitudinal (from 48° 31′ 47″ N – 49° 31′ 24″ N and 19° 12′ 45″ E – 20° 11′ 53″ E) and altitudinal range (from 1200 m a.s.l. to the upper forest limit, *i.e.*, around 1600 m a.s.l.), capturing the wide gradient of Norway spruce forests natural distribution in the Western Carpathians, including the most southern (Polana) and northern (Beskids) sites (Fig. 1). Majority of these primary forests are fragmented and scattered over the region, mainly due to intense logging practices and lenient control measures that affected their succession and distribution. They are dominated by Norway spruce (over 90% of overstory basal area), accompanied by European silver fir (*Abies alba* Mill.), Scots pine (*Pinus sylvestris* L.), rowan (*Sorbus aucuparia* L.), birch (*Betula* spp.), and at higher altitudes Swiss pine (*Pinus cembra* L.). The average annual temperature ranges from 2.5°C to 4.5°C, while the annual precipitation ranges from 1000 mm/year at the southernmost locality in the Polana massif, to 2400 mm/year on the northern slopes of the Tatra Mts (Bošela, 2010; Holekša *et al.*, 2017). Bedrock and soils varied, with podzols and leptosols atop of granitoids and limestones being the predominant soil types (Table 1). Stands chosen for the study represent a range of geographical and geological variability, regarding physiographic (*i.e.*, slope, aspect, altitude) and structural (*i.e.*, regeneration density, canopy cover) attributes, thus capturing the landscape heterogeneity of the Western Carpathian region (for more information visit www.remoteforests.org).

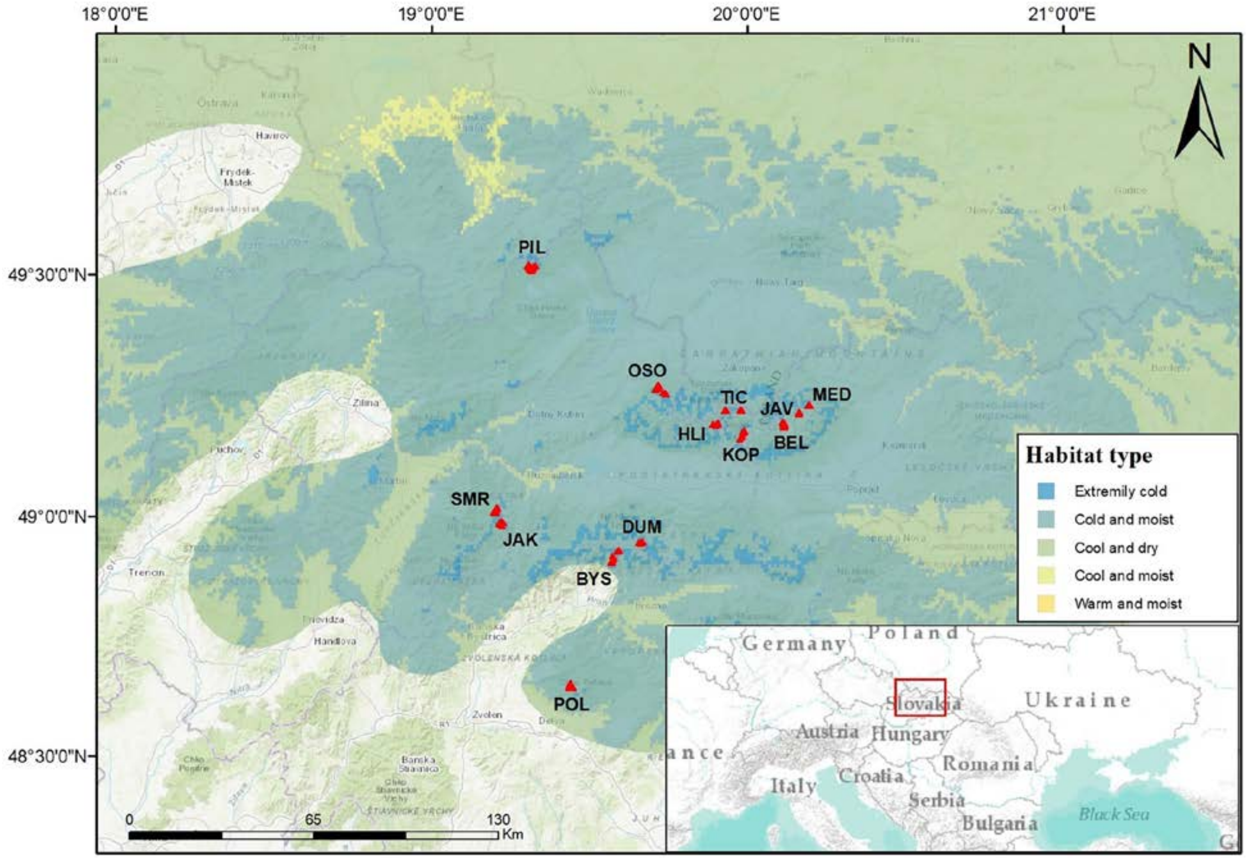

Fig. 1. Map of studied sites in the Western Carpathians.

Norway spruce habitat types given in different colours (from de Rigo *et al.* 2016). The abbreviations represent forest stands (BEL - Bielovodská dolina, BYS - Bystrá dolina, DUM – Ďumbier, HLI – Hlina, JAV – Javorova Dolina, JAK - Jánošíkova Kolkáreň, KOP - Kôprová dolina, MED – Žadné Meďodoly, OSO – Osobita, PIL - Piľsko, POL – Poľana, SMR – Smrekovica, TIC - Tichá dolina). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

4.2.2.2 SAMPLE COLLECTION AND DATA PREPARATION

A stratified random sampling design established a series of permanent sample plots (PSP) using ArcView 9.3 Environment (ESRI ArcGIS, 2011), by overlaying a gridded network of 1- or 2-ha cell sizes over each stand, depending on total stand area, and randomly placing a single PSP within the interior of each cell (0.25 ha or 0.49 ha, respectively). In each 1000-m^2 circular PSP, site parameters (*i.e.*, geospatial location, species, altitude, slope, and aspect), composition and structure of live and standing dead trees with diameter at breast height (DBH) ≥ 10 cm, and canopy status were recorded. We collected increment cores from randomly selected 15-25 living and standing dead trees per PSP with DBH ≥ 10 cm for quantifying individual tree age, growth patterns and disturbance histories. One core per tree was extracted 1 m above the ground using a 5 mm Haglöf increment borer, perpendicularly to the slope to avoid wood compression. In total, 5800 increment cores from 13 stands with 179 PSPs were collected in the period between

2013-2019. For a more detailed description of plot establishment and data collection strategy see Janda *et al.* (2019).

Increment cores were air-dried, mounted on wooden boards, and sanded with different grit-level sanding papers until reaching clear visibility of annual growth rings. Laboratory analyses were based on standard dendrochronological dating techniques described by Stokes & Smiley (1996). Annual tree-ring widths (TRW) were measured using a stereomicroscope to an accuracy of 0,01 mm using a Lintab-TM traversing measuring stage in tandem with TSAP-WinTM software (www.rinntech.de). Cores were first visually cross dated using the marker year approach (Yamaguchi, 1991), followed by statistical validation using COFECHA (Holmes, 1983; Grissino-Mayer, 2001) and CDendro softwares (Larsson, 2015). The number of missing rings was estimated by fitting a geometric pith locator to the innermost rings and converting the distance to the theoretical pith into a number of missing rings (Duncan, 1989). Crossdating of individual series was based on measures of GFK (Gleichläufigkeit; Schweingruber, 1988), T-test, and Pearson’s correlation coefficient. After excluding increment cores that could not be sufficiently cross dated, had more than 20 missing rings or more than 30 mm core missing, 5025 cores were used in the subsequent analysis (Begović, 2022).

Table 1. Stand characteristics of Western Carpathian primary forests

Mountain region	Stands (with abbreviations)	Number of plots	Elevation range (m a.s.l.)	Mean tree density (N/ha)	Mean age (years)	Max/min age (years)	Mean DBH (cm)	Soil profile	Bedrock
Eastern Tatras	Bielovodská dolina (BEL)	13	1297–1389	485	171	432/29	31.85	Leptosols	Granitoids
	Javorová dolina (JAV)	8	1395–1478	494	179	354/22	33.49	Podzols	Granitoids
	Zadné Meďodoly (MED)	7	1454–1536	447	148	254/25	34.37	Leptosols	Limestones (Dolomites)
Central Tatras	Hliná dolina (HLI)	16	1352–1493	494	120	333/22	34.57	Podzols	Metapsamites
	Kôprová dolina (KOP)	13	1367–1501	435	137	430/20	35.38	Leptosols	Granitoids
	Tichá dolina (TIC)	16	1331–1481	568	94	359/19	30.24	Podzols	Limestones (Dolomites)
Western Tatras	Osobitá (OSO)	14	1235–1461	389	157	314/31	39.21	Leptosols	Limestones (Dolomites)
Low Tatras	Bystrá dolina (BYS)	16	1339–1473	376	121	403/19	36.29	Podzols	Metapsamites, Granitoids
	Ďumbier (DUM)	17	1416–1535	483	159	438/23	37.11	Podzols	Granitoids
Great Fatra	Jánošíkova kolkáreň (JAK)	25	1223–1397	326	127	408/24	36.44	Podzols	Granitoids
	Smrekovica (SMR)	11	1334–1437	265	137	307/16	44.11	Podzols	Granitoids
Orava Beskids	Pilsko (PIL)	12	1258–1398	273	171	490/22	45.34	Podzols	Claystones, Sandstones
Poľana	Poľana (POL)	16	1353–1415	364	122	252/25	43.45	Andosols	Andesites

4.2.2.3 DATA PROCESSING

Two growth metrics were derived from individual tree-ring series: basal area increments (BAIs), used to quantify annual biomass production and preserving the long-term growth trends (Rubino & McCarthy, 2000), and detrended ring width indices (RWI) for disentangling the effects of high-frequency climate variability on tree growth, while filtering out the impact of biological and non-climatic trends (Biondi & Qeadan, 2008; Bowman, Brienen, Gloor, Phillips, & Prior, 2013).

Basal area was calculated for each tree using the tree radius and formula for circular cross-section, and BAI was calculated as the difference between current and previous year BA values. In order to evaluate growth differences across age groups, each tree was assigned to a 50-year age class based on tree age at sampling. Mean decadal growth values of individual BAI series were calculated and averaged within each age class for allowing comparison across age classes. Additionally, estimates of temporal trends in tree growth have shown to be an effective tool in interpreting growth rate changes in relation to climate change (Shestaková *et al.*, 2016; Schurman *et al.*, 2019). To this end, we adopted the mixed-modelling approach from Shestaková, Aguilera, Ferrio, Gutiérrez, & Voltas (2014) to estimate regional growth synchrony value ($\hat{a}_c$), calculated for successive 30-year periods lagged by 5-year increments (Alday, Shestaková, de Rios, & Voltas, 2018).

As we aimed to determine the climatic impact on Norway spruce LOTs across the region, a regional Western Carpathian RWI chronology from the 75th quartile of oldest and largest (*i.e.*, DBH) trees from each site was developed (Cook & Kairiukstis, 1990). Two RWI chronology versions (*i.e.*, standard and residual) were developed in order to retain the inter-annual to multi-decadal growth fluctuations. Individual TRW series were standardized by fitting a cubic smoothing spline with a 50% frequency response over 100-year periods (Cook, 1985). Ring width indices (RWI) were then produced as ratios between raw TRW and modelled values. In order to retain only high-frequency variability without the influence of autocorrelation, residual chronologies were obtained by applying an autoregressive model to the standardized chronologies and averaging them by year (Cook, 1985). The detrended chronologies were then averaged at stand-level by year as Tukey's bi-weight robust mean, developing the standard and residual stand-level chronologies, which were then averaged within the region to produce a regional Western Carpathian chronology. Mean interseries correlation (*rbar*) and expressed population signal (*EPS*) were used to assess the robustness of the chronologies (Table S3; Wigley *et al.*, 1984; Cook & Krusic, 2005).

4.2.2.4 STATISTICAL ANALYSIS

4.2.2.4.1 PREDICTOR VARIABLES

The predictor variables can be aggregated into five categories: 1) disturbance parameters, 2) individual tree-life histories, 3) tree-to-tree competition, 4) site attributes, and 5) climate factors. Full overview of all independent predictors with basic descriptive statistics can be found in Table SI1.

We include only a brief description of the quantification of disturbance metrics, as we mainly extracted disturbance histories parameters from a previously published 250-year disturbance reconstruction record from spruce primary forests (*e.g.*, Janda *et al.*, 2017, 2019; Schurman *et al.*, 2018, 2019; Čada *et al.*, 2020). Individual trees were distributed to modes of accession up the forest canopy based on their radial growth patterns (Lorimer & Frelich, 1989; Frelich, 2002) as: (1) open canopy recruitment, *i.e.* trees that initiated rapid growth shortly after canopy opening; (2) released trees, *i.e.* trees that established in the shaded understory and recruited to the canopy abruptly through growth release(s) (Frelich & Lorimer, 1991), (3) trees with a combination of both strategies (hereafter "*combo*"), and (4) trees without noticeable events. Open canopy recruitment was identified by tree juvenile growth patterns following Trotsiuk *et al.* (2014) and empirically established growth thresholds to distinguish suppressed from non-suppressed saplings (Hosmer & Lemeshow, 2004), whereas growth releases were detected using the absolute increase method following Fraver & White (2005) in years with absolute growth difference between the preceding and following 10-year means exceeding 1.25 standard deviations from the mean difference. Due to a moderately shade-tolerant nature of Norway spruce, multiple releases are often necessary for young trees to reach canopy level, so in order to minimize overestimation of disturbances, only releases occurring prior to the DBH threshold of 23 cm were counted (Janda *et al.*, 2017). Detected canopy accession events were linked to present-day crown area of sample trees as estimates of the original disturbance-induced canopy gap size. These individual tree-level gaps were summed annually and divided by the aggregate crown area of the sample trees to represent the proportion of plot disturbed in the past (Lorimer & Frelich, 1989). Ultimately, we used maximum disturbance severity (hereafter "*disturbance severity*"; defined as the proportion of the disturbed canopy area from the highest severity disturbance event) and time since maximum severity disturbance event (hereafter "*disturbance year*"; identified as the peak in kernel density function smoothed annual values from the highest severity disturbance event) as metrics of plot-level disturbance dynamics.

Several life-history traits were quantified to comprehensively assess individual tree growth strategies. Firstly, we considered mean ring width during the first 50 years of life (hereafter "*juvenile growth*") for all trees. This age represents average time for trees to reach the 10 cm DBH coring threshold, and greatly reduces the intrinsic age effect on tree-ring chronologies (Di Filippo *et al.*, 2012; Bigler *et al.*, 2016). Secondly, we computed suppression length interval (hereafter "*suppression*") over the whole length of tree-ring chronologies (excluding first 50 years), as an interval of 5 or more subsequent years with average growth rate lower than 0.5 mm/year, and no sequences of 3 or more years with growth above the 0.5 mm/year threshold (Canham *et al.*, 1990). Lastly, we calculated the average growth rate (TRW and BAI) over the whole lifespan of a tree.

Calculation of the competition indices was based on the assumption that large size and high growth imply high tree competitiveness. To that extent, we calculated the distance-dependent competition index individually for each year (CI_{Hy}) and cumulatively (CI_{Hc}), taking into account the number and size of the neighboring competitors and their distance to the focal tree (Hegyi, 1974) following the formula (eq. 1, 2):

$$CI_{Hy} = (dbh_{ny}/dbh_{ty})\,/dist_{nt} \qquad \textbf{(1)}$$

$$CI_{Hc} = \Sigma\, CI_{Hy} \qquad \textbf{(2)}$$

where dbh_{ny} represents DBH of a competitor in a specific year, dbh_{ty} DBH of target tree at a specific year and $dist_{nt}$ as the distance between trees, respectively. Hegyi index of a target tree represents the sum of individual Hegyi indices calculated for the competitors. The threshold radius above which neighbors were discarded as uncompetitive was estimated through comparative analysis of mean BAI and CI_H for all trees considering different radii (*i.e.* 2, 4, 6, 8, 10 and 12 m). The radius of 8 m exhibited the strongest correlation and was used in further calculations. An area-weighted edge correction was applied to correct for the edge effects of Cis extending outside the plot boundaries (Das, 2012). Additionally, we derived a retrospective dynamic competition index from BAI, which is a time-varying index describing changes in competitive abilities of neighbouring trees over a specific time period (Weber, Bugmann, Fonti, & Rigling, 2008). The index becomes higher with more competitors a subject tree has and the better the competitors grow in comparison to the subject tree. The index was obtained over the period 1980-2018 in order to detect the effect of changes in competitive relationships under the impacts of climate change.

The investigated site descriptors (*i.e.*, slope, aspect, and bedrock) were obtained from field measurements. To ease the interpretation of the effects of terrain aspect, aspect was transformed into a linear metric (hereafter “*northness*”) following the formula: northness = *cosine* [(aspect in degrees * π)/180)]. We considered additional predictor variables, such as latitude, longitude, and altitude, but excluded them due to high correlation with other predictors (*e.g.,* temperature vs altitude, Fig. S9), or lack of explanatory power.

Regional climate information was obtained from KNMI Climate Explorer as CRU TS 4.04 gridded 0.5° instrumental climate datasets (https://climexp.knmi.nl/start.cgi; Trouet & Van Oldenborgh, 2013; Harris, Osborn, Jones, & Lister, 2020) for the coordinates of each stand over the period 1901-2018. Annual averages of monthly mean temperature, self-calibrating Palmer drought severity index (hereafter “*scPDSI*”; see S1) and monthly precipitation totals were used in the climate-growth response analysis.

4.2.2.4.2 CLIMATE-GROWTH ANALYSIS

To identify the period of strongest overlap between the accelerating climate warming (Gazol *et al.*, 2015; Bošela, Štefančík, Petráš, & Vacek, 2016; Bošela *et al.*, 2018) and the observed regional growth trend (Schurman *et al.*, 2019), we fitted a generalized additive model to the regional RWI chronology over the period 1950-2018. Pearson’s correlation coefficients were used to quantify the underlying climatic constraints on LOT growth, and assess the relationship between the regional RWI chronology and climatic variables within a 20-month period (*i.e.*, from May of the year preceding ring formation to December of the ring-formation year; Fritts, 1976), including seasonal windows which represent the climatic variables averaged over several months (*i.e.*, May-July, June-August, July-September). The analysis was conducted for both the residual and standard chronology variants. Additionally, we quantified the temporal stability of the climate-growth association over the 20th century by computing Pearson’s correlation coefficients over 31-year moving window segments.

4.2.2.4.3 REGRESSION MODELLING

We conducted a series of linear regressions and mixed effect models to disentangle and quantify the effect sizes of drivers of tree age and growth.

Firstly, we fitted linear functions to the mean 50-year juvenile tree growth values for 5025 individual TRW chronologies and plotted against tree age and tree size (DBH) in order to identify the overall tradeoff between productivity (*i.e.*, growth) and lifespan (*i.e.*, longevity). Additionally, we tested for the effects of age and time on early-life average decadal growth rates and age of all living and dead trees, respectively, using linear mixed effect modelling. The random effect structure involved intercept terms for plots and stands to account for the hierarchical design of the study (*i.e.*, trees nested in plots and plots nested in stands).

Secondly, we built two separate models to identify the most influential drivers of age and recent growth trend of LOTs (age & DBH > 75th quantile): one for age (hereafter "*the longevity model*") and one for BAI during the period of high temperature-growth synchrony (*i.e.*, 1980-2018; SI4, Fig. 5a; hereafter "*the growth model*"). In total, a subset of 315 LOTs was used in the subsequent models.

The longevity model was fitted using a generalized linear mixed-effects model (GLMM) with a generalized Poisson distribution to account for underdispersion, with age as the response variable and tree size (DBH), growth histories (*i.e.*, mean juvenile growth and relative suppression), competition index, disturbance factors (*i.e.*, disturbance severity and disturbance year) and site attributes (*i.e.* slope and northness) as predictors. Disturbance severity, suppression, DBH and Hegyi index were log-transformed to account for non-normality and meet homogeneity of variance. Only stand identity was considered as a random component of the model.

The growth model was fitted by a GLMM with Gaussian distribution and log-transformed annual BAI values of individual trees as a response variable. Tree age, tree size (*i.e.,* DBH), cumulative dynamic index, site attributes (*i.e.,* slope, aspect, and bedrock) and disturbance factors (*i.e.,* disturbance severity and disturbance year) were included as predictor variables, along with the monthly climate data of the most significant climatic drivers from the climate-growth response analysis (see Fig. 5). Disturbance severity, DBH and cumulative dynamic index were log-transformed to account for non-normality and meet homogeneity of variance. The random effect structure was identical to the aforementioned linear mixed effects models of decadal growth (*i.e.*, trees nested in plots and plots nested in stands).

Model building was conducted over several stages. First, all potential predictor variables were tested for multicollinearity using the Spearman's correlation coefficients I and variance inflation factors (VIFs; Dormann *et al.*, 2013). Individual predictors with Spearman's correlation values $r > 0.3$ (at $P < 0.001$, Fig. S9) and $VIF > 3$ (with tolerance < 0.3) indicated high collinearity and were sequentially dropped from the analysis. Calculations of multicollinearity and removal of highly collinear predictors were repeated until all VIFs were smaller than the pre-determined threshold (Zuur, Ieno, & Elphick, 2010). Remaining predictors, based on our initial hypotheses and ecological interpretation, were fitted using maximum likelihood method (ML). Each predictor was individually dropped from the model in order to quantify their relative importance on the model fit based on differences in AIC and P-values (Chi-square test; Zuur *et al.*, 2009). Since no significant improvement to the model fit was observed (*i.e.*, $\Delta AIC < 10$, Table S4; Burnham & Anderson, 2002), the final models kept all remaining predictors, and were refitted using restricted maximum likelihood (*i.e.*, REML). Predictors were scaled (*i.e.*, z-score) prior to modelling to ensure comparability across effect sizes. The residuals were assessed for potential heteroscedasticity, zero inflation and overdispersion by visual inspection of residual plots and graphical analysis (S5, Fig. S8; Zuur *et al.*, 2009), as well as for temporal autocorrelation of residuals in the growth model using the Durbin-Watson test. Model performance was evaluated based on the proportion of variance accounted for by fixed effects only (*i.e.*, marginal R^2) and fixed and random effects (*i.e.*, conditional R^2), following Nakagawa & Schielzeth (2013). Data analysis and model fitting were performed using R software (R Development Core Team, 2021) and the following packages: *dplR* for tree-ring standardization (Bunn, 2008), *tidyverse* for data manipulation (Wickham *et al.*, 2019), *glmmTMB* for model fitting (Brooks *et al.*, 2017), *Dendrosync* for calculation of tree growth synchrony (Alday *et al.*, 2018), *MuMIn* for model-coefficients calculations (Burnham & Anderson, 2002) and *ggplot2* (Wickham, 2016) for graphical presentation.

4.2.3 RESULTS

4.2.3.1 INDIVIDUAL TREE GROWTH DYNAMICS AND DRIVERS OF LIFESPAN

Juvenile growth rates significantly explained variability in tree size and lifespan (Fig. 2). Age was inversely correlated to mean ring width during the first five decades of a tree's life ($P < 0.001$), whereas DBH increased with faster juvenile growth rates. Generally, Norway spruce trees followed a range of distinct growth trajectories (Fig. S2). Trees with fast early growth (*i.e.*, > 2 mm/year) tend to be younger, whereas the number of LOTs increased with decreasing rates of early growth (*blue* and *purple* lines in Fig. S2). The majority of LOTs exhibited slow (0.5 – 1 mm/year) to very slow juvenile growth rates (< 0.5 mm/year).

The analysis of decadal increments by age class showed overlapping growth rates, with the generally increasing basal area growth over time (Fig. 3a, 3c; Table S2). Significant differences in decadal growth rates were found amongst age classes and tree statuses (*i.e.*, live or dead; $P < 0.0001$). Youngest living trees consistently exhibited a significantly higher BAI and TRW over the first 100 years, while the oldest Norway spruce trees grew at the slowest rate. Additionally, the oldest trees grew significantly slower at the same respective age as their younger counterparts (*e.g.*, BAI of 100-400 mm^2/year of oldest age class versus 180–1000 mm^2/year in the youngest; $P < 0.0001$; Table S2). Although exhibiting rapid growth in the first 50 years, the youngest trees were eventually outperformed by trees between 150-250 years of age (Fig. 3a).

Similar growth patterns were found in dead trees during the first few decades (Fig. 3c), but with significant differences between the oldest and youngest trees (Fig. 3c, 3d). The oldest dead trees grew faster from around 50 years onwards than the youngest ones, exhibiting both a higher BAI and wider tree-rings. Additionally, dead trees over 300 years of age exhibited higher growth rates than their living counterparts at the same respective age. TRW showed a generally decreasing trend over time, generally mirroring the relationships seen in BAI (Fig. 3d). A significant part of the variability in decadal growth was explained by unobserved individual (tree level) and spatial (plot and stand levels) factors (Table S2). The models accounted for well over 55% (up to nearly 80% of variance in decadal BAI of living trees; R^2_c in Table S2) of variance in decadal BAI in live and dead trees.

Majority of LOTs established in the canopy following a release event (Fig. 4a). The oldest trees (age > 350 years) exhibited low growth rates even upon entering the canopy (*released trees*; Fig. 4b; $P < 0.001$), spending half of their lifetime under suppression with average growth rates between 0.5 – 1 mm/year. Age was inversely associated with increasing average growth rates

(Fig. 4b for TRW; BAI data not shown), as the oldest trees generally exhibited a continuation of slow growth established during juvenile years. Additionally, most of the recently dead trees exhibited faster growth than their living counterparts (Fig. 4b *triangles*). Only a few dead trees reached over 350 years of age, while one of the oldest trees found at our sites (*i.e.* 490 years in Orava Beskids; Fig. S3) was in fact a recently dead tree with a long history of slow growth.

Disturbance-related factors and life-history traits exhibited the most significant effects on age (Fig. S7, Table 2). Plot-level maximum severity disturbance ($P < 0.0001$) and shorter time since maximum severity disturbance ($P < 0.05$) had a pronounced negative effect on LOT lifespan. Slow growth was a major factor prolonging lifespan of LOTs ($P < 0.0001$), while fast juvenile growth rates significantly decreased it ($P < 0.0001$). Additionally, age significantly increased with higher DBH ($P < 0.0001$), while neither competition nor site-specific factors exhibited any significant impact on LOT age.

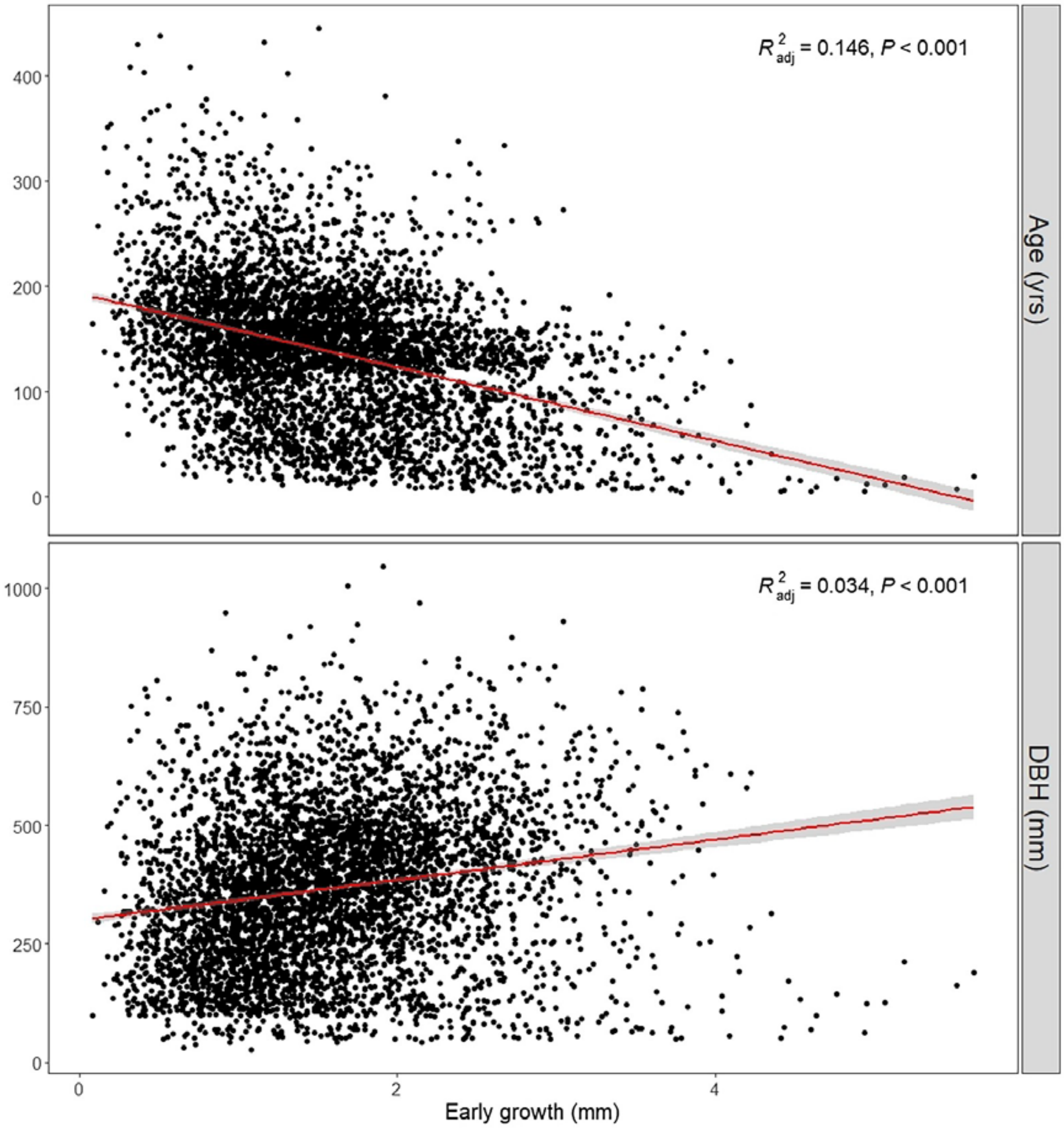

Fig. 2. Relationship between age, size, and early growth.

Relationship between age (a), and stem diameter (*i.e.*, DBH; b) with mean 50- year juvenile growth modelled by linear regression. Red lines indicate linear regression trends, while gray shaded areas represent standard error (SE). Shown are adjusted coefficients of determination R-squared (R2adj) and the probabilities significance value (p).

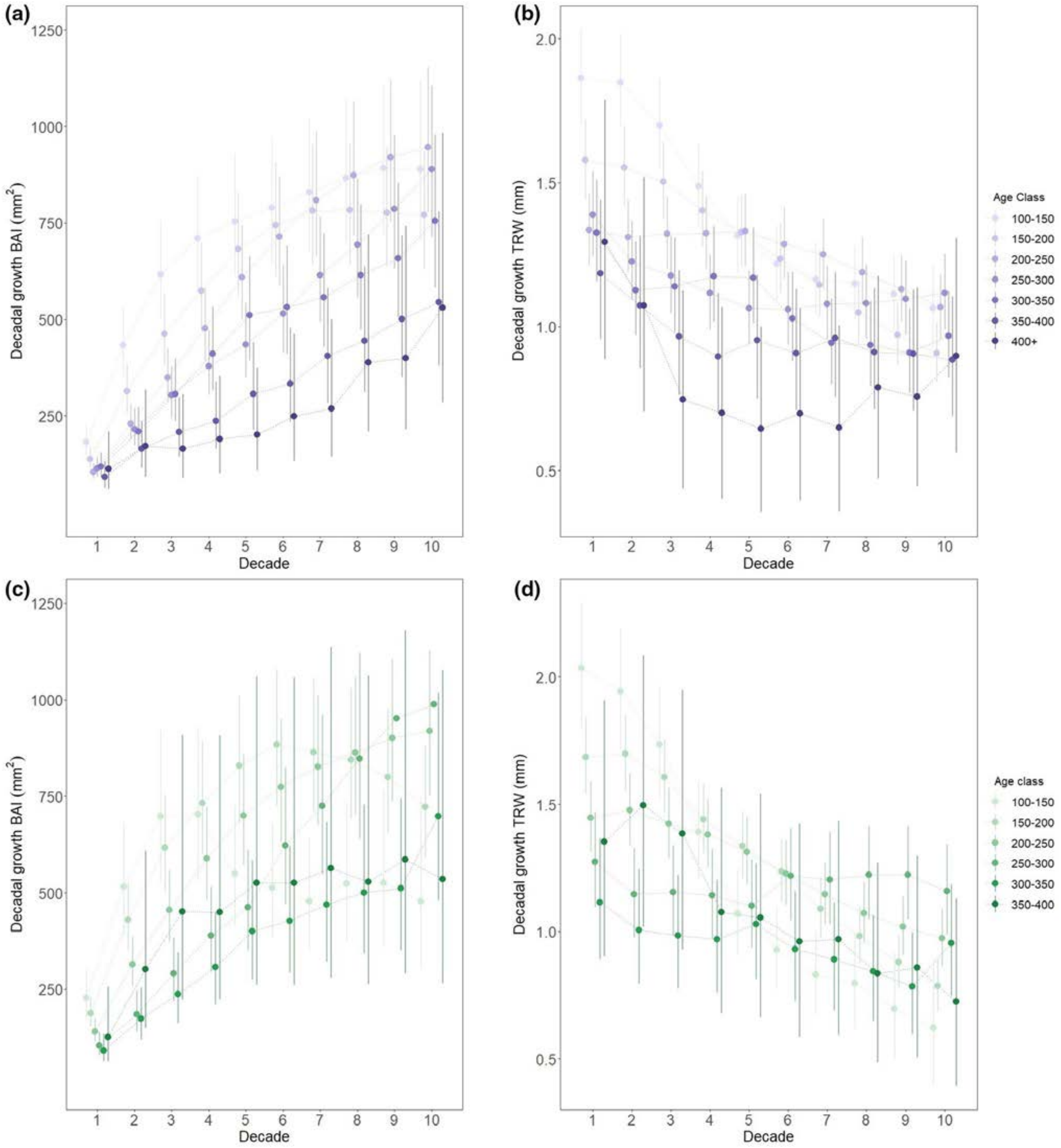

Fig. 3. Early life decadal growth rates across overlapping age classes of live and dead trees. Decadal average growth rates in BAI (a, c) and raw-ring widths (b, d) are given for each age class for the overlapping period (*i.e.*, first 100 years) of living (purple: a, b) and dead (green: c, d) trees, respectively. Each decade indicates a 10-year period of averaged growth over all trees in each data set. Age classes are given in a colour gradient and descending order. Values shown are means and standard error bars. Shown are age classes with a minimum replication of five trees.

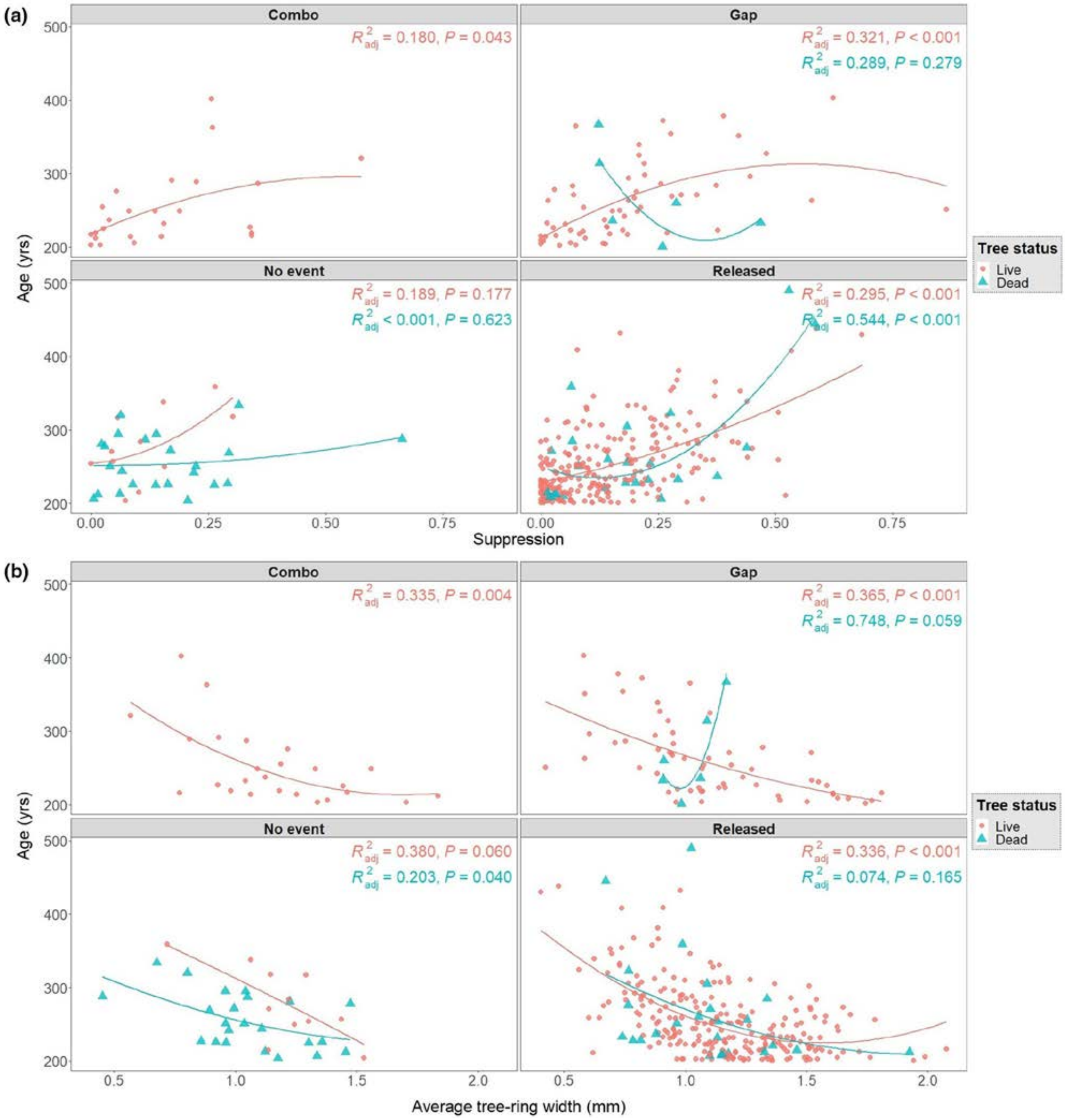

Fig. 4. Relationship between slow growth and lifespan of LOTs.

Suppression (a) is defined as the relative share of years with suppressed growth (*i.e.*, TRW < 0.5 mm/year for five subsequent years and without three consecutive years with TRW > 0.5 mm/year) over the course of a trees' life, while (b) shows the average tree-ring width relative to age. Each facet represents trees with different recruitment strategies: released trees, gap-recruited trees, trees with continuous growth (*i.e.*, no event) and trees with a combination of gap recruitment and subsequent release later in lifetime (*i.e.*, combo). Solid lines represent predictions from generalized additive models, showing the relationship between age and growth factors for live (red, circle) and dead (green, triangle) trees, respectively. Shown are also adjusted coefficients of determination R-squared (R^2_{adj}) and the probabilities significance value (p) of the models.

Table 2. Summary of the longevity model (with Generalized-Poisson distribution) and the growth model (with Gaussian distribution)

Longevity model				**Growth model**			
Age $= \alpha + \beta_{slope} + \beta_{northness} + \beta_{log(DBH)} + \beta_{juvenile\_growth} + \beta_{log(suppression)} + \beta_{log(disturbance\_severity)} + \beta_{disturbance\_year} + \beta_{log(Hegyi\ index)} + (1 \mid stand) + \varepsilon$				**log (BAI)** $= \alpha + \beta_{slope} + \beta_{northness} + \beta_{bedrock} + \beta_{log(DBH)} + \beta_{Age} + \beta_{log(disturbance\_severity)} + \beta_{disturbance\_year} + \beta_{log(Cumulative\ dynamic\ index)} + \beta_{TEMP\_JAS} + \beta_{PDSI\_March} + (1 \mid stand/plot\_id/tree\_id) + \varepsilon$			
Fixed effects	**Est (SE)**	**z**	**P**	**Fixed effects**	**Est (SE)**	**z**	**P**
Slope	.014 (.007)	2	.051	**Slope**	-.034 (.073)	-0.5	.69
Northness	-.014 (.007)	-1.8	.067	**Northness**	-.027 (.063)	-0.4	.765
DBH	.065 (.007)	8.0	< .0001***	**Bedrock_Claystones**	-.172 (.228)	-0.8	.458
Juvenile growth	-.041 (.008)	-5.3	< .0001***	**Bedrock_Granitoids**	-.146 (.271)	-0.5	.574
Suppression	.098 (.008)	12.0	< .0001***	**Bedrock_Limestones**	-.102 (.224)	-0.4	.647
Disturbance severity	-.041 (.007)	-5.4	< .0001***	**Bedrock_Metapsamites**	-.177 (.182)	-1.0	.331
Disturbance year	-.022 (.008)	-2.8	.004*	**DBH**	.486 (.055)	8.8	< .0001***
Hegyi index	-.008 (.007)	-1.1	.284	**Age**	-.302 (.049)	-6.2	< .0001***
				Disturbance severity	-.032 (.057)	-0.6	.93
				Disturbance year	-.004 (.054)	-0.1	.618
				Cumulative dynamic index	.086 (.009)	9.4	< .0001***
				TEMP_JAS	.349 (.014)	25.3	< .0001***
				PDSI_March	.045 (.008)	5.3	< .0001***
Random effects	**τ**	**χ^2**	**P**	**Random effects**	**τ**	**χ^2**	**P**
Stand	.005	.01	.92	**Stand**	.326	22.16	< .0001***
-	-	-	-	**Plot(stand)**	.164	3.20	.074
-	-	-	-	**Tree(plot(stand))**	.509	5250.8	< .0001***
Whole model	**R^2_m/R^2_c**	**χ^2**	**P**	**Whole model**	**R^2_m/R^2_c**	**χ^2**	**P**
	.495/.496	210.46	< .0001*		.310/.826	11961	< .0001***

The table shows coefficients of explanatory variables as standardized regression parameters (*Est.*) with their associated standard errors (*SE*), *z*-values (*z*), and probabilities (*p*). Model formula is Predictors were standardized previously to fitting the models. For random effects, hierarchy of variance components is shown in terms of standard deviations (*τ*) between stands, between plots, and between trees. Likelihood ratio tests statistics (χ2) and associated probabilities are given for random effect parameters and the whole models. Marginal (R^2_m) and conditional determination coefficients (R^2_c) are also tabulated. Asterisks indicate significance levels: *p < .05, **p < .001, and ***p < .0001, respectively.

4.2.3.2 CLIMATIC RESPONSE OF NORWAY SPRUCE LOTs

We found a strong temperature-growth synchrony since the 1950s between growing season temperatures and mean regional BAI of LOTs ($R^2 = 0.406$), with an almost linear trend in the period 1980-2018 ($r = 0.7$; Fig. 5a). LOT growth in that period exhibited the strongest relationship with summer season temperatures, especially during the late growing season (*i.e.*, July-September; $r \sim 0.6$, Fig. 5b). We observed a broader and stronger positive relationship with summer season temperatures (*i.e.*, June-September; $r > 0.35$), compared to other climate factors. Additionally, we found a significant positive relationship of tree growth with previous year October and current year April temperature. In contrast, only precipitation totals from previous year July and current year January exhibited significant effects on tree growth. Correlations with scPDSI were significant mainly during the winter months (*i.e.*, January-March) of the year of ring formation (Fig. 5b). The correlation analysis of the standard chronology generally reiterated the results from the residual chronology, albeit with generally stronger and/or broader correlations of current year growth with climatic parameters (Fig. S5).

Moving correlation analysis shows that the temporal variability in tree growth sensitivity to dominant climatic drivers followed the climatic variation over the studied period (Fig. 5c, Fig. S1). Regional climatic conditions fluctuated throughout the 20th century (Fig. S1), with relatively warm and wet periods around 1920s and 1940s interchanging with a distinct gradual increase in warm and dry climate in recent decades (*e.g.*, 1980-1995). Sensitivity of tree growth to late summer temperatures fluctuated over the course of the last century, increasing since the 1960s and reaching its peak in the 1990s ($r > 0.6$), followed by a generally downward trend towards the end of the century. As the climate became drier (Fig. S1b), tree-ring sensitivity to annual precipitation increased, showing a distinct upwards trend since the 1960s, while the relationship with July precipitation generally remained below the significance threshold over the whole century. On the other hand, the relationship between tree growth and March moisture generally remained significant ($r > 0.30$) throughout the 20th century.

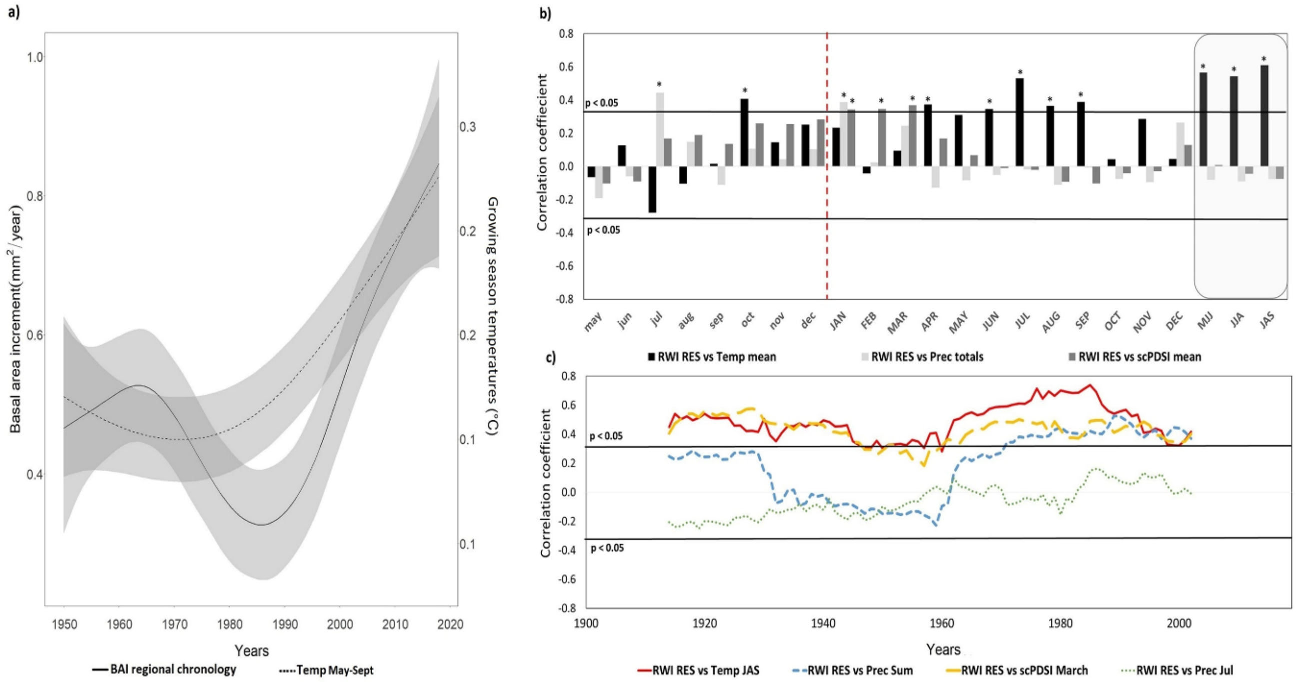

Fig. 5. Climate-growth relationships in the Western Carpathians.

(a) Demonstrates the temperature-growth synchrony between the mean regional BAI chronology (full line) and annual growing season temperature change (dashed line) in the period 1950–2018. Generalized additive model (GAM) was applied to filter out the inter-annual variation and preserve multi-decadal changes. Values were normalized using a min–max normalization technique. The shaded bands represent mean ± standard error. (b) Shows Pearson's correlation between regional residual RWI chronology in relation to monthly climatic variables (mean temperature, precipitation totals, and mean scPDSI) for the current and prior year of growth for the period 1980–2018. Relationships with precipitation (light gray stacks), scPDSI (dark gray stacks) and temperature (black stacks) are shown. Black asterisks indicate statistically significant correlations ($p < .05$). Red vertical dashed line separates prior and current year of tree-ring formation. Gray rectangle box represents the summer season windows. (c) Shows a 31-year moving window Pearson's correlation between regional residual RWI chronology and the most significant climate factors from the climate- growth response analysis over the 20th century. Residual chronology is shown against summer season temperature (summer window June– September; red line), Precipitation totals (blue dashed line), July precipitation (green dashed line) and March scPDSI (orange dashed line) values. Black horizontal lines represent the significance threshold ($p < .05$).

4.2.3.3 GROWTH TREND ANALYSIS AND DRIVERS OF RECENT GROWTH RATES

The analysis of radial growth dynamics demonstrated variability in growth histories between younger and older age classes, as well as high growth synchrony throughout the 20th century (Fig. 6a). Mean decadal BAI rates have continuously increased through time across age classes. Younger trees exhibited an almost exponential growth up to half of their lifespan, peaking early in life (BAI ~ 1350 mm^2/decade – 1800 mm^2/decade), and reaching larger sizes compared to LOTs at the same respective age. However, BAI of younger trees declined after the first few decades of a tree's life, followed by fluctuations around a mostly decreasing trend that persisted through time (Fig. 6b). The oldest LOTs in the region (*i.e.*, age > 400 years) consistently exhibited the lowest increments until the middle of the 19th century. This prominent increase in BAI is mirrored by a shift from a quasi-constant decreasing TRW trend, to a markedly increasing one (Fig. 6b). Regional growth synchrony was high throughout the 20th century ($\hat{a}_c > 0.7$), exhibiting a generally steady decline from peak value from the 1940s ($\hat{a}_c \sim 0.9$) until 1980s, with a steeper drop in the following decade ($\hat{a}_c \sim 0.7$), only to increase again in the 1990s (Fig. 6c).

Summer season temperature (*i.e.*, mean temperature of summer months July-August-September, $P < 0.0001$) proved to be the leading driver of recent growth increase (Fig. S7, Table 2). Furthermore, BAI of LOTs was significantly reduced by increasing age ($P < 0.0001$), while higher water availability before the onset of growing season (*i.e., PDSI_MAR;* $P < 0.0001$) and larger DBH ($P < 0.0001$) increased BAI growth significantly. Additionally, increasing competitive abilities of LOTs over the last couple of decades showed a positive impact on BAI ($P < 0.0001$), albeit at a lesser degree than summer temperatures. Plot-level disturbance factors and site attributes showed no association with LOTs recent growth trends.

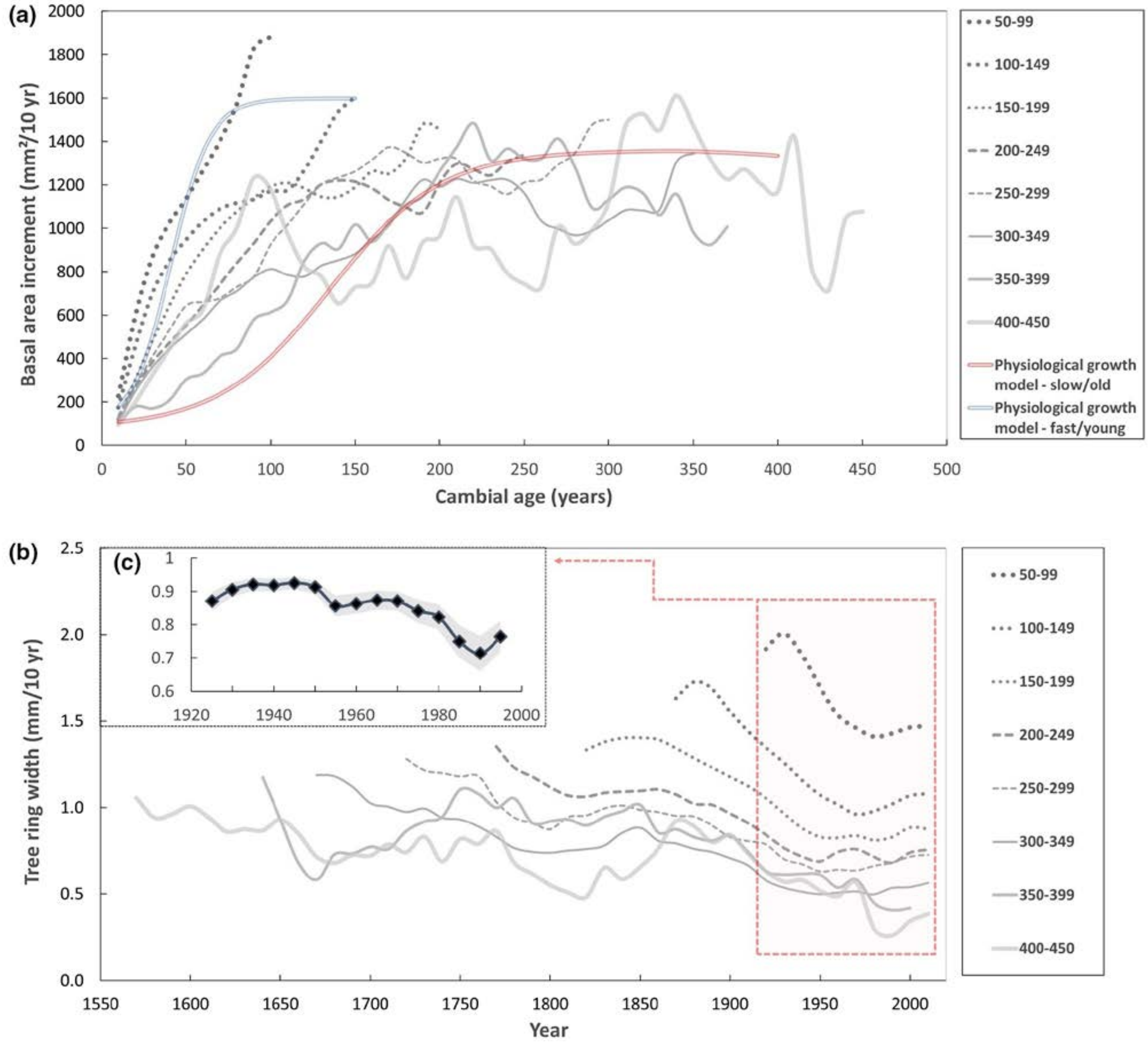

Fig. 6. Radial growth dynamics of non-overlapping 50-year age classes.

(a) Shows decadal mean basal area increment by cambial age, and (b) represents decadal mean tree-ring width by calendar year. For (a) and (b) each smoothed line represents a non-overlapping 50- year age class (see legend). Each decade represents a 10-year mean growth averaged over each age class. Sigmoidal curves in (a) represent theoretical growth trajectories for trees with fast growing strategies versus slow growing strategies, modelled according to the mean values of decadal growth rates of three oldest (slow/old) and three youngest (fast/young) age classes. Only the fully replicated portion with minimum five trees of each age class is shown. (c) Shows temporal changes in ring width synchrony (âc) between age classes. The shaded area indicates the standard error of synchrony.

4.2.4 DISCUSSION

In summary, we demonstrate the concurrent impacts of individual tree age/growth drivers and stand-level dynamics on growth-longevity tradeoffs in montane primary spruce forests. First, we show that age and mean early growth are negatively correlated. Trees growing slowly during their juvenile stage, or with a period of suppressed growth later in life, are those with a higher chance of reaching the highest ages. Second, the existence of the growth-mortality tradeoffs is further complicated by the impacts of disturbance histories as predominant drivers of tree age variability and growth dynamics. Third, radial growth patterns demonstrate diverging growth trajectories across age classes in pre-industrial times, but a general trend of increasing productivity over the last century, thus contradicting the onset of the expected age- and size-related productivity declines. Furthermore, the fluctuations in ring width synchrony over the 20th century indicate high variability in the degree of large-scale regulation of the growth trend by the macroclimatic factors. Finally, past growth histories did not hamper the growth potential of LOTs to continue accumulating biomass under rising temperatures. We discuss these findings in greater detail in the following chapters, and elaborate on the association of LOTs abundance and growth dynamics with productivity and resilience of primary forest ecosystems under intensifying environmental pressure.

4.2.4.1 PHENOTYPIC PLASTICITY AND DISTURBANCE EFFECTS MODULATE THE GROWTH-LONGEVITY TRADEOFF

Slow juvenile growth was a determining trait of old age (Fig. 2, 3, 4, S2). Norway spruce trees have an increased shade-tolerance and high nutrient-use efficiency at a young age (Grubb, 1977; Sokolov, Svyvasev, & Kubly, 1977), allowing them to survive extended stretches of time in the understory. By shifting resources from growth towards production of secondary metabolites, “slow-growers” gain selective advantage over “fast-growers” by improving their defenses against environmental stressors and increasing wood resistance, but at the cost of reduced growth (Wiley & Helliker, 2012). On the other hand, “fast-growers” get larger sooner, but rarely reach the same age as “slow-growers”, as the initial advantage of dominant canopy position (*i.e.* increased light availability) and fast growth are offset by generally declining growth rates, decreased resilience to pests and pathogens, and reduced investments in defenses and biomechanical stability (Vašíčková *et al.*, 2021). However, trees with more than half of a lifetime with suppressed growth seldom reach an age above 300 years (Fig. 4), as continuous growth suppression and limited resources increase mortality risks (Munné-Bosch, 2018).

The growth-longevity tradeoff, seen through the negative association between age and size with early growth, is additionally discernible in the contrasting early life growth patterns between live and dead trees (Fig. 3, Table S2). Young living trees consistently outperformed the oldest trees in the first decades of growth, generating wide TRWs and exhibiting exponential growth rates (Fig. 3a, 3b). Vice versa, the oldest dead trees grew faster than the youngest ones from about half of the century (Fig. 3c, 3d), indicating that younger trees that stagnated in growth became susceptible to increasing crowding effects and biotic and/or abiotic factors, which ultimately resulted in their earlier death. Additionally, the oldest dead trees exhibited a wide range of early life growth patterns compared to their living counterparts, and generally grew at a faster pace.

The observed tradeoffs have been noted in previous studies of temperate montane forests (*e.g.*, Black *et al.*, 2008; Bigler & Veblen, 2009; Johnson & Abrams, 2009; Di Filippo *et al.*, 2012, 2015; Bigler *et al.*, 2016; Piovesan *et al.*, 2019). However, by considering additional factors our study highlights disturbance histories as key drivers of age variability across the region (see S3, Fig. S3, S4, S7). Disturbance-related processes drive local resource availability through canopy openings and tree mortality, modifying the canopy ascension strategies of understory trees, and overriding the effects of environmental constraints on age and growth. Although slow growth remains the common trait for long lifespan, abundance of LOTs is largely determined by the severity and timing of local disturbances. Furthermore, the fact that the majority of LOTs established in the canopy following a release event(s), indicates disturbance dynamics are essential for multi-centennial lifespan in primary spruce forests.

4.2.4.2 SUMMER TEMPERATURES ARE THE PREDOMINANT DRIVER OF RECENT LOTs GROWTH RATES

Summer temperatures are the dominant driver of LOTs growth since 1980s (Fig. 5b, S8). Higher temperatures in summer months improve cell division and expansion in conifers (Fritts, 1976; Tranquillini, 1979; Körner, 2003; Ryan, 2010), leading to enhanced wood formation and increased growth. Furthermore, LOTs responding positively to warmer prior year October temperature (Fig. 5a) demonstrates the benefits of extended photosynthetically active period and warmer early autumn conditions (Menzel & Fabian, 1999). The extended photoperiod stimulates additional carbon uptake in LOTs (Buermann, Bikash, Jung, Burn, & Reichstein, 2013; Stinziano & Way, 2017), leading to improved carbon storage and carry-over effects for tree growth in the following year (Fritts, 1976; Oberhuber, 2004). In times of heightened stress, active carbon storage and prioritization of carbon allocation to respiration over growth could improve resistance to external mortality agents (Chapin, Schulze, & Mooney, 1990; McDowell *et al.*, 2011; Trowbridge *et al.*, 2021), and prevent drought-induced carbon starvation (Huang *et al.*, 2021).

LOTs, however, have become more sensitive to moisture availability in recent decades (Fig. 5b) while tree-ring sensitivity to summer temperatures declined (Fig. 5c). As the region becomes increasingly prone to moisture stress, increased energy and water demands could significantly impede future growth trajectories (Babst *et al.*, 2019), and benefits of extended growing season could become offset by moisture limitation and a higher risk of xylem embolism (Trenberth *et al.*, 2014; Bennett *et al.*, 2015; Grossiord, 2019; McDowell *et al.*, 2020). However, lack of a distinct summer moisture signal indicates that drought risks have not yet reached stressful levels at our sites. Although the regional climate has become hotter and drier, precipitation regimes have largely remained unaltered (Škvareniná, Tomlain, Hrvol', & Škvareninová, 2009; Fig. S1). Instead, we find a positive effect of winter moisture (Fig. 5b), highlighting the importance of snowmelt in refillment of soil moisture reservoirs for growth initiation (Barnett, Adam, & Lettenmeir, 2005). Whether LOTs will acclimate to shifting environmental constraints will depend on an array of factors outside the scope of this study, such as plant-hydraulic modifications (Woodruff & Meinzer, 2011), thermal tolerance thresholds (Kunert *et al.*, 2021), extent of CO_2-driven increase in intrinsic water-use efficiency (Buermann *et al.*, 2018), as well as the recurrence and intensity of extreme droughts (Allen, Breshears, & McDowell, 2015; Senf & Seidl, 2021b).

4.2.4.3 REGIONAL GROWTH SYNCHRONY AND LOTs GROWTH SENSITIVITY ARE LINKED WITH 20th CENTURY FLUCTUATIONS IN MACROCLIMATIC VARIATION

Increasing growth rates across all trees, regardless of age or size, were in sync with rising temperatures in recent decades (Fig. 5a). Although ring width synchrony has been steadily declining since the mid-20th century (Fig. 6c), with a substantial decrease in 1970s/1980s due to high nitrogen and sulphur depositions in the region (Oulehle *et al.*, 2016), tree growth remained highly synchronized throughout the 20th century, indicating a common environmental constraint on tree growth. However, if rising temperatures are the sole regional macroclimatic “synchronizer” of tree growth, a decrease in synchrony would be expected, as local growing conditions (*e.g.* soil, competition) grow in relevance. Thus, the observed positive spike in ring width synchrony in recent decades could indicate that an increasing warming-induced drought stress could be reducing forest resilience to moisture limitation (Shestaková *et al.*, 2016; Cailleret *et al.* 2019), in turn raising regional growth synchrony. This would, consequently, suggest a regional fluctuation in carbon sink strength as trees sync with rising temperatures (Shestaková, Camarero, & Voltas, 2021).

Nonetheless, the fact that LOTs still exhibit high growth sensitivity to improving conditions indicates these trees have not yet reached their maximum size, nor lost their growth potential. Whereas young trees generally display an inherently stronger growth response to improving growing conditions (Carrer & Urbinati, 2004; Primicia *et al.*, 2015; Sánchez-Salguero *et al.*, 2018), the fact that LOTs can reverse the slow-growing strategies established earlier in life and accumulate additional biomass, demonstrates their high adaptive capacity to changing environmental conditions. This could carry broad consequences for forest productivity, carbon storage and ecosystem dynamics. LOTs accumulate a disproportionately higher amount of biomass compared to smaller and younger trees (Fauset *et al.*, 2015; Trotsiuk *et al.*, 2016), and have a longer carbon residence time after a mortality event (*i.e.*, as standing dead trees; Shu *et al.*, 2019). If LOTs continue responding incrementally to improving growing conditions, rising temperatures could elevate carbon uptake and increase forest biomass, which would certainly benefit carbon storage, at least in areas that avoid large-scale mortality events (Lindenmayer *et al.*, 2012; Liu, Guirui, Wang, & Zhang, 2013; Gunn, Ducey, & Whitman, 2014; Calfapietra *et al.*, 2015; Senf & Seidl, 2021a).

4.2.4.4 POTENTIAL OF WESTERN CARPATHIAN PRIMARY SPRUCE FORESTS FOR INCREASED CARBON UPTAKE UNDER CLIMATE WARMING

Climate-reinforced high-severity abiotic (*i.e.*, windthrows, droughts) and biotic disturbances (*i.e.*, bark beetle outbreaks) have recently increased in frequency and severity across the Carpathians (Rouault *et al.*, 2006; Mezei *et al.*, 2014; Nikolov *et al.*, 2014). However, Western Carpathians primary spruce forests are mainly driven by low- to moderate-severity disturbances (see S4, Fig. S3, S4; Holekša *et al.*, 2017; Janda *et al.*, 2019) and exhibit high structural resilience to disturbances (Janda *et al.*, 2017, 2019). The terrain ruggedness and topographic complexity (*e.g.*, in the High Tatras) modulate the spatial patterns of disturbances, in turn creating a mosaic of small patches and heterogeneous structures across the landscape, which could carry an advantageous role for the long-term preservation of carbon storage (Senf & Seidl, 2018). Although the exacerbated effects of intensifying tree growth-moisture sensitivity may increase LOT mortality, the adverse effects of rising mortality could be attenuated by the synchronic post-disturbance tree recruitment and rapid understory growth benefiting from improved growing conditions (*e.g.*, increased light availability), while trees that invested into chemical and anatomical defenses in the past will persist as biological legacies. As an example, the dryer southern Carpathian spruce forests have experienced high-severity disturbances at the turn of the 20th century (Spînu *et al.*, 2020), yet contain some of the oldest trees, the highest living basal area and mean tree density across the Carpathians.

Furthermore, post-disturbance environmental conditions that favor higher rates of productivity relative to the rates of respiration and decomposition, also improve soil potential to store additional carbon (Mayer *et al.*, 2020), increasing soil organic matter fluxes and leading to larger carbon gains (Keith, Mackey, & Lindenmayer, 2009). Belowground carbon sinks, in tandem with the internal regulation of C allocation and mobilization of stored C, could help trees to preserve functionality under extreme events, albeit at the expense of growth. Determining the limit of biomass acquisition is, thus, complicated for naturally developing primary forest, but it will likely depend on the legacy effects of post-disturbance environmental conditions, tree life-history attributes and species-specific phenotypic plasticity (Bond-Lamberty *et al.*, 2014; Körner, 2017; Walker *et al.*, 2019), rather than a steady-state equilibrium between assimilation and respiration rates.

Nonetheless, our results offer strong empirical evidence of the stimulatory effects of climate warming, and its implications regarding the carbon budgets in montane primary spruce forests. If climate-driven accelerated rates of biomass accumulation explicitly lead to increased mortality and faster turnover rates, we would expect the co-occurring contrasting impacts of drivers promoting growth (*i.e.*, rising temperatures) and mortality vectors (*i.e.*, disturbances) to push stands towards younger age and reduced productivity (Brienen *et al.*, 2016; McDowell *et al.*, 2020). However, annual mortality rates have remained stable at our sites despite accelerated growth in recent decades (Synek *et al.*, 2020), indicating trees are still dying at the same age, but at larger sizes. As LOTs eventually do get removed from the canopy, the post-disturbance advanced regeneration will undoubtedly benefit carbon sequestration (Trotsiuk *et al.*, 2016; Pugh *et al.*, 2019; Mikoláš *et al.*, 2021), and offset potential increases in heterotrophic respiration from dead wood decomposition (Luyssaert *et al.*, 2008). Although a projected increase in disturbances and severe climate anomalies might increase contemporary mortality and offset biomass, and consequently carbon, gains on a local scale, Western Carpathian montane primary spruce forests will continue benefiting from the stimulatory effects of rising temperatures, either through an increase in overall growth rates (Pan *et al.*, 2011), or through development of a post-disturbance multi-layered canopy structure (Meigs *et al.*, 2017).

4.2.4.5 IMPLICATIONS FOR FOREST MANAGEMENT POLICIES AND FUTURE RESEARCH POTENTIAL

Results of our study provide a comprehensive understanding of how co-benefits of protecting LOTs might be leveraged in future conservation and management strategies in temperate montane forests. Relative to their scarcity in the landscape, LOTs exhibit a disproportionate impact on forest feedbacks in terms of carbon cycling, biomass dynamics, microclimatic buffering, and habitat provisioning. Even at death, LOTs are a significant carbon pool, as they can retain carbon for a long time in the forest as standing snags, while large decaying wood that eventually enter the soil as coarse woody debris promote soil development and productivity, nutrient immobilization and mineralization, and nitrogen fixation (Harmon *et al.*, 1986; Moore *et al.*, 2013; Shu *et al.*, 2019). Protecting LOTs is, arguably, the most effective strategy for accumulating atmospheric carbon and, simultaneously, benefitting other ecosystem services.

Western Carpathian primary spruce forests are a mosaic-landscape of disturbance-driven forests, where maintaining landscape heterogeneity is essential for preserving LOTs, and protecting wildlife habitats and populations of biodiversity species (Mikoláš *et al.*, 2021; Kameniar *et al.*, 2021; Kozák *et al.*, 2021). Activities that promote small- to large-scale deforestation of buffer zones and protected areas disregard disturbance dynamics as the indispensable driver of primary forest ecosystems, subsequently amplifying environmental pressures on their development. Salvage logging and other interventions that could interfere with self-regulating processes, should thus be prohibited, or at least minimized, in order to preserve LOT habitats and allow for conservation of biodiversity.

We also highlight the importance of accounting for both regional and tree-level drivers when assessing contemporary ecosystem dynamics under climate change. Under the coupled effects of ubiquitous disturbance events and intensifying climate pressures, future forest development will increasingly depend on local site properties (Babst *et al.*, 2013), and novel growth constraints (Schurman *et al.*, 2019; Svobodová *et al.*, 2019), which are harder to predict. Furthermore, it remains unclear whether accelerated growth rates will change the upper limit of forest biomass or translate into an actual increase in carbon sink capacity. Thus, continued long-term monitoring studies over regionally extensive primary forest datasets combined with mechanistic modelling are crucial for improving our understanding of long-term biomass dynamics, and future role of primary montane forests as buffer against C emissions.

4.2.5 CONCLUSION

Growth-longevity tradeoffs in Western Carpathian primary spruce forests are mainly determined by the interaction between the antagonistic impacts of natural disturbance dynamics and improving growing conditions. Whereas the potential for individual trees to attain high age remains primarily determined by their life-history traits, mainly slow early life growth rates, growth release events are essential for a multi-centennial lifespan in primary spruce forests. The clear interdependence of the recent growth trend with rising temperatures suggests that the effects of improving baseline environmental conditions transcend age/size limitations. Although faster growth may accentuate the growth-mortality tradeoffs, the fact that even LOTs can add additional carbon, suggests trees are presently not bound by past growth histories, and still exhibit ample room to grow. The landscape consequences of enhanced biomass accumulation could, thus, mediate carbon losses under intensifying climate-driven disturbances, and promote legacy sink effects of primary spruce forests for decades to come.

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CONFLICT OF INTEREST

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.z34tmpghw.

SUPPORTING INFORMATION

Additional supporting data can be found online at doi:10.1111/gcb.16461, or in the Supporting Information subsection (S2) of the Bibliography section at the end of this Thesis.

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4.3 SPATIOTEMPORAL CHANGES IN DROUGHT SENSITIVITY CAPTURED BY MULTIPLE TREE-RING PARAMETERS OF CENTRAL EUROPEAN CONIFERS

Status: *manuscript under development*

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Abstract: Global environmental changes have increased the frequency and intensity of climatic extremes, particularly heatwaves in tandem with severe droughts (*i.e.,* hotter droughts), which significantly affect inter-annual tree growth patterns and leave multi-year lags in post-drought growth recovery (*i.e.,* drought legacy effects). The effects of shifting climatic conditions on tree growth are inhomogeneous across species' natural distribution ranges due to large spatial heterogeneity and inter-population variability within a broad set of environmental conditions, but with major consequences for contemporary forest dynamics and future ecosystem functioning. Despite numerous studies quantifying the impacts of regional drought effects from tree to ecosystem scale, large uncertainties still remain regarding the mechanistic basis of drought legacy effects in wood formation, and intra-/inter-species ability to cope with increasingly drier growing conditions and rising year-to-year climatic variability across Central-Eastern European natural forest landscapes.

To unravel the complexity of climate-growth interactions and assess species-specific response to severe droughts, we combined common correlation analyses with climate (*i.e.*, mean temperature, precipitation totals, and moisture index) and growth response to extreme climate years from multiple tree-ring parameters (*i.e.*, tree-ring width and blue intensity parameters) with forward modelling of tree growth from an extensive dataset with ~1000 tree-ring series from 23 nature forest reserves across an altitudinal range in Czechia and Slovakia. These forests represent a wide range of environmental conditions of naturally developing Norway spruce and Scots pine, making them ideal for inferring general conclusions on the effects of intensifying climatic conditions on Central European forest dynamics.

Overall, we observed a large spatiotemporal variability in growth response to summer season temperature and moisture availability across species and parameters, but with the general trend of increasing moisture-growth sensitivity in recent decades over the Scots pine mountain forests and in both species lowlands sites. Furthermore, both species demonstrated temporally unstable

and nonlinear relationships with the dominant climatic controls over the 20th century. The VS-lite model captured the non-stationarity in climate-growth relationships and accurately estimated high-frequency growth variability, indicating a strong coincidence of regional drought events with growth reductions. Growth reductions during extreme drought years and discrete legacy effects identified in individual wood components were most pronounced in the low elevation forests, and together with the observed declining growth trends in recent decades, suggest an increasing vulnerability of Norway spruce and Scots pine on xeric low-elevation sites under intensifying climatic constraints.

4.3.1 INTRODUCTION

The intensifying climate warming in recent decades has increased the frequency and severity of heatwaves and droughts across the European temperate region (Allen *et al.*, 2010; Ciais *et al.*, 2005; Jones *et al.*, 2001). Extreme droughts have a pronounced effect on forest ecosystem processes, from offsetting carbon cycle feedbacks (Cook *et al.*, 2014; Dai, 2011), causing demographic shifts in tree species composition (Schuldt *et al.*, 2020), and reducing forest productivity (Anderegg *et al.*, 2015), to promoting landscape level biotic infestation outbreaks (Seidl *et al.*, 2017). Furthermore, compound drought events (*e.g.*, the 2018-2019 subsequent summer droughts) exacerbate the combined effects of rising vapor-pressure deficits (*i.e.*, VPD) and decreasing soil moisture on tree growth (Anderegg *et al.*, 2020; Bastos *et al.*, 2021; Pederson *et al.*, 2014; Dai, 2011; Park-Williams *et al.*, 2013; Zscheischler *et al.*, 2018), leading to chronic transpiration deficits, hydraulic failure, and reduced tree vigour (Brun *et al.*, 2020). As hotter droughts, *i.e.*, low water availability combined with simultaneous high air temperature, are projected to increase in frequency and severity across the temperate zone (IPCC, 2021), forest ecologists and policy makers face unprecedented challenges to develop strategies that would mitigate the impacts of climatic perturbations on forest ecosystem functioning and carbon dynamics.

Conifers exhibit a heightened sensitivity to severe and chronic water stress (Haberstroh *et al.*, 2022; McDowell *et al.*, 2016; Peltier *et al.*, 2016), mainly due to the biological limitations that inhibit rapid acclimation to rising evapotranspiration demands and prolonged periods of stomatal closure (Jump *et al.*, 2017; Peltier & Ogle, 2020), which puts them at a higher risk of hydraulic failure, embolism and carbon starvation (Adams *et al.*, 2017; McDowell *et al.*, 2008; Park-Williams *et al.*, 2013). Although the main temperate European conifer species, Norway spruce (*Picea abies* [L.] H. Karst) and Scots pine (*Pinus sylvestris* L.), exhibit relatively high plasticity to individual drought events (Knüver *et al.*, 2022; Pardos *et al.*, 2021), recurrent droughts can alter xylem and sapwood characteristics and impart persistent lagged effects on tree growth several years after the alleviation of growth limiting factors (*i.e.*, drought legacy effects; Kannenberg *et al.*, 2020). On the other hand, phenological shifts and extended growing season may mitigate drought-induced stress by extending photosynthetically active period and increasing carbon production prior to extreme environmental conditions (Arzac *et al.*, 2021), which could prevent carbon starvation. Despite their ubiquity, drought legacy effects remain heterogeneous across species (Camarero *et al.*, 2018; Kannenberg *et al.*, 2020), site conditions (Bottero *et al.*, 2017; Gazol & Camarero, 2016), and elevational gradients (Bošel'a *et al.*, 2014;

2021; Jevšenak *et al.*, 2021; Ponocná *et al.*, 2016, 2018), and could benefit from comprehensive multi-species and multi-parameter analysis to improve the interpretation of species- and site-specific growth dynamics under intensifying dry conditions.

Tree-ring studies of inherent growth responses to climatic conditions provide invaluable insight into growth-climate associations on a range of spatial and temporal scales (Fritts, 1976). The underlying principle of tree growth response to climatic extremes, visible through the formation of anomalously narrow tree-rings, can be used to derive indices of seasonal climatic information, and assess the response of populations to environmental stress (Dobbertin, 2015). However, tree-ring parameters other than tree-ring width (hereafter "TRW"), such as image-based blue reflectance (or blue intensity; hereafter "BI"), have been increasingly utilized to extract the climatic signals preserved in tree-rings (Björklund *et al.*, 2019, 2014; Rydval *et al.*, 2018, Wilson *et al.*, 2014; 2017). The BI parameter, as an indirect proxy for tree-ring density based on a measure of reflected light in the blue colour wavelengths, has become a valuable parameter for dendroclimatological studies due to its relative affordability, and a generally stronger and broader seasonal climate signal (McCarroll *et al.*, 2002). Recent studies have demonstrated the utility of BI parameters for assessing tree hydraulic and growth characteristics in drought-prone environments (Björklund *et al.*, 2020; Ho & Thomas, 2021), as cell anatomical features, particularly cell-wall and cell-lumen dimensions (Björklund *et al.*, 2021), are profoundly affected by extreme droughts. However, dendroecological studies with the application of BI parameters in drought-prone temperate forests are still generally missing (*e.g.*, Arbellay *et al.*, 2018; Begović *et al.*, 2020; Seftigen *et al.*, 2020).

Norway spruce and Scots pine growth-climate associations have been well established over the last century in Central Europe, with a predominantly temperature-limited growth at high-elevation sites (*e.g.*, Dittmar *et al.*, 2012; Hartl-Meier *et al.*, 2014; Kaczka *et al.*, 2017; Pretzsch *et al.*, 2014; Rybníček *et al.*, 2012), a mixed effect of moisture and temperature at mid-elevations (*e.g.*, Altman *et al.*, 2017; Mäkinen *et al.*, 2002; Primicia *et al.*, 2015; Tumajer *et al.*, 2017), and a generally moisture-limited growth at lower elevation sites (*e.g.*, Babst *et al.*, 2013; Lebourgeois *et al.*, 2010; Ponocná *et al.*, 2016; Trnka *et al.*, 2016). However, typical climate response function analysis are predicated on a linear relationship between tree growth and climate, thus lacking the mechanistic understanding of the underlying principles of limiting factors to wood formation (Friend *et al.*, 2019; Wilmking *et al.*, 2020). Furthermore, linear functions fail to acknowledge the nonlinearity in climate-growth relationships over time (Anchukaitis *et al.*, 2006; Babst *et al.*, 2018; D'Arrigo *et al.*, 2008), therefore potentially underrepresenting ecological reality and confounding the interpretation of contemporary and future growth trends (Eckes-Shepard *et al.*, 2022). In turn, process-based forward models have been increasingly utilized to account for the multivariate and inhomogeneous climate-growth relationships in recent decades (Anchukaitis *et al.*, 2020; Guiot *et al.*, 2014). One of such models, the Vaganov-Shashkin process-based model (Vaganov *et al.*, 2006), has become increasingly popular in dendroecological applications to different forest ecosystems (*e.g.*, Arzac *et al.*, 2021; Camarero *et al.*, 2021; Matskovsky *et al.*, 2021; Tumajer *et al.*, 2021) mainly due to its ability to jointly simulate the nonlinear effects of temperature and precipitation on tree growth, and giving a more accurate depiction of inter- and intra-annual growth variability (Tumajer *et al.*, 2022). To our knowledge, few studies have combined the linear response function analysis from multiple tree-ring parameters (*i.e.*, TRW and BI) and nonlinear modelling to disentangle the climate-growth interactions and evaluate drought legacy effects on inter- and intra-species level across a broad environmental gradient in Central European conifer forests.

To assess the fundamental differences in growth sensitivity of Norway spruce and Scots pine to average climate and extreme drought events along the wide range of environmental conditions, we used an extensive dataset of multiple tree-ring parameters from 23 monospecific Norway spruce and Scots pine forests from Czechia and Slovakia. We adopted both classical (principal component and superposed epoch analysis, and climate response functions) and novel (process-based forward modelling) methodological approaches to: (i) identify the dominant species- and site-specific growth-climate associations, (ii) evaluate inter-annual changes in climate sensitivity across the latitudinal and altitudinal gradient, and (iii) identify growth patterns during severe drought events on tree (*i.e.*, tree-ring parameter), local (*i.e.*, site) and regional (*i.e.*, altitudinal) scale in Central European nature forest reserves. We hypothesize that Norway spruce and Scots pine demonstrate elevation- and site-dependent growth responses to average and extreme climatic conditions. We predict that the local site conditions and species' functional traits determine the idiosyncratic patterns in individual species' drought sensitivity and scope of drought legacy effects. Finally, we expect that future development of Norway spruce and Scots pine will be increasingly limited by moisture limitation across the latitudinal and altitudinal range in Central-Eastern Europe.

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4.3.2 MATERIALS AND METHODS

4.3.2.1 STUDY AREA

Norway spruce and Scots pine are one of the most widespread and socio-economically valuable tree species in European temperate forests, constituting more than 60% of total forest biomass in Central Europe (Oušková *et al.* 2021; MPSR, 2019; MZe, 2018). Norway spruce is mainly distributed in mountain regions at elevations over 1000 m a.s.l., but is also found naturally in valleys and on steep slopes in the lowlands (Chytrý, 2013; Spiecker *et al.*, 1996). Scots pine generally inhabits less productive sites atop sandstones and rocky outcrops, and covers a broad elevational gradient from 400 to 1200 m a.s.l. The study area spanned across a latitudinal (from 48° 56′ 4″ N – 50° 53′ 23″ N and 13° 06′ 47″ E – 20° 26′ 29″ E) and altitudinal range (from 460 m a.s.l. to 1450 m a.s.l.), capturing the wide gradient of Norway spruce and Scots pine natural distribution in Central Europe, including the Sudetes, Ore Mts, Krkonoše Mts and Šumava region in Czechia, and the Western Carpathians (*i.e.* Tatra Mts and Slovak Ore Mts) in Slovakia (Fig. 1).

Study sites were categorized according to the hypothesized dominant climatic drivers of tree growth into moisture-limited low-elevation sites (*i.e.*, < 650 m a.s.l.; hereafter "PCAB low" & "PISY low") and temperature-limited high elevation sites (*i.e.*, > 900 m a.s.l.; hereafter "PCAB high" & "PISY high"). Stands were selected as representative of near-natural forest reserves, based on the presence of mature canopy trees and limited impact of past forest management activities. Additionally, physiographic site attributes were considered when selecting sampling populations to highlight the climatic sensitivity of tree growth (*e.g.*, shallow south-facing slopes in high-elevation sites, and steep valley slopes and rocky outcrops in the lowlands). Given the broad geographical and environmental range of the study area, mean annual temperature ranged from 0.5°C - 5.8°C and 5.5°C - 8.8 °C at high elevation and low sites, respectively, while the annual precipitation ranged from 530 mm/year at the westernmost locality in the Rabštejn area, to 1530 mm/year on the southern slopes of the Low Tatra Mountains (Fig. 2), with the regional trend of rising temperature and decreasing soil moisture (Fig. S1).

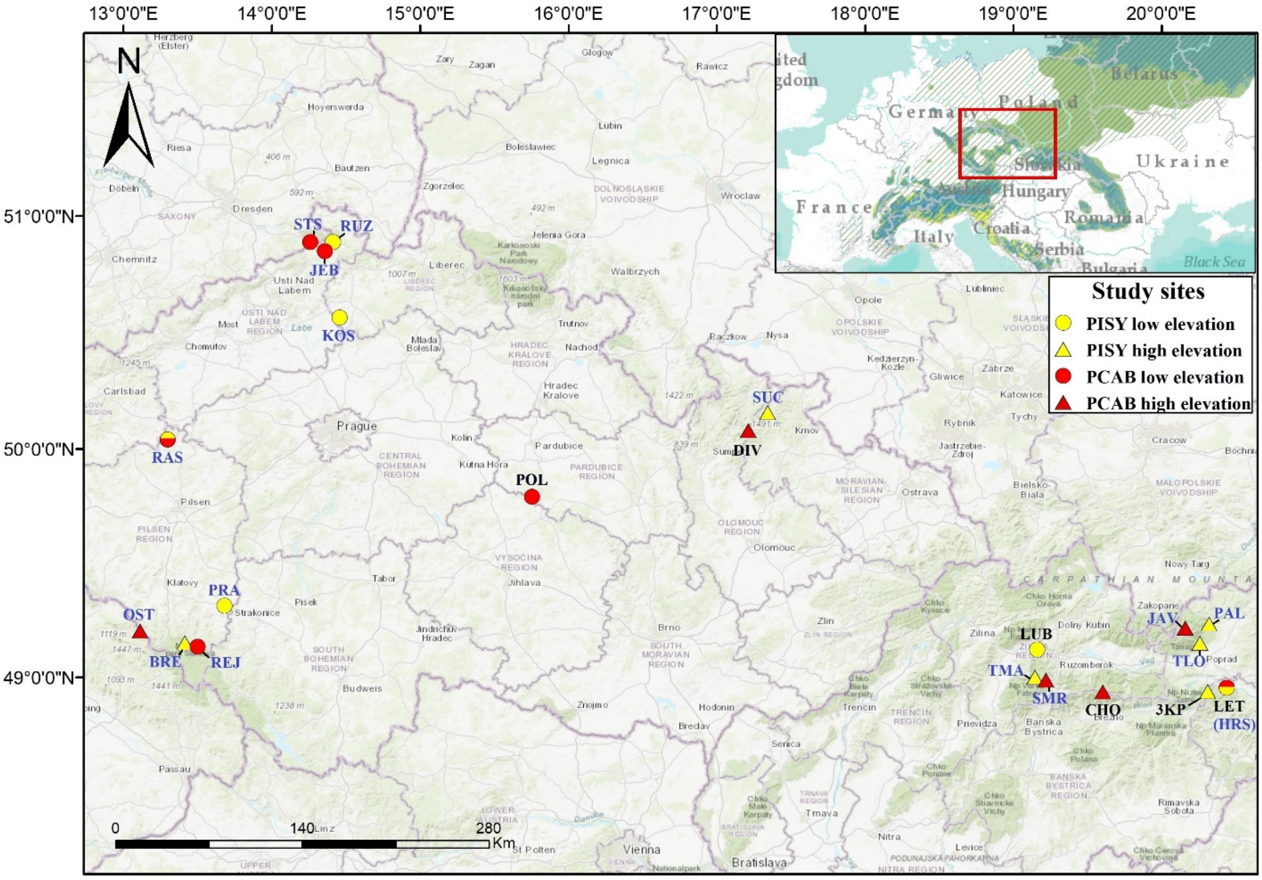

Fig. 1. Distribution of studied sites in Czechia and Slovakia.

Low elevation (**circles**) and high elevation (**triangles**) Norway spruce (**red**) and Scots pine (**yellow**) sites are shown. Abbreviations represent individual sites (see Table 1 for full site name). Blue colour site abbreviations indicate availability of blue intensity chronologies. Multi-coloured sites indicate both Norway spruce and Scots pine populations from the same stand. Norway spruce (*colour*) and Scots pine (*dashed lines*) Map lines delineate study areas and do not necessarily depict accepted national boundaries.

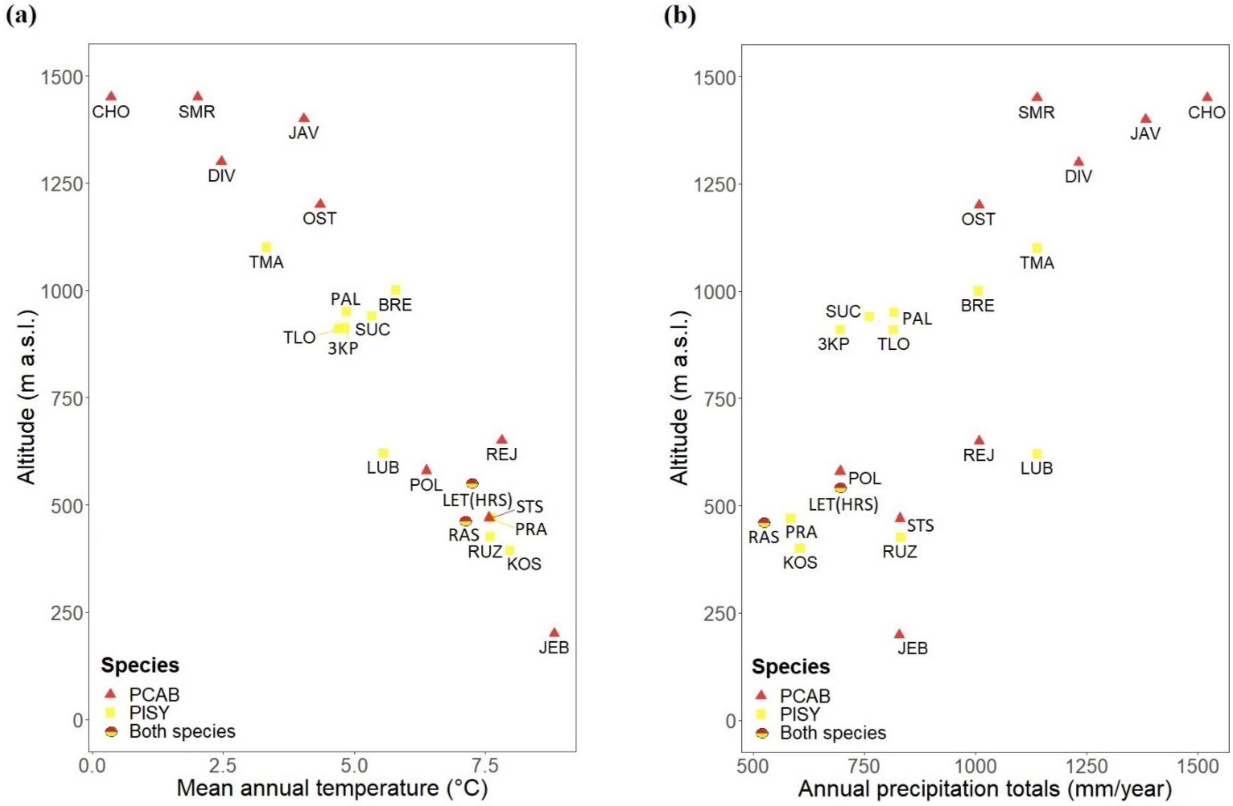

Fig. 2. Distribution of studied sites across the climatic gradient in Czechia and Slovakia. Shown are (**a**) mean annual air temperature and (**b**) total annual precipitation at the study sites across an altitudinal gradient during the instrumental period 1950–2018. Abbreviations denote individual forest stands (see Table 1 for full site name).

4.3.2.2 SAMPLE COLLECTION AND DATA PREPARATION

The study area consisted of 12 low-elevation (*i.e.*, 6 Norway spruce and 6 Scots pine) and 11 high-elevation (*i.e.*, 5 Norway spruce and 6 Scots pine) sites covering the regional distribution range of both tree species in Central Europe (Fritts, 1976). In each stand, site parameters (*i.e.*, geospatial location, species, altitude, slope, and aspect), and tree characteristics (*i.e.*, stem diameter at breast height, canopy status and taxa) were recorded. Increment cores were collected from 40-60 dominant and co-dominant per stand. At each site, one core per tree at breast height was extracted using a 5 mm Pressler increment borer. In total, ~1100 increment cores from 23 Norway spruce and Scots pine sites were collected in the period 2019-2020.

Increment cores were processed and analysed following the standard dendrochronological methodology established by Stokes & Smiley (1996). Increment cores were glued on wooden mounts and progressively sanded using different-grit paper until achieving clear visibility of annual growth rings. Annual tree-ring width (TRW) measurements were obtained using a stereomicroscope with a Lintab-TM traversing measuring stage in tandem with TSAP-WinTM software (www.rinntech.de). Cores were visually cross dated using the marker year approach (Yamaguchi, 1991), followed by statistical validation using COFECHA (Holmes, 1983; Grissino-Mayer, 2001) and CDendro softwares (Larson, 2015). Cross dating of individual series was based on measures of GFK (Gleichläufigkeit; Schweingruber, 1988), T-test, and Pearson's correlation coefficient. Increment cores that could not be adequately cross dated, or were missing more than 20 rings, were excluded from the analysis. Ultimately, 1042 cores were used in the subsequent analysis.

Blue intensity (BI) measurements were conducted on a subset of cores for the purpose of assessing maximum latewood and average earlywood BI, as surrogates for maximum density and earlywood density, respectively. Prior to BI measurements, individual cores were immersed in acetone for 24 hours to remove extractives (*e.g.*, resin) that could alter the measurements and induce biases during data analysis (Buckley *et al.*, 2018; Rydval *et al.*, 2014). Samples were then surfaced with sanding paper up to 1200 grit grade to ensure visibility of annual growth rings. Images of samples were acquired using an Epson Expression 10000XL scanner at a resolution of 2400 dpi combined with SilverFast Ai (v.6.6 - Laser Soft Imaging AG, Kiel, Germany) scanning software. The scanner was calibrated following the SilverFast IT8 calibration procedure using a Fujicolour Crystal Archive IT8.7/2 calibration target to prevent drift of BI measurements and allow for comparison of BI data across different scanning facilities. To minimize potential ambient light impact on image quality, cores were isolated with a dark and non-reflective cloth (Rydval *et al.*, 2014). Earlywood BI (EWBI) and latewood BI (LWBI or MXBI) values from scanned images were measured using the CooRecorder software (Cybis, 2019). Raw LWBI measurements were inverted according to Rydval *et al.* (2014), to express a positive relationship with TRW and instrumental data (no such inversion was necessary for EWBI). Additionally, we derived a third BI-parameter (delta BI; DBI or ΔBI), defined as the difference between the LWBI and the EWBI parameters (Björklund *et al.*, 2014).

4.3.2.3 DATA PROCESSING

4.3.2.3.1 TRW AND BI STANDARDIZATION PROCEDURE

Two sets of chronologies were developed for each site, species and tree-ring parameter using the detrend function from the *dplR* package (Bunn, 2008; Bunn *et al.*, 2013) in R software (v. 4.1.0, R Core Team, 2021). To remove the age/size biological trend and retain the inter-annual to multi-decadal growth fluctuations (Cook & Kairiukstis, 1990), individual TRW series were standardized by fitting a negative exponential function with adaptive power transformation, to compensate for variance differences related to the local mean of the tree-ring indices (Cook, 1985; Cook & Peters, 1997), thus producing a standard site chronology. To retain only high-frequency variability without the influence of autocorrelation (or non-climatic trends), we applied an autoregressive model and ring width indices (RWI) were calculated as ratios between the observed TRW and modelled values. The detrended series were averaged by year using Tukey's robust mean to produce residual site chronologies (Mosteller & Tukey, 1977; Cook *et al.*, 1995). Rbar-weighted stabilization was imposed to stabilize potential changes in variance related to decreasing sample depth and mean inter-series correlation (Rbar) over time (Osborn *et al.*, 1997). Rbar and expressed population signal (EPS) were used to assess the robustness of the chronologies (Table 1; Cook & Krusic, 2005; Wigley *et al.*, 1984).

Standardization and calculation of BI chronologies was performed similarly to TRW data, with the exception that age-related growth trends were removed using 67-year cubic smoothing splines with a 50% frequency cut-off, which has shown to adequately remove longer-term frequency variations, and account for the potential heartwood/sapwood discolouration (Seftigen *et al.*, 2020; Wilson *et al.*, 2014). Site chronologies for each BI parameter were produced by averaging the dimensionless indices and truncating the series where sample replication dropped below 5 series. In total, 23 TRW and 51 BI-related site chronologies (*i.e.*, EWBI, $LWBI_{inv}$, and ΔBI) were used in the analysis (Table 1).

Table 1 Site information and summary statistics of RWI/BI site chronologies.

Shown are residual site information and homogeneity statistics of RWI and BI site chronologies for the common interval 1950–2018. The acronyms stand for: mean inter-series correlation (*rbar*), expressed population signal (*EPS*), signal-to-noise ratio (*SNR*) and mean sensitivity (*MS*).

Site category	*Region*	*Site*	*Lat*	*Long*	*Elevation*	*Tree ring parameter*	*Replication*	*r-bar*	*EPS*	*SNR*	*MS*
PCAB LOW	*Rabštejn*	*Rabštejn (RAB_PCAB)*	50° 2' 34''	13° 17' 53"	460	TRW	41	0.582	0.982	55.291	0.34
						EWBI	37	0.233	0.916	10.861	0.028
						DBI		0.294	0.937	14.951	0.138
	Šumava	*Rejštějn (REJ)*	49° 8' 12"	13° 30' 8"	650	TRW	41	0.401	0.964	26.659	0.249
						EWBI	30	0.266	0.913	10.517	0.042
						DBI		0.296	0.925	12.316	0.149
	Czech Switzerland	*Stříbrné stěny (STS)*	50° 53' 23"	14° 15' 35"	470	TRW	35	0.402	0.958	22.737	0.305
						EWBI		0.119	0.822	4.61	0.066
						DBI		0.156	0.864	6.369	0.151
		Jetřichovická Bělá (JEB)	50° 51' 1"	14° 21' 30"	200	TRW	38	0.363	0.955	21.028	0.253
						EWBI		0.145	0.862	6.261	0.023
						DBI		0.151	0.868	6.579	0.112
	Iron Mountains	*Polom (POL)*	49° 47' 32"	15° 45' 17"	580	TRW	42	0.369	0.96	23.726	0.242
	Prielom Hornadu	*Havraní skály (HRS)*	48° 57' 12"	20° 25' 44"	540	TRW	43	0.369	0.96	23.803	0.264
						EWBI		0.155	0.882	7.471	0.046
						DBI		0.154	0.881	7.438	0.139
PCAB HIGH	*Šumava*	*Ostrý (OST)*	49° 12' 13"	13° 6' 44"	1200	TRW	40	0.393	0.962	25.04	0.24
						EWBI		0.165	0.885	7.661	0.038
						DBI		0.318	0.948	18.15	0.124
	Jeseniky	*Divoký důl (DIV)*	50° 4' 46"	17° 12' 51"	1300	TRW	48	0.493	0.977	41.725	0.244
	Great Fatra	*Smrekovica (SMR)*	48° 59' 9"	19° 13' 22''	1450	TRW	48	0.422	0.971	33.288	0.25
						EWBI	34	0.184	0.879	7.28	0.054
						DBI		0.303	0.933	13.945	0.176
	Low Tatras	*Chopok (CHO)*	48° 56' 4"	19° 36' 18"	1450	TRW	33	0.42	0.968	30.362	0.197
	High Tatras	*Javorová (JAV)*	49° 13' 01"	20° 9' 46"	1400	TRW	60	0.454	0.979	47.225	0.254
						EWBI	44	0.268	0.938	15.185	0.033
						DBI		0.385	0.963	25.912	0.16
PISY LOW	*Rabštejn*	*Rabštejn (RAS_PISY)*	50° 2' 35"	13° 17' 53"	460	TRW	51	0.377	0.968	30.025	0.293
						EWBI	21	0.293	0.894	8.452	0.037
						DBI		0.323	0.908	9.884	0.145
	Czech Switzerland	*Ružova Zahrada (RUZ)*	50° 53' 23"	14° 24' 47"	425	TRW	49	0.313	0.949	18.424	0.364
						EWBI	42	0.168	0.877	7.147	0.071
						DBI		0.2	0.897	8.745	0.222
	Kostelec	*Kostelec (KOS)*	50° 34' 2"	14° 27' 30"	400	TRW	49	0.411	0.97	32.499	0.32
						EWBI	27	0.157	0.831	4.92	0.044
						DBI		0.299	0.919	11.292	0.175
	Šumava	*Prachen (PRA)*	49° 18' 58"	13° 40' 51"	470	TRW	51	0.257	0.944	16.9	0.312
						EWBI	20	0.191	0.821	4.588	0.048
						DBI		0.379	0.923	11.962	0.233
	Great Fatra	*Lubochna (LUB)*	49° 7' 21"	19° 9' 46"	620	TRW	43	0.434	0.977	42.894	0.306
	Prielom Hornadu	*Letanovsky mlyn (LET)*	48° 57' 12"	20° 26' 29"	550	TRW	58	0.268	0.939	15.289	0.254
PISY HIGH	*Šumava*	*Breznik (BRE)*	49° 9' 3''	13° 24' 50"	1000	TRW	42	0.363	0.958	22.996	0.28
						EWBI		0.194	0.908	9.819	0.05
						DBI		0.268	0.937	14.984	0.138
	Jeseniky	*Suchy vrch (SUC)*	50° 9' 22"	17° 20' 43"	940	TRW	50	0.27	0.947	17.7	0.233
						EWBI	33	0.251	0.915	10.786	0.025
						DBI		0.306	0.934	14.091	0.137
	Great Fatra	*Tmava (TMA)*	49° 0' 54"	19° 9' 26"	1100	TRW	44	0.317	0.952	19.924	0.32
						EWBI	38	0.29	0.938	15.118	0.051
						DBI		0.366	0.955	21.394	0.219
	Slovakian Paradise	*Tri kopy (3KP)*	48° 56' 10"	20° 18' 40"	910	TRW	53	0.249	0.942	16.391	0.278
	High Tatras	*Palenica (PAL)*	49° 14' 5"	20° 19' 18"	950	TRW	42	0.361	0.958	22.683	0.283
						EWBI		0.276	0.939	15.405	0.034
						DBI		0.356	0.957	22.39	0.162
		Tatranska Lomnica (TLO)	49° 9' 00"	20° 15' 34"	910	TRW	47	0.318	0.955	21.162	0.272
						EWBI	35	0.232	0.912	10.346	0.03
						DBI		0.298	0.936	14.511	0.125

4.3.2.3.2 CLIMATE DATA

Climatic information was obtained through geospatial interpolation of meteorological data from the nearest local weather stations. Monthly mean temperature data was interpolated using orographic regression from a triplet of nearest weather stations, while monthly precipitation totals were interpolated using the inverse distance weighted method from at least 7 stations closest to each site (Treml *et al.*, 2022). The standardized precipitation evaporation index (hereafter "SPEI") was computed using the Thornthwaite method following Vicente-Serrano *et al.* (2010)**.** Monthly climatic data, including the seasonal windows which represent the climatic variables averaged over several months, covered the period between 1950-2018.

4.3.2.4 STATISTICAL ANALYSIS

4.3.2.4.1 SPATIAL VARIABILITY IN GROWTH PATTERNS

Multivariate factorial analysis can be a useful tool for identifying site and regional differences based on common growth patterns or differing growth-climate associations (Buras *et al.* 2018; Lange *et al.*, 2018). To this end, we applied principal component analysis (PCA) on residual site chronologies over the period 1950-2018. The PCA transforms RWI chronologies into principal components with scores (*i.e.*, nodes of common growth variation) and loadings (*i.e.*, the association of chronologies with the component loadings) by ordination of the covariance matrix from the original data. Additionally, PCA was performed separately on a parameter-level to evaluate the common variability of each individual wood component. Additionally, we used a hierarchical cluster analysis (HCA; Ludwig & Reynolds, 1988) on the principal components to statistically validate the heterogeneity between sites and verify grouping consistency. HCA was based on Ward's minimum variance method (Everitt *et al.*, 2011), and we used Euclidean distance as the optimal measure of similarity between sites.

4.3.2.4.2 CLIMATE-GROWTH ANALYSIS

Pearson's correlation coefficients with stationary bootstrapping were used to quantify the climate-growth relationships between the monthly climatic drivers and tree growth over the truncated period 1950–2018 using the R package *treeclim* (Zang & Biondi, 2015). Climate-growth correlations were calculated between RWI site chronologies and local climatic variables (*i.e.*, temperature, precipitation, and SPEI-3) within an 18-month period (*i.e.*, from July of the year preceding ring formation to December of the ring-formation year), including seasonal summer windows expressed as mean values over aggregated months (*i.e.*, June-August & April-September). Additionally, we analyzed the temporal stability of the most significant climate-growth associations by computing Pearson's correlation coefficients over 31-yr moving window segments. The subsequent analyses were also performed on the subset of BI site chronologies that exceeded the EPS threshold of 0.80 in all BI-parameters over the 1950-2018 period (*i.e.*, 8 Norway spruce and 9 Scots pine sites).

4.3.2.4.3 VS-LITE FORWARD MODELLING

To evaluate potentially nonlinear and non-stationary climate response patterns in dominant climatic controls of inter-annual growth variability of Norway spruce and Scots pine, we employed the simplified version of the Vaganov-Shashkin model (hereafter “VS-lite model”; Tolwinski-Ward *et al.*, 2011, 2013) over the period 1940–2018. VS-lite model is adapted to simulate temperature- and moisture-driven annual tree growth rates at a monthly temporal resolution, using nonlinear equations with three main input parameters: site latitude (used for modulating day length or insolation; gE), the growth-temperature, and the growth-soil moisture parameters (gT, gM) with four adjustable model parameters reflecting the climatic minima for cambial reactivation (T1, M1; Rossi *et al.*, 2007; 2008) and the maxima for optimal growth without the dominant control of the respective climatic factor (T2, M2). The soil moisture submodule from the original VS-model (*i.e.*, “the leaky-bucket” model) was replaced by the soil moisture field data measured at each site. Optimal values of the four adjustable model parameters, defining the shape of the response functions between climatic factors and annual growth rates, were estimated by randomization with 4000 parameter combinations within an ecologically reasonable range (*sensu* Tumajer *et al.*, 2022). The set of optimal model parameters producing the highest correlation between the modelled and the observed RW chronologies were retained (Table SI3).

The VS-Lite model was calibrated separately for each site to maximize the effects of local growing conditions on tree growth, by splitting the period of interest into the calibration interval used for model parameter optimization (*i.e.*, 1940/1950–1979) and the verification interval for growth prediction based on overlapping climate data (*i.e.*, 1980-2018). The integration window of the VS-Lite model was set from January to December of the current year to differentiate the current and antecedent climate drivers. Additionally, we aggregated mean modelled RWI site chronologies within each site category, to improve spatial coherence between observed and modelled RWI chronologies (Breitenmoser *et al.*, 2014; Tumajer *et al.*, 2017). Finally, to assess the temporal impacts of shifting climatic constraints on tree growth, we also calculated average partial monthly growth responses to temperature and moisture over 20-year moving window periods (*i.e.*, 1940–1959, 1960–1979, 1980–1999, 2000-2018). VS-lite modelling and model parametrization was accomplished using the "VS-Lite" MATLAB scripts published by Tolwinski-Ward *et al.* (2011).

4.3.2.4.4 SUPERPOSED EPOCH ANALYSIS

Extreme climatic events can impart lag effects in tree-ring chronologies and confound the detected climate responses of tree growth. To complement the interpretation of growth-climate associations established by linear and nonlinear analysis, and identify the behavior of RW and wood density under extreme drought events, we used a superposed epoch analysis (*i.e.*, SEA; Haurwitz & Brier, 1981). SEA is a nonparametric test based on compositing and averaging matrices of high-frequency response signals to extreme events within a specified time window (D'Arrigo *et al.*, 1993). In this study, we followed the application discussed by Rao *et al.* (2019) to quantify the tree growth response of Norway spruce and Scots pine during extreme drought years. We calculated mean normalized (*i.e.*, z-score) epochal responses of RWI and BI chronologies for each species and site using the *dplR* package in R software (Bunn, 2010). We calculated average departures from the mean RWI values 5 years pre- and post-drought year and tested against 1000 randomized 11-yr sets to determine the significance thresholds ($p < 0.05$). SEA was conducted separately for both TRW and BI parameters. Extreme drought years were based on the extreme negative deviations of the regional mean moisture index (*i.e.*, scPDSI < -2) and validated by recent studies of drought dynamics in Central Europe (*e.g.*, Brázdil *et al.*, 2009; 2010; 2015; Čejková & Kolař, 2009; Spinoni *et al.*, 2015; Trnka *et al.*, 2015). The identified severe drought years utilized in SEA were 1921, 1943, 1973, 1976, 1983, 1990, 1992, 1993, 2003, 2007, 2012, and 2017.

4.3.4 RESULTS

4.3.4.1 SIGNAL STRENGTH AND CHRONOLOGY METRICS IN RWI AND BI RESIDUAL CHRONOLOGIES

Since the $LWBI_{inv}$ and ΔBI parameters demonstrated largely the same relationships with dominant climatic controls, $LWBI_{inv}$ analysis were omitted from the main text and can be found in the supplementary material (Fig. S2, S5, S10). Norway spruce and Scots pine residual chronologies displayed considerable high-frequency variability across sites and parameters, with a generally higher variability at low elevation sites compared to high elevation sites in both species (Fig. 3, Fig. S3-S6). PISY chronologies extended further back in time, exhibiting comparable medium- to low-frequency growth patterns compared to PCAB high and PCAB low. This relationship is further reflected in both high-frequency extremes and the observed mean decadal trends, particularly in recent decades when PCAB high chronologies demonstrate a diverging upwards trend compared to a relatively sharp decline in the remaining categories (Fig. 3).

Mean sensitivity was generally similar for site chronologies of both species, with respect to each parameter (Table 1), albeit TRW mean sensitivity was by an order of magnitude higher ($ms_{PCAB} = .197$, $ms_{PISY} = .233$) compared to EWBI ($ms_{PCAB} = .023$, $ms_{PISY} =.025$), and significantly higher than ΔBI ($ms_{PCAB} = .112$, $ms_{PISY} = .125$). RWI chronologies generally contained a stronger common signal than either EWBI or ΔBI ($r_{RWImean} = .369$, $r_{EWBImean} = .194$, $r_{\Delta BImean} = .299$; Fig. 4.), and with a significantly broader range ($.249 < r_{RWI} < .582$) compared to EWBI ($.119 < r_{EWBI} < .293$) and ΔBI ($.151 < r_{\Delta BI} < .385$). EPS decreased gradually back in time for all chronologies, reflecting a combination of decreasing sample size and inter-series correlation prior to the 1950s (Fig. S3-S6). The average EPS values of RWI and ΔBI chronologies generally exceeded the EPS threshold of 0.80 throughout the 20th century for both species, whereas the EWBI site chronologies were constricted to about middle of the 20th century (Fig. S4).

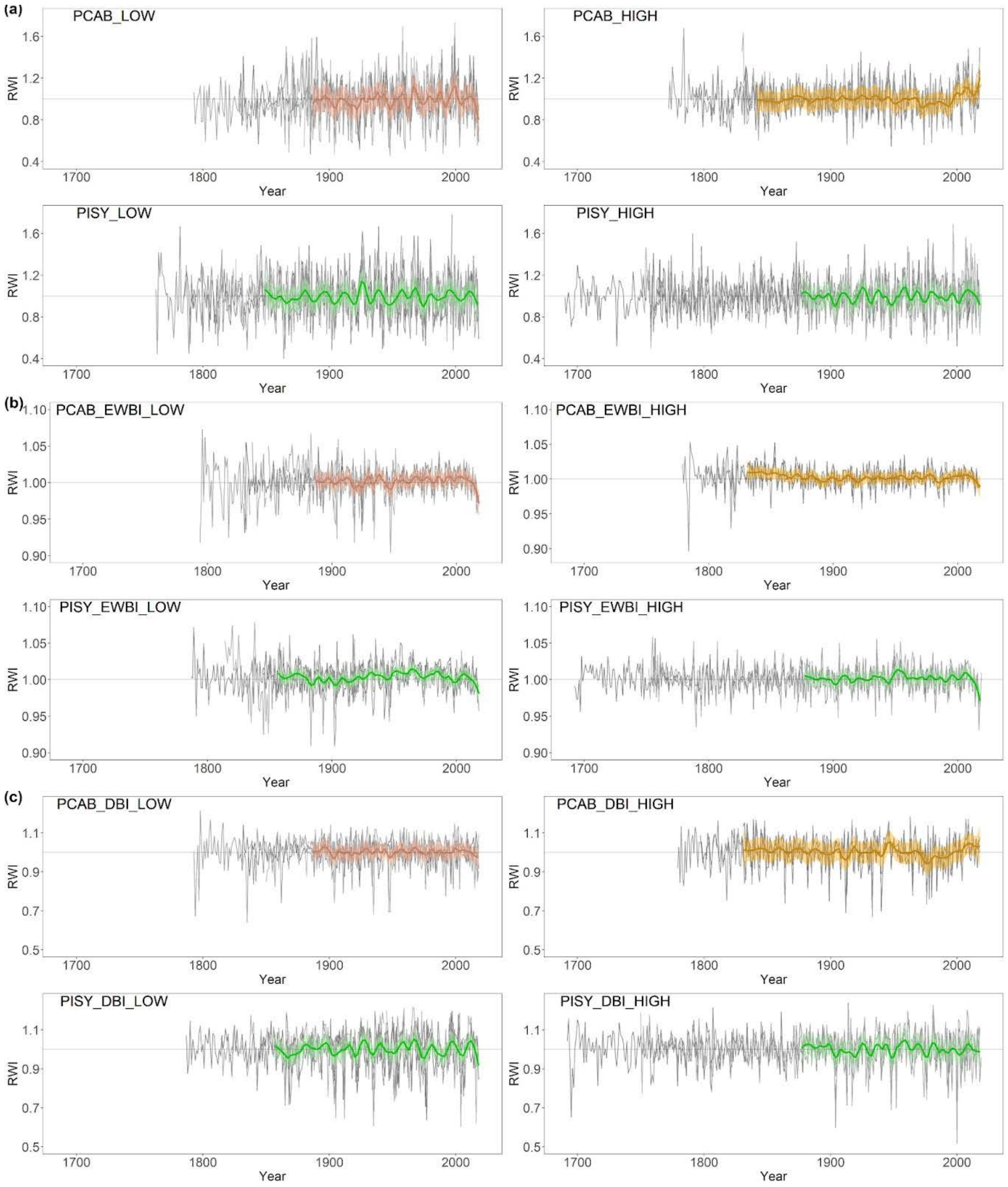

Fig. 3. RWI and BI site chronologies.

Shown are individual residual RWI (**a**), EWBI (**b**) and ΔBI (**c**) site chronologies in gray colour and mean chronologies in corresponding colours for each site category (see Table 1). Mean chronologies are smoothed based on local regression with minimized sum of squared errors (*loess* function in *ggplot*) and are shown in overlapping years between all site chronologies. Shaded areas represent standard deviation. The individual site chronologies are truncated to the year when the respective minimum replication falls below 5 individual series.

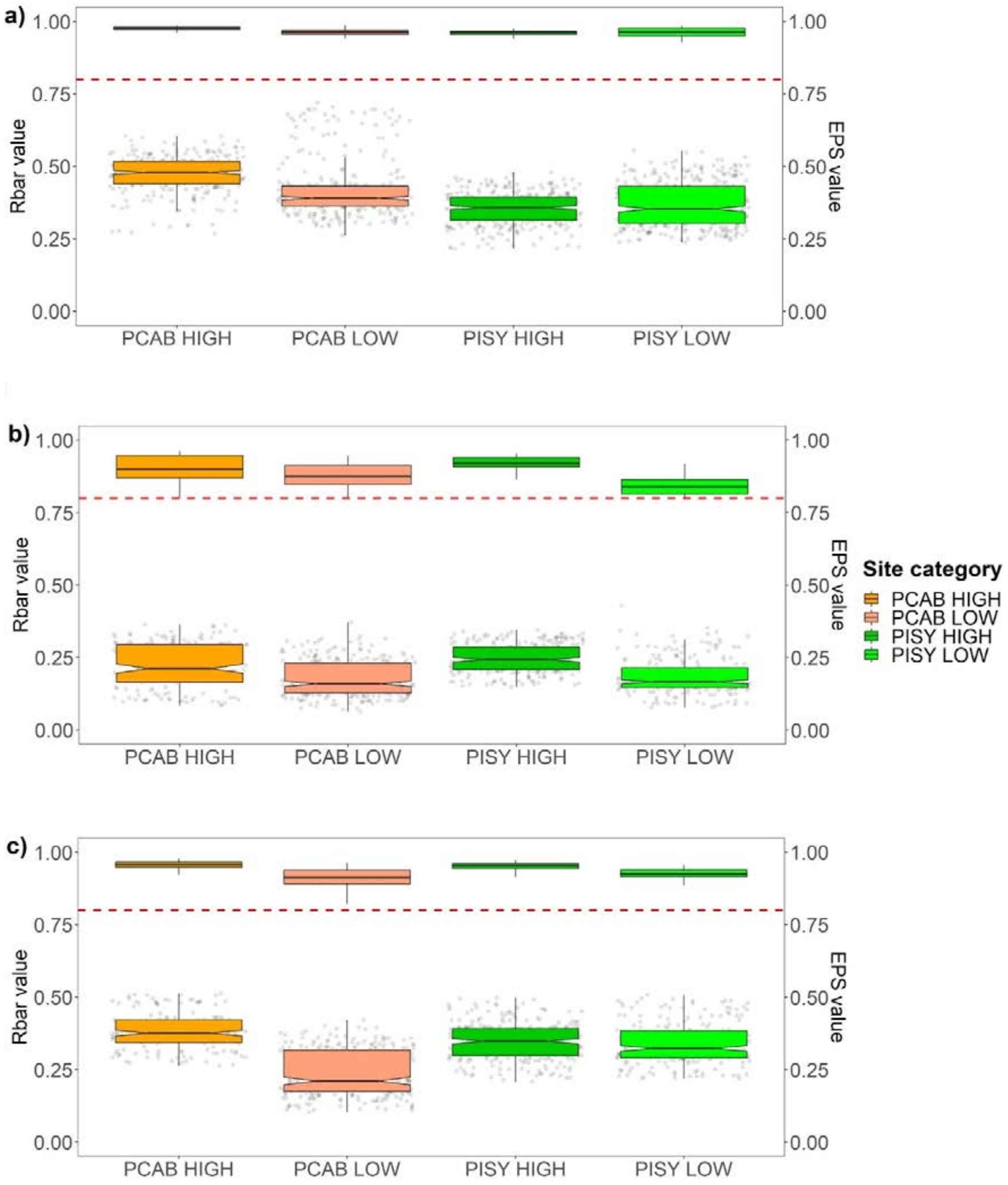

Fig. 4. Running r-bar and EPS of RWI and BI site chronologies in the period 1950-2018.

Whisker-box plots show Rbar and EPS statistics of RWI (**a**), EWBI (**b**), and ΔBI (**c**) residual site chronologies over the period 1950-2018.

4.3.4.2 SPATIAL VARIABILITY IN COMMON GROWTH PATTERNS

The PCA biplot and the hierarchical clustering analysis of RWI site chronologies validated the elevational categorization of sites, but demonstrated significant variability in common growth patterns across sites (Fig. 5). The first two modes of PCA analysis explained ~ 46% of total variability across RW site chronologies. All low elevation sites load positively and more-or-less equally strong on the first component, while the PCAB high cohort strongly loads the second component, indicating a pronounced departure of growth patterns in PCAB high from the remaining sites. Moreover, the hierarchical cluster analysis indicates a large regional variability within the "mixed-signal" groups (height > 2) in contrast with the relatively uniform PCAB high sites (height < 1). Additionally, the PCA analysis of individual RW and BI parameters explained ~ 33% of total variability and demonstrated a distinct separation of the EWBI parameter from the RW, $LWBI_{inv}$ and ΔBI (Fig. S7), suggesting the presence of distinct climate-signal patterns in the dataset.

4.3.4.3 CLIMATIC RESPONSE OF NORWAY SPRUCE AND SCOTS PINE

Pearson's correlations between the residual RWI, EWBI and ΔBI chronologies and monthly temperature and moisture variables revealed significant altitudinal- and species-specific climatic associations over the second half of the 20th century (Fig. 6-7, S8-S11). Since the growth relationships with the standardized evapotranspiration index (*i.e.*, SPEI) exhibited significantly stronger correlations with both RW and BI chronologies, the relationship with precipitation was omitted from the main text and can be found in supplementary material (S8-S11).

Summer and growing season temperatures were identified as the dominant drivers of PCAB high growth variability, and generally demonstrated the strongest correlation values across all sites and parameters ($r_{medianRWI}$ ~ 0.65, $r_{median\Delta BI} > 0.65$; Fig. 6a, 7a). Furthermore, PCAB high RWI manifested a significant positive correlation with late winter/early spring moisture index. PCAB low demonstrated mixed-climatic signals and generally the largest variability of monthly temperature- and moisture-responses across all site categories (Fig. S8-S11), with significant site-specific adverse relationships with summer and growing season temperatures ($-0.5 < r_{medianRWI} > 0.45$), and a significant positive correlation with summer season moisture availability.

On the other hand, both PISY high and PISY low showed generally weak correlations with current year temperatures ($r_{medianRWI} < 0.25$), with site-specific significant relationships with previous year late summer and current year spring temperatures (Fig. 6b, Fig. S8a). The strongest relationship with temperature was found to be a negative correlation with September in the previous year in the KOS site ($r = -0.43$). Relationships with the moisture index were seasonal and more pronounced across the whole PISY RWI network, with both PISY high and PISY low exhibiting high dependence on summer months moisture availability (Fig. 6b, Fig. S8c). The strongest summer moisture signal across the PISY RWI network was found in the LET site ($r \sim 0.50$). On average, PISY sites displayed stronger and broader relationships with the moisture index compared to the PCAB sites.

Climatic signals captured by the BI parameters generally complemented the climate-growth relationships displayed by the RWI response analysis (Fig. 7, Fig. S9-S11), but with distinct differences across site categories and contrasting seasonal relationships between the two BI parameters. Whereas EWBI showed a generally significant negative correlation with summer season temperatures (apart from June temperatures in PCAB high), ΔBI exhibited inverse associations with temperature across the network, ranging from a significant positive correlation with summer season temperatures in PCAB high ($r_{median\Delta BI} > 0.65$) and several PCAB low sites (*e.g.*, STS, JEB; Fig. S9 & S11), to significant negative correlations with previous and current August temperatures in PISY sites. The contrast between the BI parameters was also found in the relationship with moisture availability in PISY and PCAB low (Fig. 7b), where the most significant positive relationship of ΔBI with previous year late summer moisture was mirrored by a significant negative correlation in EWBI, and vice versa in the relationship with current year summer and early autumn moisture availability (*i.e.*, significant positive relationship in EWBI, but negative correlation in some ΔBI site chronologies, respectively). Overall, the response analysis of BI parameters with monthly moisture values yielded stronger correlations in both species than RWI ($r_{mediandiff} \sim \pm 0.15$), particularly in PISY sites. A full overview of individual RWI and BI (including $LWBI_{inv}$) site chronology correlations with climate is provided as supplementary material (Fig. S8-S11).

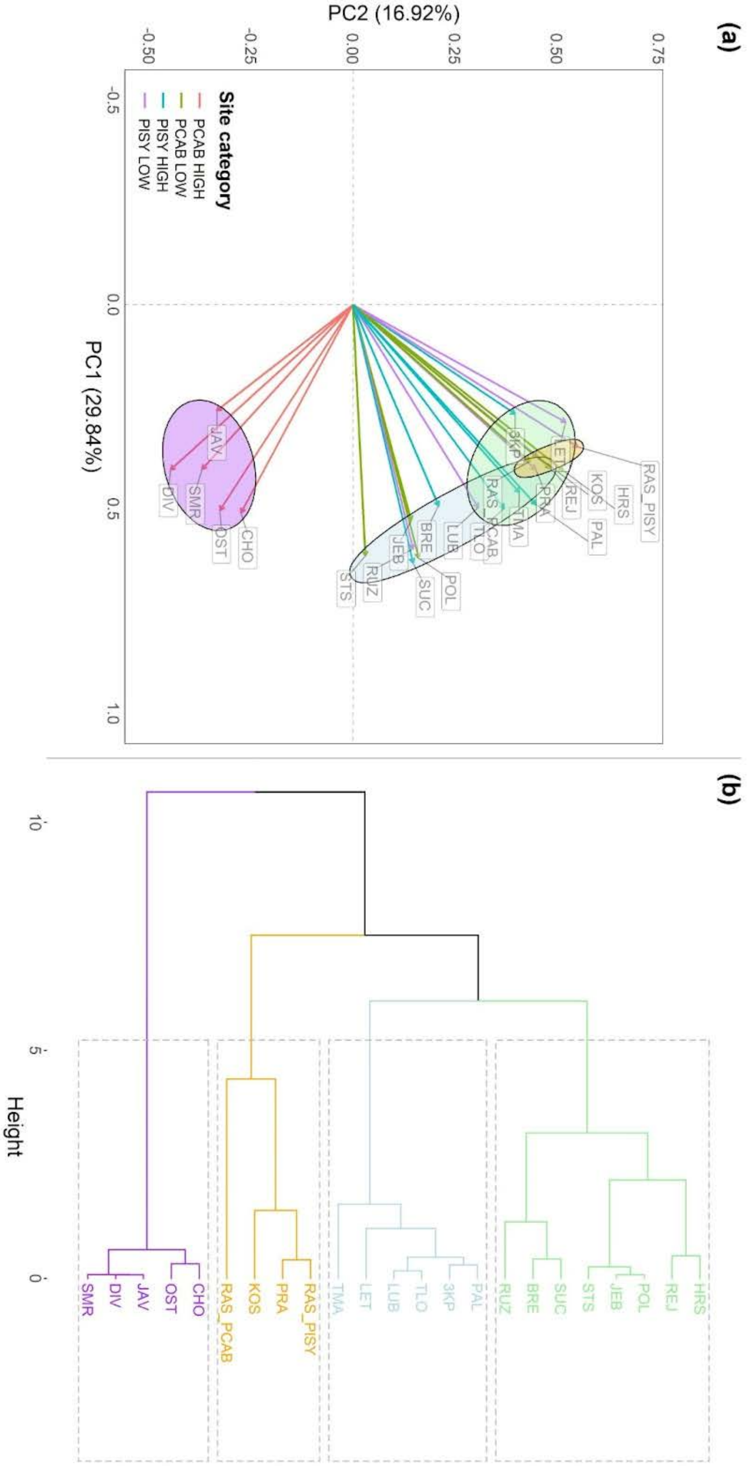

Fig. 5. Biplot of the principal components and the cluster dendrogram of RWI site chronologies. Shown are the first two principal components of the PCA performed over the common 1950–2018 period. Axis labels in (**a**) report the percentage of variance explained by the first two components; each arrow corresponds to one of the analysis variables projected onto a two-dimensional plane and proportional to its component loading. Identified group cohorts from the HCA are highlighted accordingly. The colour of the vectors corresponds to the site categories. The height values on the x-axis in (**b**) show the squared Euclidean distance between variables according to the clustering algorithm and based on Ward’s method. Identified parameter cohorts are highlighted.

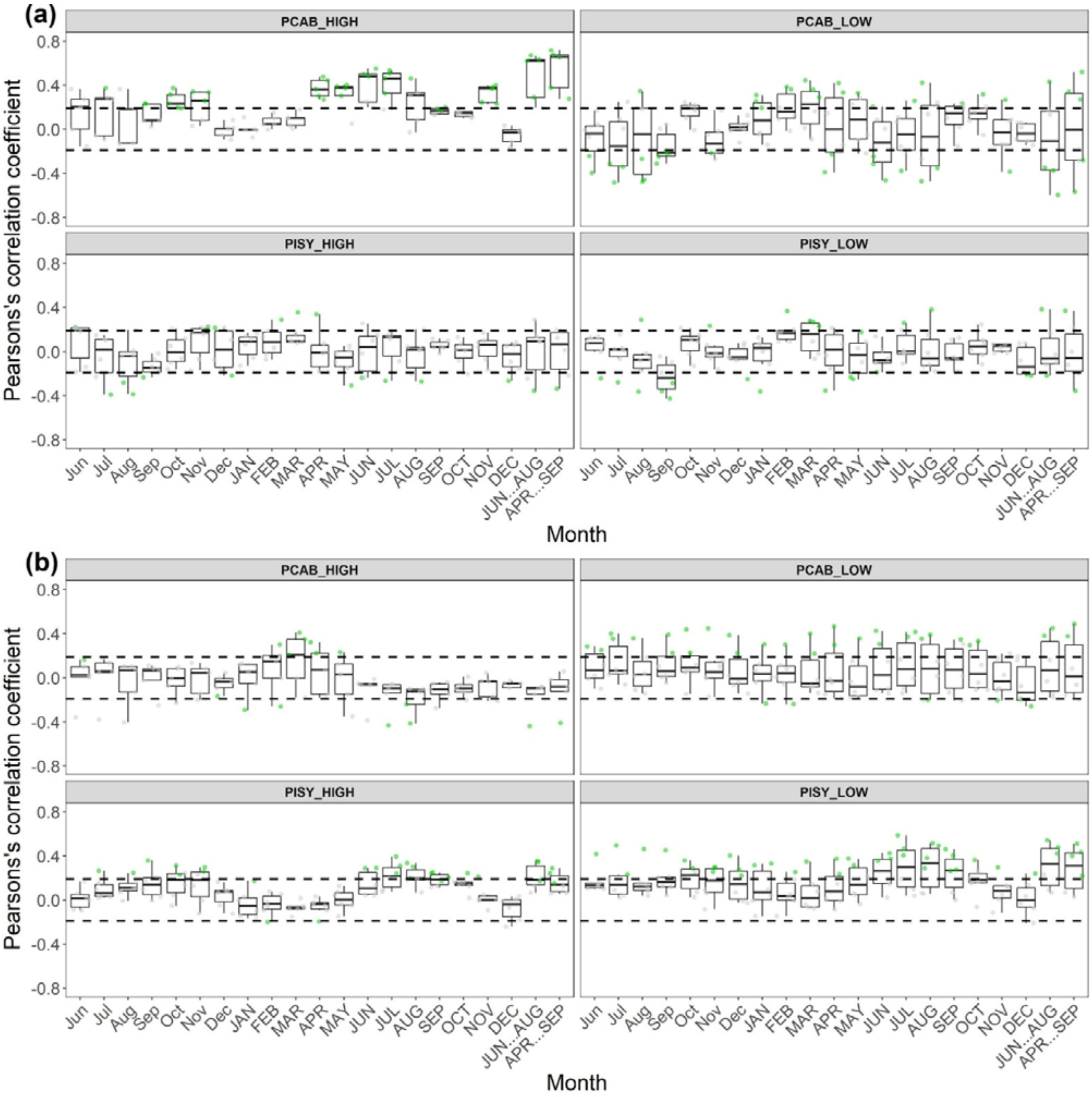

Fig. 6. Correlation response function analysis of RWI site chronologies.

Shown are temperature-growth (**a**) and moisture-growth (**b**) bootstrapped Pearson's correlations between residual RWI chronologies for each site (circles) and site category (box-whisker plots). Tukey's box-whisker plots represent the correlation values per site category, whilst circles represent the correlation value of individual site chronologies (significant in green, insignificant in gray). The upper and lower whiskers of boxplots are defined as the third quartile +1.5* interquartile range (IQR) and the first quartile −1.5*IQR, respectively. Dashed horizontal lines indicate the level of significance (*p* < .05).

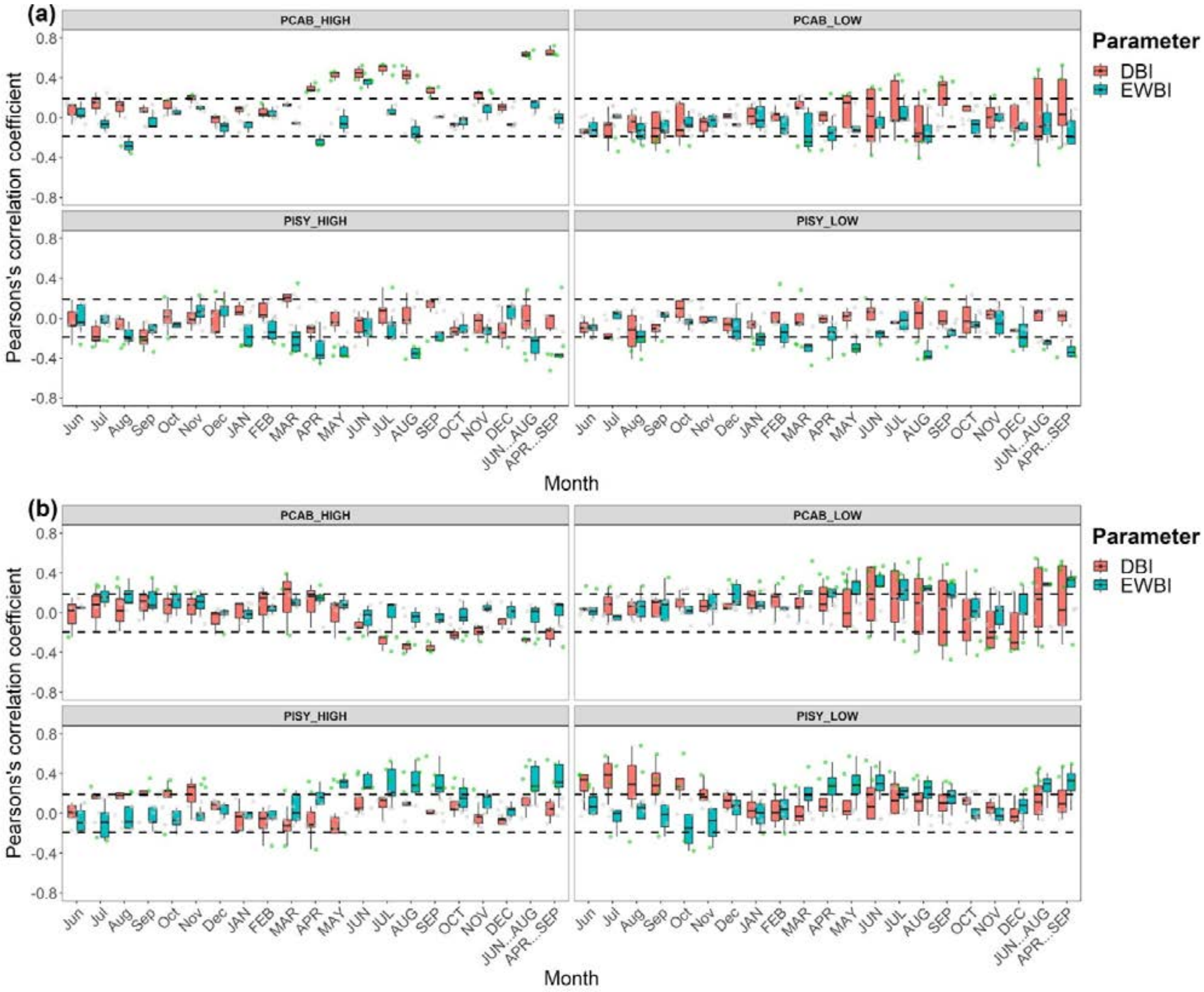

Fig. 7. Correlation response function analysis of EWBI and ΔBI site chronologies.

Shown are temperature-growth (**a**) and moisture-growth (**b**) bootstrapped Pearson's correlations between residual EWBI (**blue**) and ΔBI (**red**) chronologies and mean temperature for each site (**circles**) grouped by altitudinal category. Boxplots represent the mean correlation values per month, whilst circles represent the correlation value of individual site chronologies (significant in green, insignificant in gray). The upper and lower whiskers of boxplots are defined as the third quartile +1.5* interquartile range (IQR) and the first quartile −1.5*IQR, respectively. Dashed horizontal lines indicate the level of significance (*p* < .05).

4.3.4.4 TEMPORAL (IN)STABILITY OF CLIMATE-GROWTH RELATIONSHIPS

The moving window correlation analysis of RWI and BI parameters with summer season temperature and the moisture index show the strongest and most consistent relationship in PCAB high RWI and ΔBI with summer temperatures, a decreasing to negatively increasing correlation with summer temperatures in EWBI and ΔBI chronologies across the network, and an increasing sensitivity to summer moisture availability over all sites in recent decades (Fig. 8). Overall, the temperature and moisture signals in both PCAB high and PISY high ΔBI chronologies, and the temperature signals in PCAB low and PISY high EWBI chronologies were comparatively stronger than in RWI, respectively.

Correlation coefficients with summer temperatures were highest in PCAB high (in RWI and ΔBI; $r_{medianRWI} > 0.45$, $r_{median\Delta BI} > 0.6$), and remained significant throughout the 20th century. The ΔBI parameter at PCAB high displayed the most stable (*i.e.*, stationary) relationship with temperature, but exhibited a downward trend in temperature sensitivity across the PISY high and both species' low elevation sites in recent decades (Fig. S12-S15). The only significant relationship of the EWBI parameter with temperature is noted in individual PISY high and low sites around the 1950s and in PCAB high and low sites in recent decades (Fig. S12-S15).

On the other hand, PISY low RWI remained consistently positively associated with summer moisture availability throughout the 20th century. Significantly higher correlations were noted in PISY high and PCAB low EWBI chronologies' relationships with summer moisture compared to RWI, particularly in recent decades (Fig. 8, Fig. S13). Whereas RWI and ΔBI chronologies demonstrate a loss of sensitivity to summer moisture in high elevation sites, EWBI of all site categories show an increase in moisture sensitivity in recent decades. Generally, the moving window correlation analysis demonstrates a high degree of signal instability across all parameters and significant variability across the network in the 20th century (Fig. S12-S15).

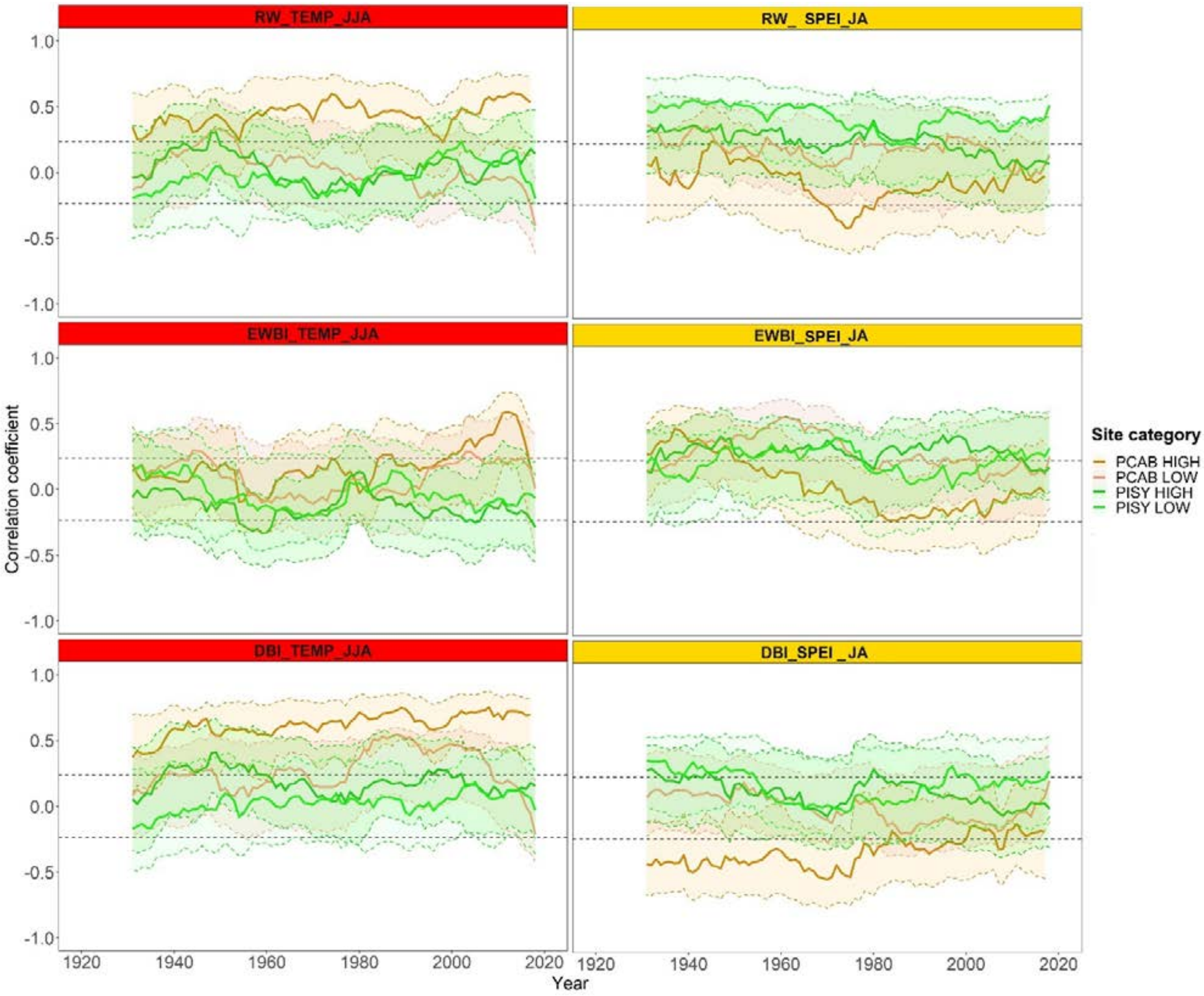

Fig. 8. Temporal climate signal stability of the RWI and BI site chronologies.

Figure shows a 31-year moving window Pearson’s correlation analysis between mean residual RWI and BI (*i.e.*, EWBI & ΔBI) chronologies per site category with summer season temperatures and the moisture index. Coloured areas with dashed lines indicate 95% confidence intervals. Each 31-year window is plotted in the last year of the window span (*e.g.*, 1988 – 2018 plotted in 2018). Black horizontal dashed lines represent the significance threshold ($p < .05$).

4.3.4.5 MONTHLY CLIMATE-GROWTH RESPONSE DERIVED FROM VS-LITE MODELLING AND MODEL PERFORMANCE

The four estimated model parameters (T1, T2, M1, and M2) demonstrated high variability among and within sites (Table S4). PISY high sites generally had a higher optimal temperature threshold than PCAB high elevation sites ($T2_{medianPISY}$ = 19.2 °C, $T2_{medianPCAB}$ = 12°C), while the opposite was true for low elevation sites ($T2_{medianPISY}$ = 12.95 °C, $T2_{medianPCAB}$ = 17.25°C). On average, PCAB have a lower value of optimal moisture for growth than PISY (Table S4). According to the modelled partial monthly growth responses averaged over elevational categories, tree growth in PCAB high is generally moisture-limited from late June to August months, with the rest of the growing season being predominantly temperature-limited (Fig. 9a). On the other hand, PCAB and PISY growth in the lowlands is broadly moisture-limited over the whole growing season (*i.e.*, April-October). Moreover, temporal evaluation of decadal mean partial growth responses indicates a distinct shift of the temperature-response curve to earlier growing season and a progressive extension of intra-annual moisture limitation towards present-times across the network (Fig. 9b, S17).

The VS-lite models exhibited relatively high growth coherence as RWI fitted well with the observed RWI across majority of sites and aggregated site categories ($p < 0.05$; Table S4, Fig. 9a, Fig. S16). On average, the correlation coefficients ranged from .47 to .55 ($p < .05$) for the calibration period, and .31 to .49 for the verification period, respectively, with exception of PISY high elevation sites ($r_{mean} \sim .07$). The highest mean correlation for an individual site was in the PCAB low site STS (r_{cal} & $r_{ver} > .60$), while the lowest mean correlation was obtained for the PISY high elevation site SUC (r_{cal} & $r_{ver} < .30$). However, the VS-lite model largely underestimated the high-frequency growth depressions (releases) during (after) recent drought periods.

4.3.4.6 SUPERPOSED EPOCH ANALYSIS AND DROUGHT LEGACIES IN RW AND BI PARAMETERS

The SEA of growth response to extreme drought events demonstrates distinct species-, site- and parameter-specific variability during severe drought years (Fig. 10). In general, PISY sites exhibit growth reductions under severe droughts uniformly across the network, compared to a more site-specific response in PCAB low, and no growth reductions in PCAB high (at $p < 0.05$). PCAB did however show strong reductions in RW and ΔBI in high-elevation sites, and EWBI in low-elevation sites, under suboptimal summer season temperatures prior to extreme drought events (Fig. 10b, 10c). Additionally, PCAB low and PISY sites without a significant growth response during severe droughts subsequently exhibited RW reductions several years following the extreme drought events, although average temperature-moisture conditions were optimal. Overall, SEA with EWBI and ΔBI parameters reiterated the conspicuous species-specific differences in severity and timing observed in RWI response (Fig. 10b, 10c).

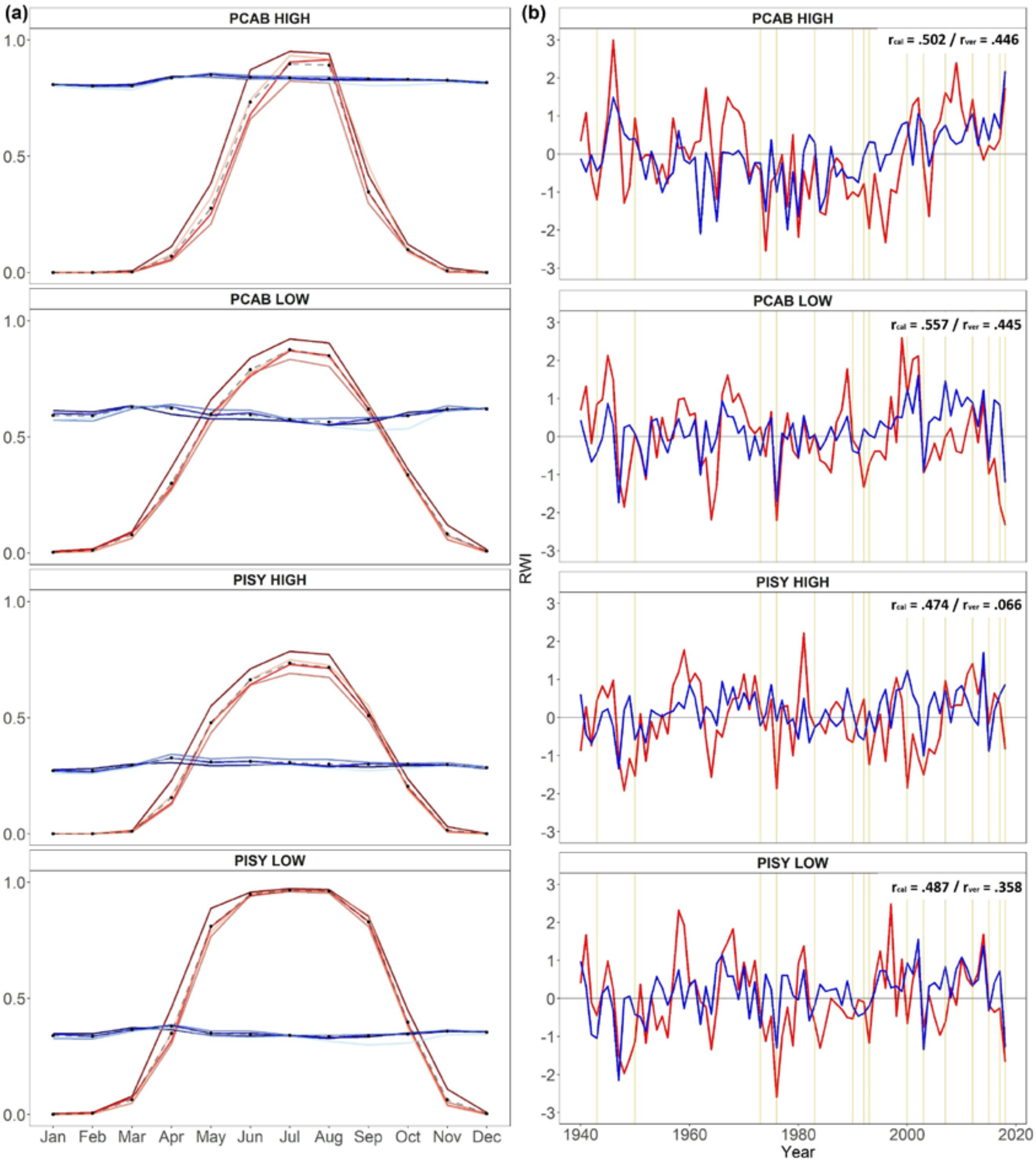

Fig. 9. VS-Lite modelling output.

VS-lite estimation of growth modulated by either temperature (***gT; red lines***) or moisture (***gM; blue lines***) per 20-yr periods (***thin lines***) and over the period 1940-2018 (***black dashed lines***) are shown for each site category in (**a**). Darker colours indicate a more recent 20-yr period (*i.e.*, darkest red/blue denotes period 2000-2018, lightest red/blue denote the 1940-1959 period). The yellow vertical lines denote severe drought years identified as significant negative deviations (SD < -2) of the regional moisture index. Overlap between modelled (***blue***) and observed residual (***red***) RWI site category chronologies are shown over the period 1940-2018 (**b**), together with their Pearson's correlation coefficient (*r*).

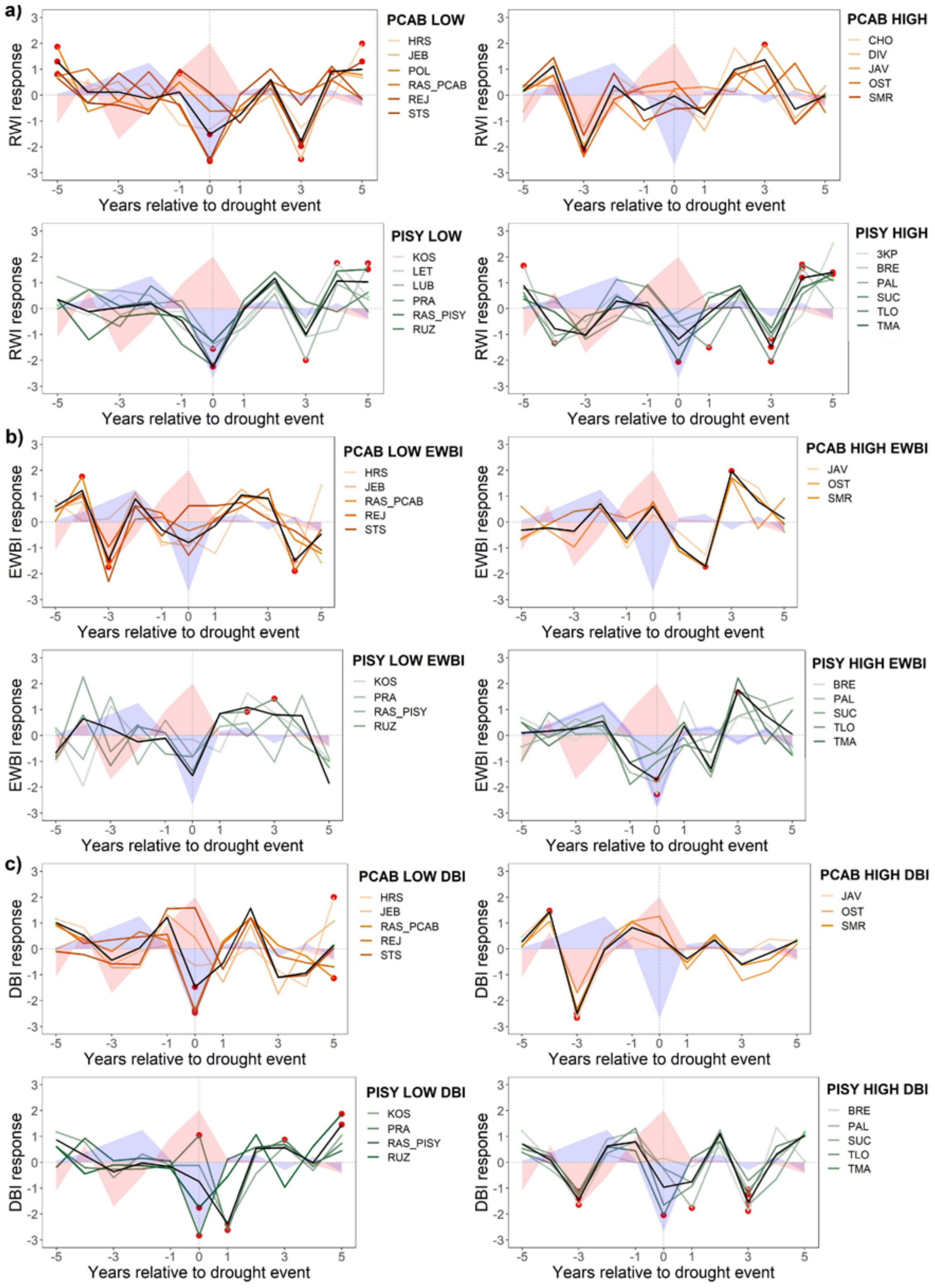

Fig. 10. SEA of Norway spruce and Scots pine RWI and BI chronologies under extreme summer droughts.

Shown are superposed epochal anomalies of scaled (*i.e.*, z-score) Norway spruce and Scots pine RWI (**a**), EWBI (**b**) and ΔBI (**c**) low- and high-elevation site chronologies to extreme drought events. Black line indicates the mean of each epochal response for each site and parameter, while the red and blue areas denote mean regional summer temperature and SPEI values, respectively. Red dots indicate statistically significant epochal anomalies ($p < 0.05$).

4.3.5 DISCUSSION

This study shows how the prevailing growth-climate associations are increasingly modulated by micro-climatic and local site conditions across Central European conifer forests, but with a general trend of intensifying hotter droughts inducing pronounced impacts on Scots pine and Norway spruce development in recent decades. Mountainous Norway spruce forests are predominantly temperature sensitive, whereas the remaining sites demonstrate a multi-faceted and mixed-climate response, indicative of a nonlinear relationship. Scots pine is strongly inhibited by decreasing moisture availability in recent decades, but both species exhibit distinct legacy effects following a severe drought. Individual wood components show clear and strong seasonality with the corresponding seasonal climatic drivers (*i.e.*, EWBI with growing season moisture availability, ΔBI with both summer temperatures and moisture availability), and improve the interpretation of drought impacts on tree growth. Finally, the process-based VS-lite model estimates the high-frequency growth variability in Norway spruce and majority of Scots pine sites fairly well, producing realistic estimates of nonlinear growth-climate associations and highlighting the broadening of the seasonal moisture-growth sensitivity in recent decades. We discuss in detail the differences in climatic responses observed across the latitudinal and altitudinal range, advantages of adopting BI tree-ring parameter to disentangle the impacts of mean climatic conditions and extreme drought events on wood anatomical features, and infer conclusions on future impacts of intensifying drought stress and shifting climatic constraints on Norway spruce and Scots pine forest development.

4.3.5.1 GROWTH-CLIMATE ASSOCIATIONS ARE MODULATED BY SITE- AND SPECIES-SPECIFIC VARIABILITY

We found large variability of climate-growth relationships across the latitudinal and altitudinal gradient of natural Norway spruce and Scots pine distribution in Central Europe since the 1950s (Fig. 6-8, S8-11). The PCA and HCA analysis demonstrated a clear dissociation of PCAB high sites from the remaining sites at the inter-annual level, indicating a strong climatic signal in PCAB high forests common growth patterns (Fig. 5). High elevation Norway spruce forests have shown to be predominantly driven by high summer temperatures, which is consistent with the findings from the Carpathian montane spruce forests (Bošel'a *et al.*, 2014; 2021; Schurman *et al.*, 2019; Sidor *et al.*, 2015) and the Alpine regions (Carrer *et al.*, 2012; Hartl-Meier *et al.*, 2014; Piovesan *et al.* 2019; Stephenson *et al.*, 2014). High summer temperatures improve cell growth processes and lead to enhanced wood production (Fritts, 1976). Additionally, previous year high autumn temperatures stimulate active carbon storage through extended period of photosynthesis (Menzel & Fabian, 1999), whereas large snow accumulation during winter ensures increased water availability at the onset of the growing season (Barnett *et al.*, 2005; Oberhuber, 2004).

Low elevation Norway spruce forests demonstrated opposing relationships with current year summer temperatures across the region, a generally uniform significant negative effect of previous year high summer temperatures, and a positive relationship with all-year high moisture availability (Fig. 6). Lagged negative effects of high summer temperatures are likely a result of reduced carbohydrate reserves for growth initiation in the following growing season, due to increased respiration losses under the compound impacts of high summer temperatures and low water availability in the previous year (Bouriaud & Popa, 2009; Kahle, 1996; van der Maaten-Theunissen *et al.*, 2012). Adverse relationships with summer season temperatures are likely related with annual precipitation regimes in different regions, where high summer temperatures at dry sites exacerbate the effects of reduced water supply (*i.e.*, negative response; RAB site), whereas Norway spruce trees from regions with optimal soil conditions profit from higher temperatures through enhanced wood formation (*i.e.*, positive response; JEB site), thus emphasizing the importance of local site conditions (*i.e.*, microclimate and topography) for tree growth sensitivity to changing environmental controls.

Contrary to our expectations that growth-climate associations remain generally elevation-dependent, Scots pine growth was predominantly limited by summer moisture availability across the whole network, indicating a heightened species-specific drought sensitivity even at cold and wet high-elevation sites. Scots pine generally grows atop rocky, shallow, and nutrient deficient soils with low top-soil water retention and low productivity (Chytrý, 2013; Treml *et al.*, 2021), which increases its dependence on water availability during dry summer spells (Haberstroh *et al.*, 2022). Furthermore, compound drought events and reduced winter precipitation can reduce soil water reserves prior to the onset of tree growth in early spring, which is the dominant period of wood and xylem formation in Scots pine (Gruber *et al.* 2010; Michelot *et al.* 2012), whereas an increase in water availability improves stomatal conductance and leads to higher carbon uptake and, ultimately, enhanced wood production (Feichtinger *et al.*, 2014; Larcher, 2003; Ruehr *et al.*, 2012). The predicted intensification of arid conditions and hot summers will likely drive future growth declines of Scots pine across the altitudinal gradient.

4.3.5.2 EWBI AND ΔBI REVEAL SPECIES-SPECIFIC CLIMATE RESPONSE IN EARLYWOOD AND LATEWOOD FORMATION

Climate-growth relationships derived from BI parameters revealed distinct impacts of shifting climatic constraints on the seasonality of wood formation, but a generally stronger climatic response and less variability across species and sites compared to the RWI analysis (Fig. 7, S9-S11). EWBI and ΔBI, as surrogates for earlywood and latewood cell (tracheid) size and density (Campbell *et al.*, 2007) provide fundamental information on the climatic interactions with individual wood components which are generally confounded in growth-climate associations with RWI. This partitioning of the climatic controls on tree growth is clearly indicated by the visible separation of EWBI from the rest of the parameters in our analysis (Fig. S7). Furthermore, compartmentalization of tree growth can be used to interpret the changes in xylem-hydraulic conductivity and assess species' drought sensitivity under shifting climatic constraints (Eilmann *et al.*, 2012).

Previous studies of xylogenic processes have shown strong dependence of earlywood formation on carbohydrate storage from previous years (Eilmann *et al.*, 2009; 2012; Kagawa *et al.* 2006; Weber *et al.* 2007). We identified significant negative correlations of EWBI with previous and current summer temperatures, and strong positive associations with moisture availability during both previous and current year growing season (Fig. 7). During the preceding year, chronically dry conditions in tandem with high temperatures can inhibit synthesis of growth sustaining carbohydrates, which leads to fast depletion of carbon storage when trees experience drought stress in the following year. In turn, this induces formation of cells with narrower lumen due to the positive stimulus of high temperatures on cell wall thickening going from earlywood to latewood, thus producing higher earlywood density (Björklund *et al.*, 2014; Cuny *et al.*, 2014). A generally stronger response of EWBI to summer season conditions in PISY compared to PCAB sites indicates a stronger sensitivity of Scots pine earlywood formation to early growing season moisture availability, which is further reflected by generally broader and left-skewed window of moisture-growth limitation predicted by the VS-lite model (Fig. 9a).

On the other hand, latewood density is generally a factor of cell-wall thickening processes and variation (Björklund *et al.*, 2017; Carrer *et al.*, 2017; Cuny *et al.*, 2014). In our study, ΔBI was utilized as a surrogate for latewood density and demonstrated a generally positive association with current early spring and late summer season temperatures, and a negative association with previous late summer temperatures across all low-elevation sites and PISY high sites (Fig. 7). The positive temperature-growth association could be explained by optimal water availability at the beginning/end of the growing season making higher transpiration rates under rising temperatures more tolerable, in turn increasing latewood density. The lagged negative effects of late summer temperature can be attributed to early stomatal closure to prevent hydraulic failure during hot and dry late summer conditions, which comes at a cost of reduced carbon assimilation rates (Jones, 2009; Martin-Benito *et al.*, 2013; McDowell *et al.*, 2008) and reduced resource allocation to cell-wall thickening (Willey & Helliker, 2012). Similarly, prioritization of hydraulic safety over growth efficiency is further reflected by the positive association of ΔBI with the previous year summer moisture index. However, the distinct site-specific differences in ΔBI response to current year moisture conditions suggests localised coping strategies and latewood modifications under increasing drought stress, and highlights the role of local site conditions on late summer carbon assimilation (Mayr, 2007; Oberhuber, 2004; Rehschuh *et al.* 2021, Rigling *et al.*, 2003).

4.3.5.3 WEAKENING OF TEMPERATURE-GROWTH SENSITIVITY IS MIRRORED BY INCREASING MOISTURE-GROWTH LIMITATION AND DECLINING GROWTH RATES UNDER MORE FREQUENT DROUGHTS

Temporal coherence analysis identified four general trends in growth sensitivity of Norway spruce and Scots pine to summer season climate over the period 1940 (1950) – 2018: a stable and continuously significant temperature sensitivity in PCAB high, a decreasing to negatively increasing sensitivity to summer temperatures across PISY sites and PCAB low sites captured by all tree-ring parameters, a generally increasing sensitivity to summer moisture availability across majority of sites captured by the EWBI and RWI tree-ring parameters (Fig. 8, S12-S15), and a progressive extension of the seasonal moisture-growth limitation towards present times (Fig. 9a, S17-S18).

We identified a rising adverse importance of summer temperature and moisture controls on tree growth sensitivity across the altitudinal range (Fig. 6, 9a, Fig. S12-17). Whereas the unprecedented warming enhanced Norway spruce growth at high elevations since the 1980s, rising summer temperatures have likely exacerbated the impacts of summer drought stress in the lowlands by increasing evapotranspiration rates and, thus, moisture availability pressure on tree growth (Briffa *et al.*, 2009, Kašpar *et al.* 2021). Some low-elevation site chronologies did demonstrate a positive increase in summer temperature sensitivity in recent decades (*e.g.*, mesic REJ & STS sites; Fig. S12), which could partially reflect an alleviation of summer drought stress due to extended growing season allowing for cambial reactivation and additional carbon storage (Pretzsch *et al.*, 2014, Tumajer *et al.* 2017). However, the general trend of intensifying

RW sensitivity to hotter droughts was followed by a notable growth decline along all tree-ring parameters over recent decades (Fig. 3, Fig. 9b), suggesting that the soil moisture deficits during the growing season and extreme regional drought events ultimately offset any benefits of a prolonged growing season and additional carbon production. Furthermore, factors outside of the scope of this study, such as stand structural features (*e.g.*, mean DBH and age, horizontal and vertical structure) and/or topographical attributes (*e.g.*, soil type, slope, exposition), are likely contributing to the large spatiotemporal variability in response to drought impacts observed across the network (Mašek *et al.*, 2021; Mazza *et al.*, 2014; Trotsiuk *et al.*, 2020). The significant divergence in growth synchrony between Norway spruce and Scots pine growing at the same site (*i.e.*, Rabštejn; Fig. S16) further highlight the importance of understanding species-specific functional traits and physiological mechanisms to cope with increasing drought stress on a local spatial scale (Bošel'a *et al.*, 2019; Kolář *et al.*, 2017; Vitali *et al.*, 2017).

VS-lite derived partial monthly growth response analysis predicted an intra-annual increase in the proportion of tree growth developed under moisture limitation over recent decades, particularly in the early growing season and at high elevations (Fig. 9b, Fig. S17). This ties in well with the results of the linear correlation analyses and temporal analysis of growth-climate sensitivity over the 20th century, furthermore highlighting the rising importance of water availability and optimal temperatures at the onset of the growing season for annual growth. However, the observed decoupling between the modelled and observed PISY high chronologies since 1970s, and the relatively underestimated magnitude of growth reductions following extreme drought events in recent decades (Fig. 9a), reveal limited capacity of the VS-lite model for modelling complex growth-climate interactions from environments with an intricate mixed-climate relationships under global warming. Scots pine sites represent a marginal niche of its natural ecological distribution and exhibit more complex response under rising temperatures at the inter-annual scale, which likely complicates predicting tree growth under increasing climatic variability (Bose *et al.*, 2020; Tumajer *et al.*, 2022). Moreover, high-elevation forests exhibited significant growth declines due to a period of high air pollution and increased acid deposition in the region, where we recognized the largest divergence between the modelled and observed growth rates (*i.e.*, 1970s & 1980s; Kolář *et al.*, 2015; Rydval & Wilson, 2012).

4.3.5.4 SCOTS PINE EXHIBIT STRONG GROWTH REDUCTIONS DURING SEVERE DROUGHTS, BUT BOTH SPECIES DEMONSTRATE PRONOUNCED LEGACY EFFECTS IN INTRA-ANNUAL TREE-RING FORMATION

Superposed epoch analysis (SEA) has been widely used in dendroclimatological evaluation of drought legacy effects (*e.g.*, Lévesque *et al.*, 2014; Martin-Benito *et al.*, 2008; Pederson *et al.*, 2014). In this study, SEA of growth response to extreme drought events tested over multiple tree-ring parameters demonstrated significant growth reductions across majority of Scots pine sites during severe droughts, and notable legacy effects several years after extreme drought events in both species across the lowlands (Fig. 10; $p < 0.05$). Furthermore, SEA with EWBI and ΔBI parameters proved useful in capturing average pre- and post-drought anomalies in xylem formation across the network (Fig. 10b, 10c). To our knowledge, few studies have utilized BI parameters in analysis of epochal growth anomalies under extreme (non-)climatic events (*e.g.*, Reid & Wilson, 2020).

Scots pine exhibited strongest negative response in RW and ΔBI during severe drought years across the altitudinal range, as well as several years after the extreme drought event (Fig. 10). This could indicate a specific optimization strategy in Scots pine trees under drought stress: as a more isohydric species, Scots pines ensure the preservation of hydraulic efficiency under recurrent droughts by down-regulating stomatal conductance (Oberhuber *et al.*, 2015; Swidrak *et al.*, 2011) and producing a lower number of cells (*i.e.*, narrower rings), while maintaining the relative proportion between the cell wall and cell size stable through reduced resource investments into cell-wall thickness (*i.e.*, lignification phase; Eilmann *et al.*, 2009). Furthermore, Scots pines that exhibited severe growth reductions in extreme drought years generally did not exhibit significant growth fluctuations in the following years, thus potentially demonstrating higher growth resistance to subsequent moderate droughts or non-climatic perturbations, as a result of higher investments into to non-structural carbohydrate storages and root structural pools, ensuring mechanical stability and maintaining the hydraulic function (Fonti *et al.*, 2010; Galván *et al.*, 2014; Hacke *et al.*, 2001). However, increasing sensitivity to moisture availability in recent decades (Fig. 8, Fig. 9a) and significant drought legacy effects identified across PISY sites (Fig. 10) support the findings from ecophysiological studies of potentially limited resilience and recovery of Scots pine following recurrent severe droughts (*e.g.*, Lloret *et al.* 2011; Serra-Maluquer *et al.*, 2018**,** Schwarz *et al.*, 2020).

In Norway spruce, RW reductions in drought years were less pronounced and significant only at the extremely dry (*i.e.*, RAS) and/or mesic site (*i.e.*, REJ; Fig. 10). However, majority of lowland sites showed an abrupt RW reduction in the 3rd year following a severe drought event. The fact that the lagged response in RW occurred during optimal growth conditions and was not mirrored by an earlywood and/or latewood response could indicate an intrinsic maladaptation of Norway spruce to metabolically acclimate under extreme growing conditions (Hentschel *et al.*, 2014; Lévesque *et al.*, 2013) and suggests a generally higher vulnerability to non-climatic perturbations in the following years (Jactel *et al.*, 2012). Moreover, recent trends in Norway spruce growth reductions (*e.g.*, Treml *et al.*, 2021) and a generally declining growth trend observed in lowlands over recent decades (Fig. 3, 9b) could indicate a decreasing potential of Norway spruce for physiological acclimation to moisture stress and increasing frequency of recurrent severe droughts (Knüver *et al.*, 2022), and may be the first warning signs of incoming mortality (Buras *et al.*, 2020; Cailleret *et al.*, 2019; Cienciala *et al.*, 2018; Treml *et al.*, 2022).

4.3.5.5 IMPLICATIONS OF INTENSIFYING DROUGHTS ON NORWAY SPRUCE AND SCOTS PINE FUTURE DEVELOPMENT IN CENTRAL EUROPE UNDER GLOBAL CLIMATE CHANGE

Protracted heatwaves and recurrent droughts exhibit pronounced short-term and long-term effects on carbon production needed for sustaining tree growth, thus leading to hydraulic failure, rapid depletion of carbon storage and carbon starvation (McDowell *et al.*, 2022; Sedmáková *et al.*, 2022). The resulting depletion of carbon pools leads to growth declines that ultimately reduce trees' resistance against future mortality vectors (Bréda *et al.* 2006; Wiley & Helliker, 2012). The physiological mechanisms that affect individual tree growth can accumulate over time as legacies and scale up to disproportionately affect forest landscapes (Kannenberg *et al.*, 2020; Sippel *et al.*, 2018), either through distinct declines in radial growth (*i.e.*, reduced carbon uptake; Bigler *et al.*, 2007) or widespread mortality events (*i.e.*, increased carbon source; Vanoni *et al.* 2016). Climate-induced growth declines have already been linked with rising mortality in Norway spruce and Scots pine forests across the Carpathians (*e.g.*, Parobekova *et al.*, 2016; Seidl *et al.* 2017; Sidor *et al.*, 2019), the Alps (*e.g.*, Seidl *et al.* 2017; Thom *et al.*, 2018) and Central European regions (Buras *et al.* 2020; Haberstroh *et al.*, 2022; Senf & Seidl 2021a; 2021b).

In general, the large spatial and temporal differences in growth sensitivity under increasing climatic pressures observed across our network suggest that the future development of Central European conifer forests with nonlinear and mixed-response will heavily depend on micro-environmental variability (Babst *et al.*, 2013; Svobodová *et al.*, 2019; Zang *et al.*, 2014) and the general interplay between species' functional traits (*i.e.*, plasticity) and growth factors promoting/inhibiting tree growth (*e.g.*, prolonged growing season and abundant growing season soil moisture vs periodic extreme drought events), making projections of forest ecosystem resilience increasingly challenging. Norway spruce high-elevation forests have largely benefitted from rising temperatures in recent decades, although it remains unclear whether accelerated growth rates will translate into a higher carbon sink capacity (Begović *et al.*, 2022), nor whether increasing moisture sensitivity will eventually decouple enhanced tree growth from temperature (Camarero *et al.*, 2021). On the other hand, more frequent and severe droughts will likely drive radial growth declines across xeric and mesic low elevation Norway spruce and both low- and high elevation Scots pine sites across the network, albeit higher xylogenetic plasticity of the isohydric Scots pine and conservative carbon allocation strategies might mediate transient drought effects (Körner, 2015; Phillips *et al.*, 2016). However, persistent moisture pressures caused by more frequent heatwaves and growing season droughts will likely affect future growth trends of both species and push these monospecific forest ecosystems beyond their hydraulic limits (Peltier & Ogle, 2019; Serra-Maluquer *et al.* 2021), which could ultimately trigger large-scale tree-dieback and ecosystem carbon cycle feedbacks, in turn reducing the climate mitigation potential of Central European forest ecosystems.

4.3.6 CONCLUSION

Norway spruce and Scots pine demonstrated large spatiotemporal variability in growth-climate associations and distinct species-specific growth response patterns under severe droughts in Central Europe. Effects of shifting dominant climatic controls enhance growth in temperature-driven mountainous Norway spruce forests, but induce a broad magnitude of effects in mixed-response Scots pine montane forests, and moisture-driven Scots pine and Norway spruce lowlands. Growth reductions under extreme droughts and discrete legacy effects in wood components are most pronounced in the low elevation forests, and together with the observed declining growth trends in the 21st century, suggest that the predicted increase in frequency and duration of summer droughts will likely drive future growth declines across the region, through increased evapotranspiration demands, depletion of stored carbohydrates and, ultimately, decreased resistance to extrinsic mortality factors. Considering the inconsistent and spatiotemporally variable (nonlinear) growth relationship with dominant climatic drivers, the long-term performance and future development of Central European conifer forests will be increasingly dependent on local site and microclimatic conditions. Finally, we highlight the advantage of utilizing the BI parameters as robust proxies of short-term drought impacts and long-term trends of antecedent and contemporary climatic drivers on wood anatomical features from trees developing in moisture-limited environments.

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SUPPORTING INFORMATION

Additional supporting data can be found in the Supporting Information subsection (S3) of the Bibliography section at the end of this Thesis.

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4.4 ECOLOGICAL AND METHODOLOGICAL DRIVERS OF NON-STATIONARITY IN TREE GROWTH RESPONSE TO CLIMATE

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Abstract: Radial tree growth is sensitive to environmental conditions, making observed growth increments an important indicator of climate change effects on forest growth. However, unprecedented climate variability could lead to non-stationarity, that is, a decoupling of tree growth responses from climate over time, potentially inducing biases in climate reconstructions and forest growth projections. Little is known about whether and to what extent environmental conditions, species, and model type and resolution affect the occurrence and magnitude of non-stationarity. To systematically assess potential drivers of non-stationarity, we compiled tree-ring width chronologies of two conifer species, *Picea abies* and *Pinus sylvestris*, distributed across cold, dry, and mixed climates. We analyzed 147 sites across the Europe including the distribution margins of these species as well as moderate sites. We calibrated four numerical models (linear vs. non-linear, daily vs. monthly resolution) to simulate growth chronologies based on temperature and soil moisture data. Climate–growth models were tested in independent verification periods to quantify their non-stationarity, which was assessed based on bootstrapped transfer function stability tests. The degree of non-stationarity varied between species, site climatic conditions, and models. Chronologies of *P. sylvestris* showed stronger non-stationarity compared with *Picea abies* stands with a high degree of stationarity. Sites with mixed climatic signals were most affected by non-stationarity compared with sites sampled at cold and dry species distribution margins. Moreover, linear models with daily resolution exhibited greater non-stationarity compared with monthly-resolved non-linear models. We conclude that non-stationarity in climate–growth responses is a multifactorial phenomenon driven by the interaction of site climatic conditions, tree species, and methodological features of the modelling approach. Given the existence of multiple drivers and the frequent occurrence of non-stationarity, we recommend that temporal non- stationarity rather than stationarity should be considered as the baseline model of climate–growth response for temperate forests.

4.4.1 INTRODUCTION

Understanding past responses of tree growth to climate is a crucial prerequisite for predicting future forest dynamics (Soja *et al.*, 2007). More precisely, the development of reliable numerical climate–growth models is essential to assess the relationship between tree growth and climate to infer tree growth patterns beyond meteorological records. However, assessing these climate–growth responses is becoming increasingly challenging as climate change accelerates. In particular, there is an increasing risk that environmental conditions outside the calibration period could exceed certain physiological thresholds, that are unprecedented in the time period covered by the calibration data set (Vaganov *et al.*, 2006). Such a situation might lead to non-linear and temporarily unstable relationships between tree growth and climatic factors (Wilmking *et al.*, 2020). Consequently, calibrated climate–growth response functions might not accurately reflect growth variability outside the calibration period, which might reduce the validity of both climate reconstructions and forecast models of forest growth (Jevšenak *et al.*, 2018). This phenomenon, referred to as the “divergence problem” (D'Arrigo *et al.*, 2008) or “non-stationarity” (Wilmking *et al.*, 2020), is likely widespread and might affect most forest biomes across the globe (Buchwal *et al.*, 2020; Büntgen *et al.*, 2006; Kirdyanov *et al.*, 2020; Wilmking *et al.*, 2020). Although the existence of non-stationarity is increasingly recognized and novel approaches to detect non- stationarity have been developed (Buras *et al.*, 2017), our understanding of the processes causing non-stationarity remains limited.

For instance, it is unclear to what extent certain environments and species are more susceptible to non-stationarity than others. Climate–growth non-stationarity was initially reported from cold environments such as high latitudes (Briffa *et al.*, 1998; D'Arrigo *et al.*, 2008; Kirdyanov *et al.*, 2020) and high elevations (Büntgen *et al.*, 2006), where tree growth gradually began to decouple from summer temperatures. However, a recent meta-analysis revealed that non-stationarity is a global phenomenon, which affects all forested biomes (Wilmking *et al.*, 2020). Temperate forests represent a transitional biome between cold and drought-limited ecosystems, where both temperature and moisture availability interact in influencing tree growth. This interaction can make ring-width chronologies from temperate regions prone to switching between temperature and moisture sensitivity over time (Babst *et al.*, 2013; Neuwirth *et al.*, 2007; Tumajer *et al.*, 2017). In addition to climate change, forest growth dynamics of temperate forests have been recently observed to shift in response to unprecedented CO2 concentrations (Frank *et al.*, 2015), nitrogen fertilization (Scharnweber *et al.*, 2019) or air pollution (Ponocná *et al.*, 2018).

Moreover, different temperate regions and species might be prone to non-stationarity to varying degrees, as specific regional chronologies can experience considerable variability in the degree of climate–growth non-stationarity (Esper *et al.*, 2016; Ljungqvist, Piermattei, *et al.*, 2020).

In addition to environmental factors, non-stationarity might reflect methodological biases of specific transfer functions used to describe the link between climate and radial growth (Esper & Frank, 2009; Wilmking *et al.*, 2020; Wolkovich *et al.*, 2021). Although decoupling of observed chronology from its numerical simulation might help to identify important ecological, phenological and physiological shifts (Camarero *et al.*, 2021; Kirdyanov *et al.*, 2020), it also represents a significant bias for applied research focused on, for example, long-term predictions of forest growth and productivity (Charney *et al.*, 2016). This increases the need for identifying models capable of coping with shifting climatic responses. Climate–growth correlations represent the standard statistical approach in tree-ring research, where climatic data are linearly correlated with tree ring-width chronologies to identify the climatic variable with the strongest statistical relationship to tree growth (Fritts, 1976). Statistical climate–growth correlations can be easily applied to any site across the world where climatic data and tree-ring width chronologies are available, without the need to estimate ecologically reasonable parameters (Babst *et al.*, 2019). However, statistical models lack a mechanistic link to the processes behind wood formation (Friend *et al.*, 2019). Furthermore, the presumed linear relationship between tree growth and its climatic limiting factor(s) does not represent ecological reality under changing climatic conditions and growth-limiting factors (Wilmking *et al.*, 2020). Consequently, some studies reported that non-stationarity might be amplified by using unrealistic linear models to approximate the non-linear response of tree-ring width to climate (Ljungqvist, Thejll, *et al.*, 2020; Wilmking *et al.*, 2020; Wolkovich *et al.*, 2021). In contrast to linear climate–growth correlations, non-linear process-based models of wood formation represent an approximation of current knowledge of the mechanisms driving wood formation at fine temporal scales (Eckes-Shephard *et al.*, 2022; Guiot *et al.*, 2014). Many process-based models provide highly reliable simulations exhibiting high coherence with observational data sets (Cabon *et al.*, 2020; Drew *et al.*, 2010; Gennaretti *et al.*, 2017; Vaganov *et al.*, 2006). Indeed, non-linear process-based models should be less prone to divergence bias (Kirdyanov *et al.*, 2020; Tolwinski-Ward *et al.*, 2011). However, a systematic comparison of the predisposition to non-stationarity of linear versus non-linear models has so far not been presented (but see Jevšenak *et al.*, 2018).

In this study, we aim to test how climatic conditions, tree species, and model structure affect the level of non-stationarity of climate– growth response functions. We established 22 new sampling sites of *Picea abies* (L.) Karst. and *Pinus sylvestris* L. across local species distribution margins in Central Europe and downloaded additional 125 site chronologies spread across South-Eastern, Central and Northern Europe from publicly available databases (Schurman *et al.*, 2019; Zhao *et al.*, 2019). Sites were distributed across dry (predominantly moisture-limited), cold (predominantly temperature-limited) and climatically mixed environments. We used linear regression models and non-linear process-based models of wood formation—each with monthly and daily resolution—to predict ring-width chronologies based on soil moisture, precipitation, and temperature. We then compared stationarity between models, climates, and species using bootstrapped transfer function stability tests (Buras *et al.*, 2017). We hypothesized that (i) non-linear process-based models would be less prone to non-stationarity compared with linear models, and (ii) models with daily temporal resolution would be more stationary compared with monthly resolved models (Jevšenak, 2019). Furthermore, we expected (iii) a stronger degree of stationarity at sites with a simple (either temperature- or moisture-limited) climatic signal compared with sites with a complex (mixed) climatic signal.

4.4.2 MATERIALS AND METHODS

4.4.2.1 STUDY DESIGN AND DENDROCHRONOLOGICAL SAMPLING

We based our study on two tree-ring width data sets (Figure 1; Table S1). First, we sampled 11 new sites for each of two species (*P. abies* and *P. sylvestris*) distributed across their distribution margins in the Czech Republic and Slovakia (hereafter referred to as the "CZSK" database). During the site selection for the CZSK database, we focused on the presence of mature canopy trees in forests subjected to a limited level of forest management and whose expected age ranged from 120 to 250 years (Treml *et al.*, 2022). Since we aimed to study climate–growth responses at sites where growth is predominantly driven by climate, we selected sites in the lowest (below 650 m), presumably moisture-limited, and highest (above 900 and 1200 m for *P. sylvestris* and *P. abies*, respectively), presumably temperature-limited, sections within the regional distribution range of these species (Fritts, 1976). For each site, we sampled 35–60 dominant individuals using a Pressler borer during the summer months of 2019 and 2020. One core was extracted from each sampled tree at breast height. The cores were air dried, glued to wooden supports, and sanded to enhance tree-ring visibility. Individual cores were scanned, and tree-ring widths were measured with a precision of 0.001 mm and cross dated using WinDENDRO software (Régent Instruments).

To extend our data set of site chronologies, we downloaded tree-ring width data for 63 sites of *P. abies* and 62 sites of *P. sylvestris* spread across Europe from the publicly available International Tree-Ring Data Bank (ITRDB; Zhao *et al.*, 2019) and REMOTE Forest (Schurman *et al.*, 2019) databases (hereafter referred to as the "ITRDB" database). First, we downloaded all available individual tree-ring width series for *P. abies* and *P. sylvestris* from the ITRDB (Zhao *et al.*, 2019; https://www.ncei.noaa.gov/products/paleoclimatology/tree-ring). We then removed all sites located outside of Europe, sites with a temporal span not fully overlapping with the 1950–2010 period, and with a replication of less than 10 series. To improve the spatial coverage of the ITRDB data set in South-Eastern Europe, we included 13 P. *abies* sites from the REMOTE Forest database (Schurman *et al.*, 2019; https://www.remoteforests.org/).

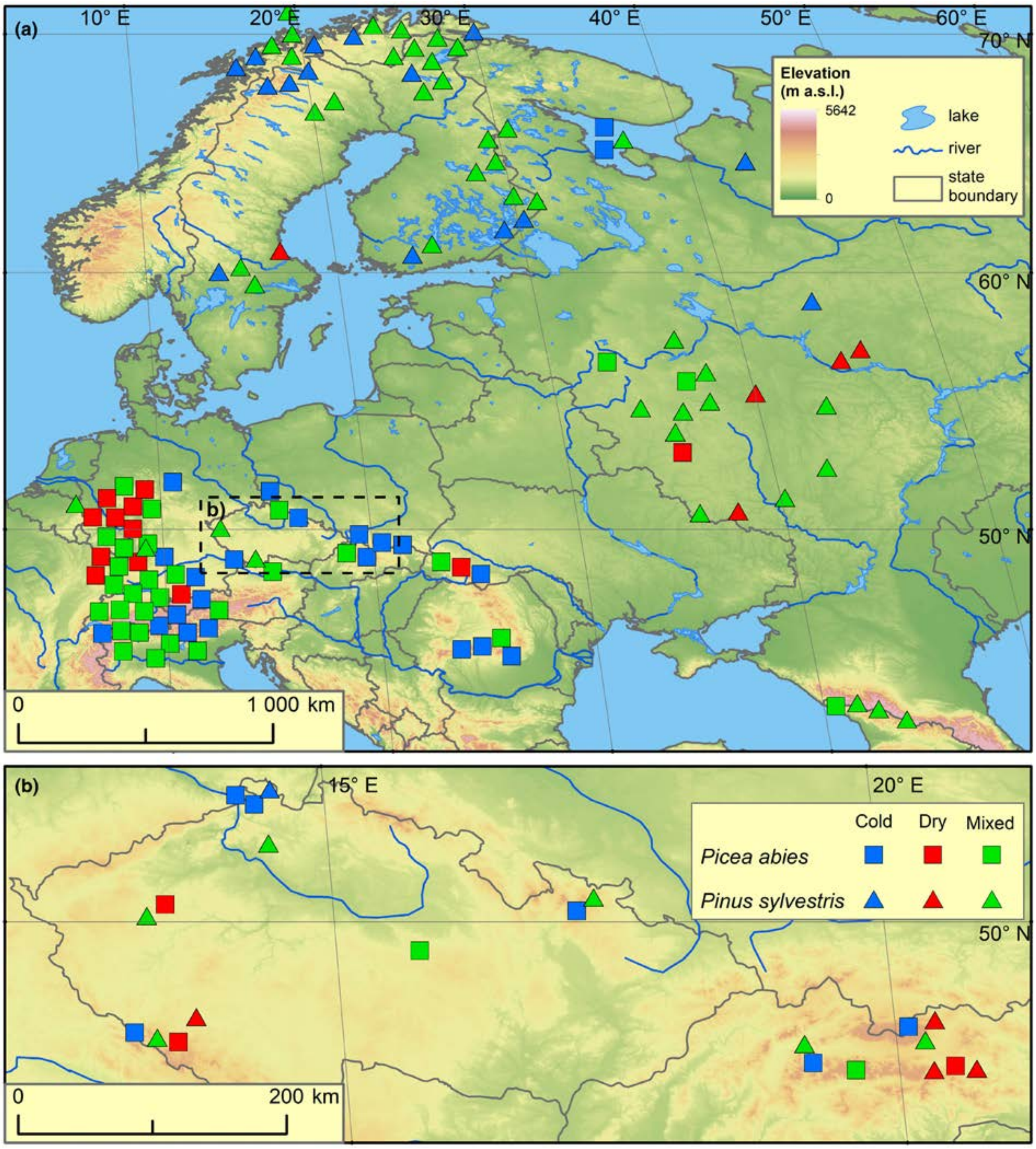

Fig. 1. Distribution of sites from (a) the International Tree-Ring Data Bank and (b) CZSK databases across Europe.

The position of some sites in regions with high site density (mainly Switzerland) was geometrically offset to improve their visibility on the map. For the exact coordinates of each site, see Table S1. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

4.4.2.2 PROCESSING OF DENDROCHRONOLOGICAL DATA

We used the same approach to process tree-ring width series from both the ITRDB and CZSK databases. To remove age trends from raw tree-ring width series, we fit a 100-year smoothing spline with a 50% frequency cut-off to each series (Cook & Peters, 1981). The indexed series were obtained by dividing the observed ring width measurements by the respective value of the spline. Finally, individual series from the same site were averaged into standard site chronologies using bi-weight robust averaging. For the rest of the analysis, we truncated all chronologies to the period 1940–2018 (Czech Republic) or 1950–2018 (Slovakia, ITRDB database), because this interval coincides with the period of available daily climatic data (see Section 2.3) and ensures sufficiently long calibration and verification periods (Figure 2a). All processing of dendrochronological data was performed in R 4.1.2. (R Core Team, 2021) using the pack- age “*dplR*” (Bunn, 2008).

4.4.2.3 CLIMATIC DATA

We acquired daily mean air temperature and precipitation data for each of the sites (Figure 2a). The approaches of data acquisition differed between the Czech Republic and the rest of the sites. For the Czech Republic, we used spatial interpolation based on a network of meteorological data from the Czech Hydrometeorological Institute and German Weather Service (for border regions). Daily mean air temperature for each site was interpolated from the nearest set of climate stations (maximum distance was 70 km from the specific sampling site) using orographic regression (Bivand *et al.*, 2013). Precipitation was interpolated from station data using the inverse-distance weighted method (maximum distance 50 km). For Slovakia and the ITRDB database, station data were not publicly available, and we, therefore, acquired daily resolved air temperature and precipitation data from the EOBS v22.0 gridded database with a resolution of 0.1° × 0.1° (Cornes *et al.*, 2018). The time period of climatic data used in this study was 1940– 2018 for the Czech Republic and 1950–2018 for Slovakia and the ITRDB sites. Both climatic data sets showed a sufficient density of climatic stations for the purpose of this study (Figure S1). There was a slight increasing trend in the number of temperature-measuring stations over time. The increase in the number of stations with precipitation measurements during the 1940s–1980s was followed by a slight decline in the most recent decades in both climatic data sets.

4.4.2.4 SOIL SAMPLING AND SOIL MOISTURE MODEL (CZSK DATABASE)

We simulated volumetric soil moisture variability at a daily scale for each site of the CZSK database (Figure 2a). To feed the soil moisture model with realistic parameters, we measured soil depth and obtained soil samples to assess their physical properties related to the water-holding capacity. In addition, we directly measured soil moisture at six sites using VIRRIB sensors and a MINILOG datalogger (Fiedler company, Czech Republic) in 10-min steps during the 2019 and 2020 growing seasons. Mean soil depth was estimated with a soil probe hammered into the soil at 10 points at each site. The soil samples were taken from dominant soil layers, mixed together, and analyzed for soil texture. Water-holding capacity was derived from soil texture using the pedo-transfer function in the ROSETTA model (Schaap *et al.*, 2001). The model estimates soil hydraulic parameters such as saturated volumetric water content (θs) and residual volumetric water content (θr) according to retention curves (van Genuchten, 1980). Their difference ($\theta s - \theta r$) represents the water-holding capacity. All soil depths were recalculated to a depth of 1 m, and the water-holding capacity was adjusted for estimated rock content and soil moisture.

Next, a soil moisture model was set up to simulate the daily volumetric soil moisture at each sampling site. The model estimates soil moisture based on daily precipitation, evapotranspiration, and snowmelt data. The model is based on the frequently used SWBM-GA model (Brocca *et al.*, 2008; 2014) represented by the following equation:

$$\begin{cases} \dfrac{d\theta(t)}{dt} = f(t) - e(t) - g(t), \text{ if } \theta(t) < \theta_s \\ \theta(t) = \theta_s, \text{ if } \theta(t) \geq \theta_s \end{cases} \quad \textbf{(1)}$$

where $\theta(t)$ (mm d−1) is the soil moisture at time t and $f(t)$ (mm d−1) is the amount of water which infiltrates into the soil either directly as liquid precipitation or as snowmelt. The daily snow-water equivalent to differentiate between snowfall and rain was calculated based on a threshold air temperature and the snowmelt was calculated using the degree-day method (Hock, 2003). Actual evapotranspiration e(t) (mm d^{-1}) was calculated from potential evapotranspiration (Oudin *et al.*, 2005) as a function of the actual soil moisture and temperature. Finally, g(t) (mm d^{-1}) is the drainage rate, which represents interflow and water percolation, and is calculated using saturated hydraulic conductivity and saturated soil moisture, θs (Brocca *et al.*, 2014).

For the six sites of the CZSK network where measured soil moisture data were available, the simulated saturated soil moisture and hydraulic conductivity were calibrated against observed data. The coherence of observed and simulated soil moisture was evaluated by a combination of several goodness-of-fit criteria, namely the Nash–Sutcliffe criterion (Nash & Sutcliffe, 1970), the Spearman rank correlation coefficient, and the volume error (Table S2). For sites of the CZSK database without *in situ* soil moisture measurements, the model parameters were derived directly from soil samples and retention curves. We did not simulate soil moisture for sites of the ITRDB database, because we had no access to site level soil data.

4.4.2.5 CLIMATE-GROWTH MODELS

We used four established approaches to study the effects of temperature, precipitation, and soil moisture on the inter-annual variability of tree growth (Figure 2b). The approaches differed in their mode (linear regression vs. non-linear process-based modelling) and temporal resolution (daily vs. monthly). Inputs for all models included the measured and standardized tree-ring width site chronologies, site coordinates, air temperature, and volumetric soil moisture content (CZSK) or precipitation (ITRDB). For approaches operating on a monthly scale, the climatic data were aggregated into monthly means (temperature, soil moisture) or monthly totals (precipitation).

All four models were used to simulate one ring-width chronology per site for 1940–2018 (Czech Republic), 1950–2018 (Slovakia), and 1950–2011/2018 (ITRDB, depending on the last year of the chronology, Table S1). The interval was split into an early period (1940/1950– 1979) and a late period (1980–2011/2018). First, the early period was used as a calibration interval to identify the optimal parameters of the four models. Next, the calibrated models were used to predict the site chronology for the verification (late) period based on climatic data for that period. This forward-modelling approach with the early calibration (1940/1950–1979) and late verification (1980–2011/2018) assessment is hereafter referred to as “chronological calibration/verification” (Figure 2a). Conversely, we also performed all analysis steps in reverse by switching the calibration (1980–2011/2018) and verification (1940/1950–1979) periods. We refer to this reverse approach as “retrospective calibration/verification.” Each of the four modelling approaches is described in detail below.

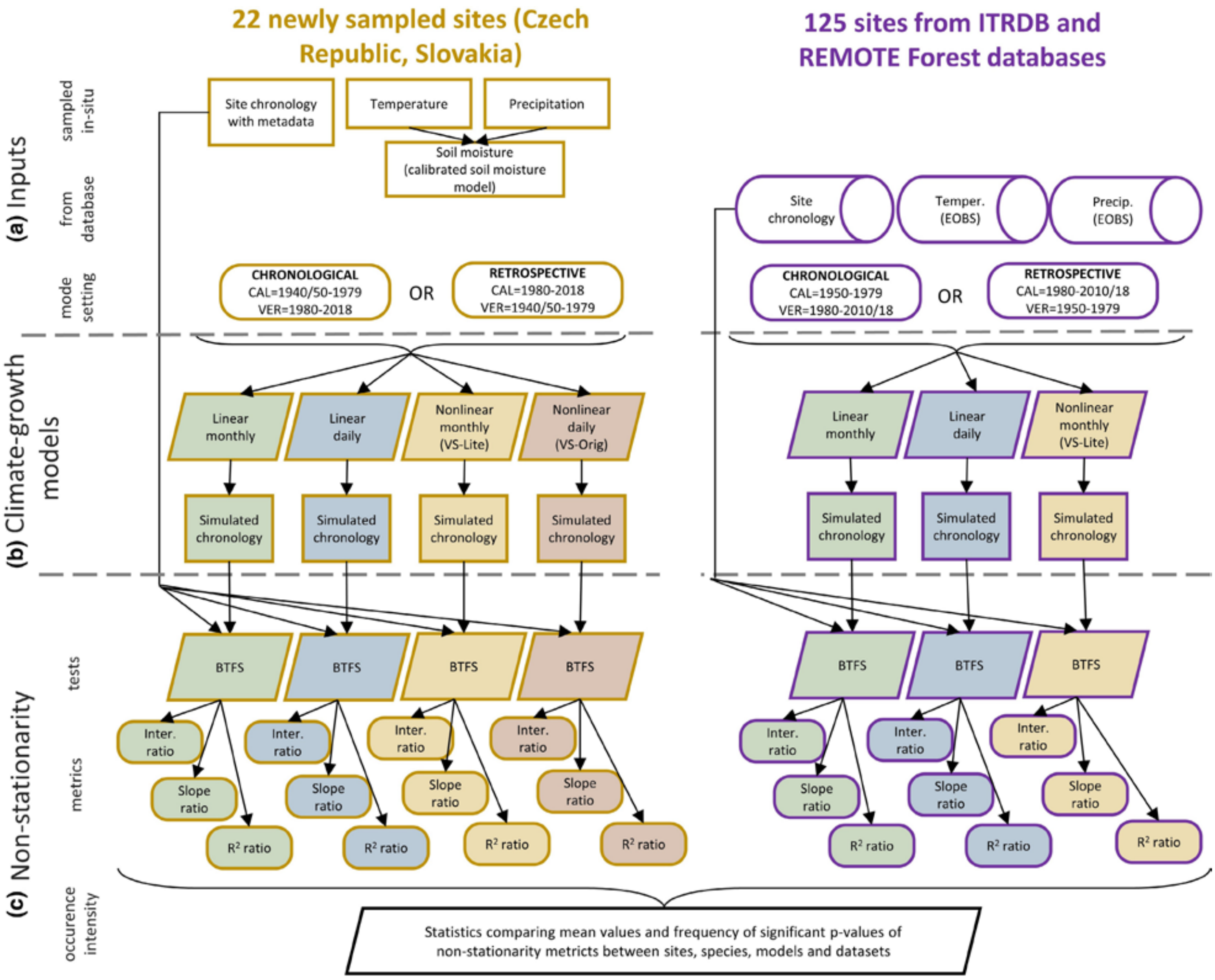

Fig. 2. Simplified workflow chart depicting the methodology applied throughout this study to assess non-stationarity for two tree-ring width data sets (outline colour) and four statistical models of climate–growth response (fill colour).

BTFS refers to the bootstrapped transfer function stability test (Buras *et al.*, 2017). Rectangles = variables, parallelogram = function, oval = parameter or statistics value, horizontal cylinder = database.

4.4.2.5.1 LINEAR STATISTICS OPERATING ON A DAILY SCALE

For each site, we calculated Pearson correlations between seasonal means of climatic data and the tree-ring width chronology (Jevšenak & Levanič, 2018). To do so, we first calculated mean temperature and soil moisture (CZSK) or mean temperature and total precipitation (ITRDB) for all possible seasons of consecutive days with a duration from 30 to 150 days for each year. To ensure consistency with process-based models, which do not take into account legacy effects of previous year conditions (Vaganov *et al.*, 2006), only seasons which were fully within the tree-ring formation year were considered (1st January–31st December of the current year). In the next step, we correlated time series of climatic data for each sea- son with the site chronology. We identified seasons with the highest correlations between the tree-ring chronology and temperature and soil moisture/precipitation. Finally, we simulated site chronologies by calibrating a transfer function which represents the relationship between the site chronology, temperature and soil moisture/precipitation during the highest-correlating seasons. The structure of the function was as follows:

$$\mathrm{TRW}_{\mathrm{mod}} = a + b.\ \mathrm{Temperature}_{seasonT} + c.\ \mathrm{SoilMoisture}_{seasonSM/} \qquad \mathbf{(2)}$$

where *TRWmod* represents the simulated tree-ring width chronology for a specific site, *a* is the intercept, *b* and *c* represent the slopes of climatic variables, and *seasonT* and *seasonSM/P* refer to the peak correlation seasons between each climatic variable and the tree-ring width chronology.

4.4.2.5.2 LINEAR STATISTICS OPERATING ON A MONTHLY SCALE

The monthly linear approach was similar to the linear correlations based on daily data described above. We identified consecutive seasons with strongest correlations between tree-ring width chronologies and aggregated monthly climatic data. All possible seasons with a duration between one and five consecutive calendar months fully within the tree-ring formation year were considered. The transfer function predicting the simulated TRWmod chronology had the same structure as in the case of the linear model operating on a daily scale (Eq. 2).

4.4.2.5.3 NON-LINEAR STATISTICS OPERATING ON A DAILY SCALE

We used the Vaganov–Shashkin model of wood formation and parameterized its so-called “environmental block” (further abbreviated as VS-Orig; Vaganov *et al.*, 2006). VS-Orig represents a moderately complex sink-oriented process-based model (Guiot *et al.*, 2014), which is based on the assumption that tree growth during a specific day reflects the simultaneous influence of temperature, soil moisture, and photoperiod. We replaced the soil moisture submodel in the VS-Orig model by our soil moisture data based on field observations at CZSK sites (see Section 4.2.4). For the remaining eight parameters of the model describing the non-linear response functions between climatic variables (temperature and soil moisture) and daily growth rates, as well as the three parameters delimiting growth phenology, we obtained optimal values for each site by generating 15,000 random sets of parameters within ecologically reasonable intervals (Table S3). We calculated TRWmod for each of the sets of parameters and retained the one with the highest correlation to ob- served site chronology for the model calibration period.

The parameterization of VS-Orig was time consuming for the CZSK database and computationally impossible for the much larger ITRDB database. Long processing times are a known limitation of the applicability of VS-Orig that was previously overcome by subjective model parameterization (Shishov *et al.*, 2016) or by ignoring between-site differences in values of parameters (Evans *et al.*, 2006). None of those approaches were applicable to our study, where we aimed to maximize the correlation between the observed chronology and TRWmod in the calibration period and to test the stability of the relationship in the independent verification period. Accordingly, VS-Orig parameterization was only conducted for sites comprising the CZSK database (Figure 2b).

4.4.2.5.4 NON-LINEAR STATISTICS OPERATING ON A MONTHLY SCALE

The VS-Lite process-based model is based on the mechanisms of VS-Orig and represents its substantial simplification (Tolwinski-Ward *et al.*, 2011). The main difference between both models is that VS-Lite is adapted to operate with monthly climatic input data and a reduced number of model parameters. Accordingly, it can be applied to large data sets including the ITRDB (Breitenmoser *et al.*, 2014). Similar to VS-Orig, the simplified model determines temperature and moisture-driven growth rates by means of non-linear equations. The soil moisture submodel in the VS-lite model was omitted and replaced by our soil moisture data based on field observations for the CZSK database, and run with default parameter values (Tolwinski-Ward *et al.*, 2011) for sites from the ITRDB database. We obtained optimal values of the four remaining model parameters defining the shape of the response functions between climatic variables and growth rates by randomly generating 4000 combinations within an ecologically reasonable range (Table S3) and retaining the set of parameters that produced the highest correlation between the observed chronology and TRWmod. The lower number of random combinations for VS-Lite compared with VS-Orig is due to the lower number of randomized parameters. In total, we simulated 926 chronologies for individual sites using different models and chronological and retrospective modes. Climate–growth models were parameterized using the R package "*dendrotools*" (Jevšenak & Levanič, 2018; linear correlations) and Matlab scripts published by Anchukaitis *et al.* (2020) (VS-Orig) and Tolwinski-Ward *et al.* (2011) (VS-Lite).

4.4.2.6 DENDROCLIMATIC CLUSTERS

We used the results of linear correlations to delimit clusters of sites with similar climate–growth response, hereafter called "dendroclimatic clusters." Specifically, we included all sites with positive peak-season daily and monthly correlations with temperature and negative peak-season daily and monthly correlations with soil moisture/precipitation into a "cold" dendroclimatic cluster. Conversely, sites with positive peak-season daily and monthly correlations with soil moisture/precipitation and negative peak-season daily and monthly correlations with temperature represented a "dry" dendroclimatic cluster. The remaining sites formed a "mixed" dendroclimatic cluster. We used correlations produced for the chronological mode to define these dendroclimatic clusters. We preferred to define clusters based on positive and negative values of climate–growth correlations due to the simplicity of the approach. However, an objective approach based on numerical hierarchical clustering of sites yielded similar groupings (Figure S2).

4.4.2.7 ASSESSMENT OF GROWTH STATIONARITY

Non-stationarity was previously assessed using various methods with different levels of complexity (Allen *et al.*, 2018; Buras *et al.*, 2017). However, it was shown that traditional non-stationarity metrics, such as RE and CE (Cook & Kairiukstis, 1990), might not be sufficient to distinguish between specific forms of climate–growth decoupling, that is, they might fail to differentiate between shifts in mean values, amplitudes or coherence of the observed site chronologies and TRWmod over time (Buras *et al.*, 2017). To test for stationarity at different complexity levels, we used the bootstrapped transfer function stability test since it evaluates the aforemen- tioned non-stationarity patterns in a single function, is less sensitive to outliers and less prone to false-positive results (BTFS, Buras *et al.*, 2017, Figure 2c). BTFS fits two linear regression models between observed and simulated chronologies during their respective calibration and verification periods. Both regression models are defined by an intercept (similarity of mean values between observed and simulated chronologies), slope (similarity of amplitudes), and R^2 (coherence between observed and simulated chronologies). For each of these variables, BTFS calculates the ratio of the value in the verification period and the value in the calibration period. A ratio equal to 1.0 indicates perfect stationarity, that is, the given regression parameter does not change between calibration and verification windows, while a significant deviation from 1.0 indicates non-stationarity. We hereafter refer to these ratios as "non-stationarity metrics." To assess the significance of non-stationarity metrics at each site, we performed calculations using 1000 randomly subsampled data sets and used empirical cumulative distribution functions to derive their 95% confidence intervals. Each of subsamples had a length equal to the chronology length and replacement was permitted during subsampling (Buras *et al.*, 2017).

Accordingly, the outputs of the BTFS for each site and model included three non-stationarity metrics with *p*-values, namely the intercept ratio, slope ratio, and R^2 ratio. For the interpretation of the results, we focused on both the occurrence and degree of non-stationarity events. To assess the occurrence of non-stationarity, we plotted Venn diagrams showing the frequency of significant ($p<.05$) non-stationarity metrics among simulated models. We performed this analysis for the entire data set as well as separately for (i) CZSK and ITRDB databases, (ii) the four different types of models, (iii) *P. sylvestris* and *P. abies* chronologies, (iv) cold, dry, and mixed dendroclimatic clusters, and (v) retrospective and chronological modes. To evaluate mean degree of non-stationarity, we calculated the mean values of intercept, slope and R^2 ratios for each of the aforementioned subsamples of our data set. We determined 95% confidence intervals for the mean values of each of the non-stationarity metrics to assess whether they significantly overlap with the 1.0 ratio. Finally, to assess possible effects of stand age (Trouillier *et al.*, 2019) and site conditions on the stationarity of climate–growth interactions, we regressed values of non-stationarity metrics against mean stand age (approximated as the mean number of tree rings) and mean inter-series correlation at a given site. For the calculation of BTFS, we used and slightly modified the "*dendRolAB*" package in R (the intercept ratio was centered around 1.0; Buras *et al.*, 2017).

4.4.3 RESULTS

4.4.3.1 MODEL PERFORMANCE IN CALIBRATION AND VERIFICATION PERIODS

The modelled chronologies showed varying coherence with observed chronologies during their respective calibration windows (Table S4). The highest mean correlations between observed and simulated chronologies during the calibration period were observed for linear daily models (0.64), followed by linear monthly models (0.57), daily non-linear models (0.54), and monthly non-linear models (0.46). However, the ranking was reversed during the verification period, with linear models showing the lowest mean correlations with observed chronologies (both models 0.18) compared with monthly non-linear (0.26) and daily non-linear models (0.32). The results of linear climate–growth correlations for each site with their peak correlation values and periods are presented in Table S5. Optimal values of the VS-Orig and VS-Lite model parameters are listed in Tables S6 and S7.

4.4.3.2 OCCURRENCE OF NON-STATIONARITY

We detected at least one significant non-stationarity metric in 68% of the models, while 32% of the models showed full stationarity of all three metrics (Figure 3a). We observed a systematically higher occurrence of significant non-stationarity metrics in cold and mixed dendroclimatic clusters compared with the dry cluster (Figure 3b), for the ITRDB compared with the CZSK database (Figure 3d), for linear compared with non-linear models, and for daily compared with monthly models (Figure 3e). By contrast, the frequency of significant non-stationarity metrics did not differ remarkably between species (Figure 3c) and between retrospective and chronological modes (Figure 3f). The distribution of significant non-stationarity metrics among databases, clusters, and species was not affected by using the non-linear daily model for sites of the CZSK database but not for ITRDB (Figure S3).

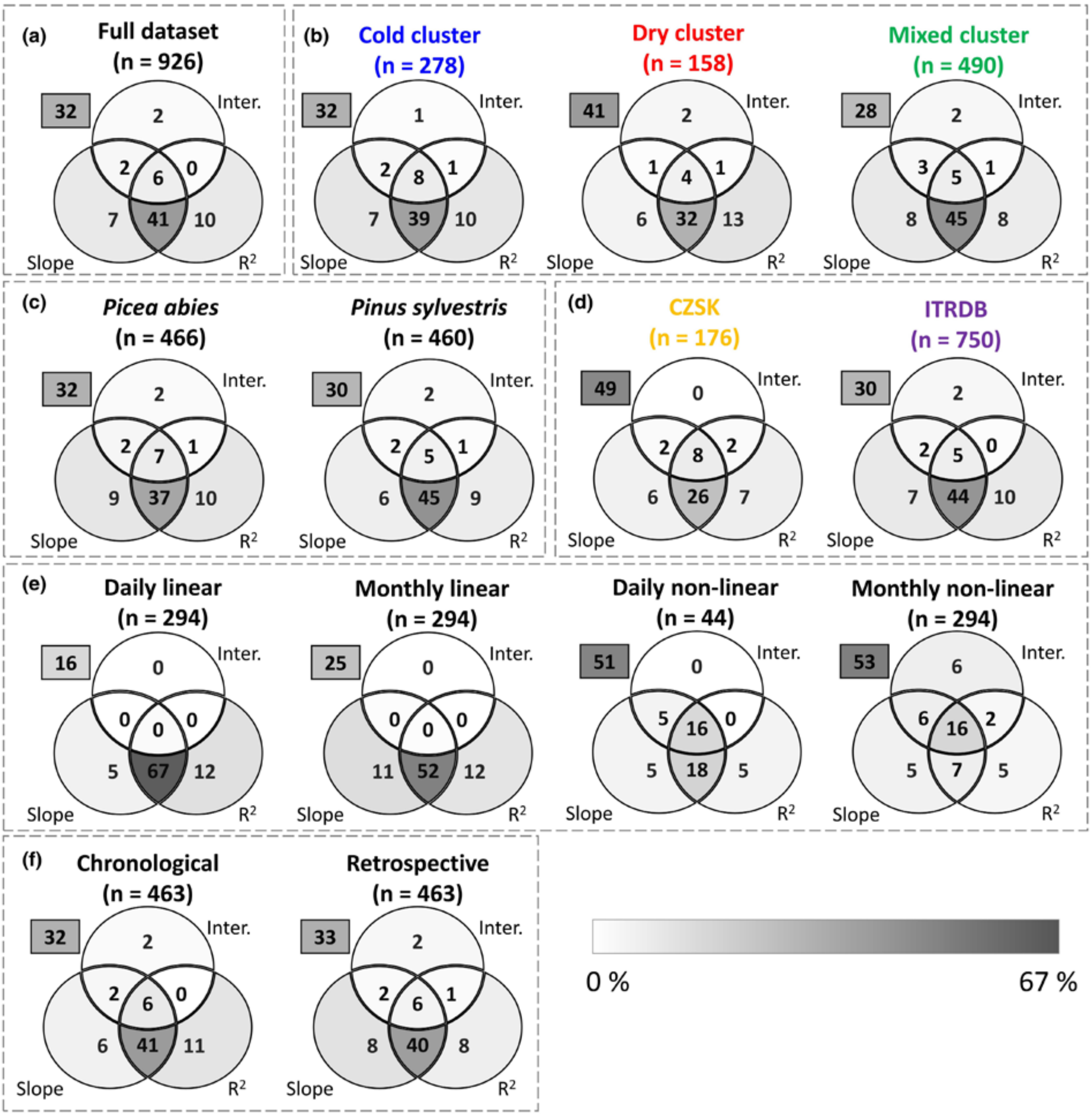

Fig. 3. Venn diagrams showing the percentage of significant and non-significant values of the three non-stationarity metrics calculated by the bootstrapped transfer function stability tests (Buras *et al.*, 2017).

Numbers inside the polygons show the percentage of models with a significant value ($p < .05$) of each non-stationarity metric. The rectangle in the top-left corner indicates full stationarity, that is, the percentage of models with significant stationarity of all three regression parameters. The Venn diagrams are shown for (a) the full data set and separately for each (b) dendroclimatic cluster, (c) species, (d) database, (e) model, and (f) chronological and retrospective modes. “n” indicates the number of climate–growth response models calculated for each data set.

4.4.3.3 DEGREE OF NON-STATIONARITY

Considering differences in mean values of non-stationarity metrics between climate–growth models, we observed a higher degree of non-stationarity for linear compared with non-linear models, and for daily compared with monthly-resolved models (Figure 4). For instance, the mean R^2 ratio across all sites was close to the value of 1.0 (indicating stationarity) for non-linear monthly models (0.87) but was lower for the non-linear daily models (0.49, calculated only for the CZSK data set), linear monthly models (0.27), and linear daily models (0.21). The models were ranked in the same order when examining the intercept and slope ratios, with non-linear monthly models showing the strongest stationarity and linear daily models the strongest non-stationarity. In most cases, the mean non- stationarity metrics of the non-linear models were closer to 1.0 compared with linear models for our entire data set as well as for specific subsamples including ITRDB and CZSK sites, chronological and retrospective modes, dendroclimatic clusters, and both species (Figures 4 and 5).

The mean values of non-stationarity metrics differed systematically between *P. abies* and *P. sylvestris* from the CZSK database in the chronological mode (Figure 5). The mean values of slope and R^2 ratios were higher for *P. abies* compared with *P. sylvestris*, indicating stronger non-stationarity of the latter species. This difference was statistically significant for sites from dry and cold dendroclimatic clusters and for linear models, but not for the mixed dendroclimatic cluster with wide confidence intervals of mean non-stationarity metrics for both species. The intercept ratio did not show systematic differences between species. For the retrospective mode of the CZSK database and for both modes of the ITRDB database, the differences between species did not show a clear pattern and were mostly non-significant (Figure 5; Figure S4).

The cold, dry, and mixed dendroclimatic clusters consisted of 7, 7, and 8 sites from the CZSK database and of 37, 17, and 71 sites from the ITRDB database, respectively (Figure 1). Individual dendro- climatic clusters differed systematically in mean climatic conditions since the 1950s (Figure S5). Most of the non-stationarity metrics were on average close to 1.0 (*i.e.*, models were rather stationary) for sites belonging to the cold dendroclimatic cluster from the CZSK database and for sites of the dry dendroclimatic cluster from the ITRDB in the chronological mode. However, the differences were often statistically non-significant (Figure 5). The differences between dendroclimatic clusters were less pronounced and not systematic in the retrospective mode (Figure S4).

By contrast to the identified differences in mean values of non- stationarity metrics between models, species, and dendroclimatic clusters, there was no relationship between non-stationarity metrics and stand age (Figure S6) or mean inter-series correlation (Figure S7).

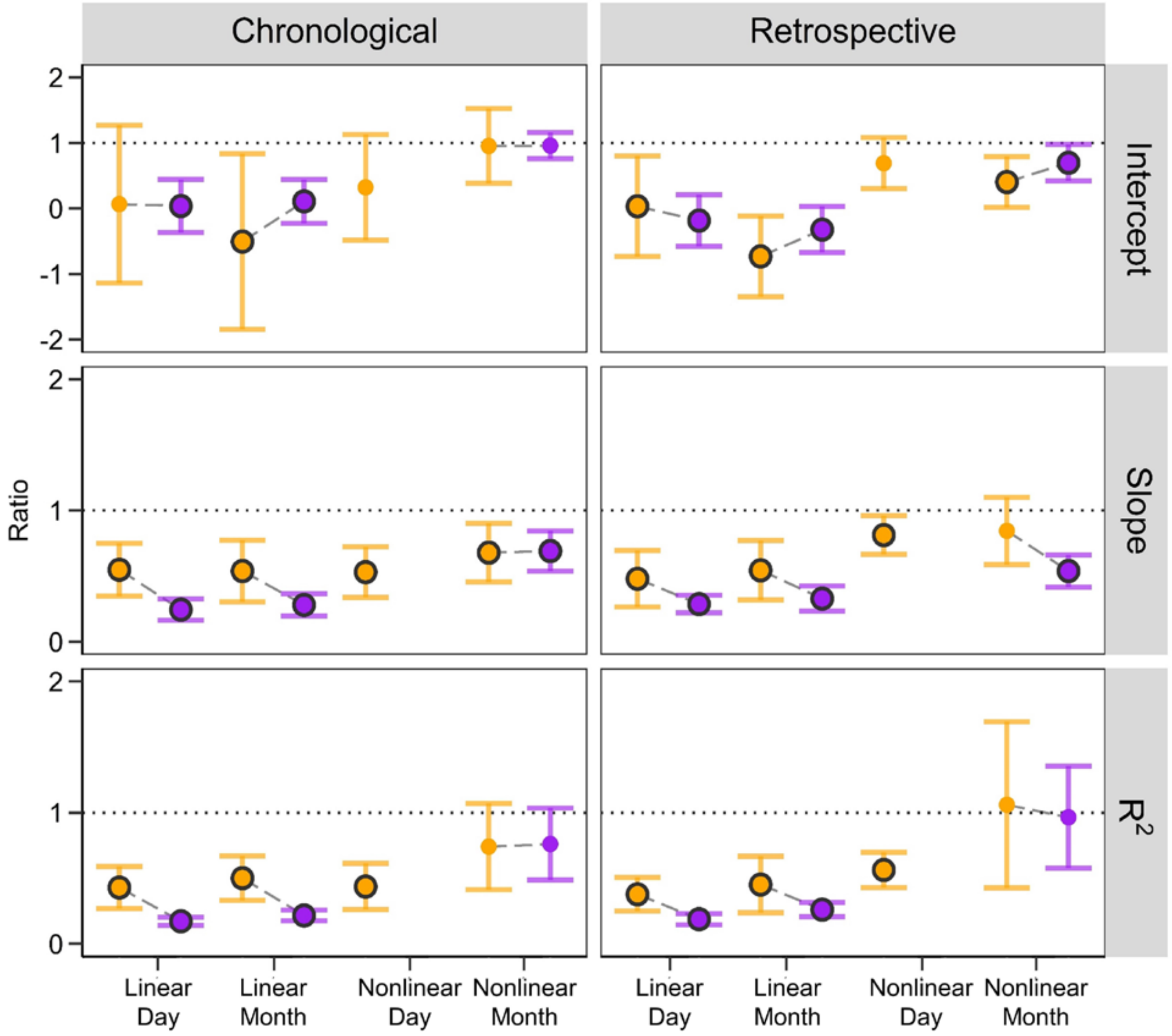

Fig. 4. Mean values (circles) and confidence intervals (95%, error bars) of non-stationarity metrics for different models of climate–growth responses obtained for chronological and retrospective modes of calibration.

The colour of the symbols refers to the tree-ring width database (orange = newly assembled CZSK database, purple = data from the ITRDB database). Symbols with a grey outline highlight parameters whose mean value significantly deviates from 1.0 ($p < .05$).

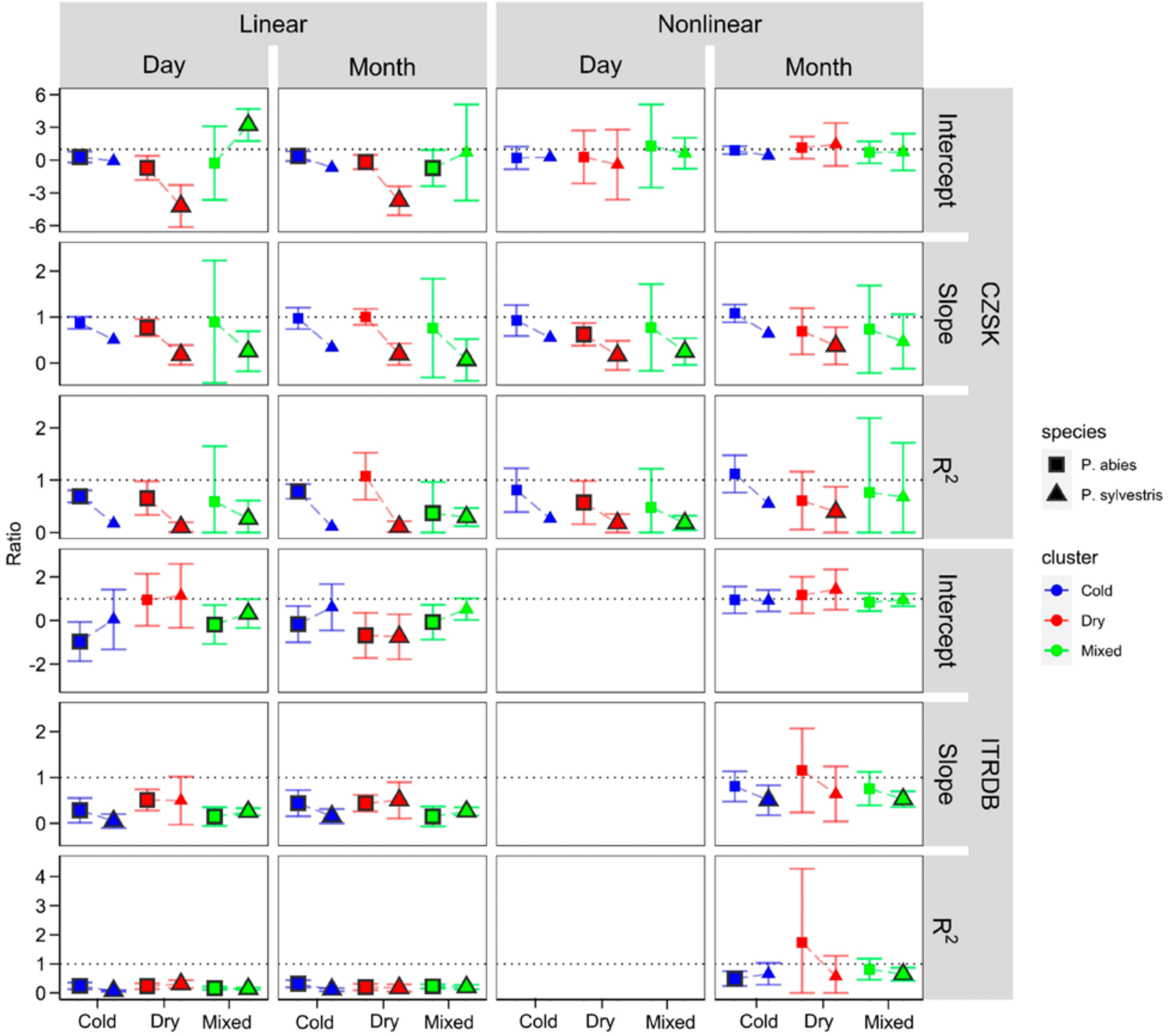

Fig. 5. Mean values (squares, triangles) and confidence intervals (95%, error bars) of non-stationarity metrics of different dendroclimatic clusters and species obtained by climate–growth models in the chronological calibration mode.

Symbol colour refers to the site dendroclimatic cluster (blue = cold, red = dry, green = mixed) and symbol shape refers to species (square = *Picea abies*, triangle = *Pinus sylvestris*). Symbols with a grey outline highlight metrics which significantly deviate from 1.0 ($p < .05$). Note, that in the CZSK database there was only one *P. sylvestris* site in the cold dendroclimatic cluster, and, therefore, an assessment of statistical significance was not performed in this case. Note, that charts might have different *y*-axis scales to aid visual comparison between clusters and species. A chart with results for the retrospective calibration mode is shown in Figure S4.

4.4.4 DISCUSSION

Our results highlight how environmental factors and the choice of methodological approach interact in driving climate–growth non-stationarity in two major European conifer species. The occurrence and degree of non-stationarity was systematically higher for linear and daily resolved models compared with non-linear and monthly-resolved models. Climate–growth non-stationarity was more frequent in sites with mixed climate–growth responses com- pared with dry and cold sites. Moreover, there was significantly stronger stationarity at *P. abies* stands compared with *P. sylvestris* stands in the regional CZSK data set. We discuss how climatic conditions, species, and methodological approach affected the level of non-stationarity in our study and highlight practical consequences for future dendroecological and dendroclimatological analyses.

4.4.4.1 THE EFFECT OF MODEL STRUCTURE AND TEMPORAL RESOLUTION OF NON-STATIONARITY

Comparing the degree and occurrence of non-stationarity between linear and non-linear climate–growth models revealed a systematic pattern: non-linear process-based models showed lower frequency (Figure 3e) and lower degree (Figure 4) of non-stationarity compared with linear statistical models. As hypothesized, this suggests that climate–growth analyses relying on linear methods, which is the standard approach in dendrochronology (Fritts, 1976), are more prone to non-stationarity, probably due to the shifting of climate–growth responses beyond the limits of quasi-linear response functions over time (Wilmking *et al.*, 2020; Wolkovich *et al.*, 2021). Such a shift can occur when climate conditions change in a way that they become either less or more limiting for tree growth over time, or no longer limit growth because optimal growth conditions have been reached (Vaganov *et al.*, 2006). Non-linear process-based models are capable of reducing non-stationarity by reflecting abrupt thresholds in the response of wood formation to environmental variability (Rossi *et al.*, 2008). The higher stationarity we found for non-linear models argues for the use of non-linear process-based models as the preferred tool for improving forecasts of forest ecosystem dynamics under global change (Eckes-Shephard *et al.*, 2022).

Moreover, we found a higher probability of non-stationarity for daily models compared with monthly models (Figure 3e). Daily-resolved models run on a data set which is approximately 30.5 times larger compared with that of monthly-resolved models and, on average, the probability of the occurrence of spurious fitting, (*i.e.*, a high statistical coherence between observed chronologies and climatic parameters, which is achieved by chance without a true ecological basis) is also 30.5-times higher. Consequently, we observed high coherence of daily linear models with observed chronologies in their calibration periods but very low coherence in verification periods (Table S3). Daily temporal resolution in models has recently been used to improve the delimitation of optimal seasons for climate–growth correlations (Jevšenak, 2019). However, because growth phenology strongly responds to climate change (Menzel *et al.*, 2020), intra-annual climate–growth relationships at finer temporal resolution (days) may become more susceptible to temporal shifts compared with relationships at coarser temporal resolution (calendar months). This may considerably hinder the applicability of daily-resolved models—otherwise valuable tools for analyzing contemporary climate–growth response—for long reconstructions or future forecasts of phenological shifts on fine intra-annual temporal scales.

Both the VS-Orig and VS-Lite non-linear models belong to the category of climate-driven models (Eckes-Shephard *et al.*, 2022), that is, they only require climatic data and observed tree-ring width site chronologies for calibration. Although we showed their significant stationarity, we are aware of the limitations that restrict their application to large data sets. Most importantly, we were not able to calibrate the more complex VS-Orig model on the large ITRDB due to unrealistic computation time requirements. Moreover, the quality and availability of daily climatic data might not be sufficient in some regions. Accordingly, we suggest the monthly-resolved non-linear VS-Lite model to be an optimal balance between climate–growth stationarity and model applicability. Operating at monthly temporal resolution and using a simplified set of non-linear response functions, this model can be readily used on global (Breitenmoser *et al.*, 2014) and continental scales (Dannenberg, 2021). Moreover, compared with linear models, VS-Lite showed smaller and often non-significant differences in mean values of non-stationarity metrics between databases (Figure 4), clusters, and species (Figure 5), suggesting its applicability to contrasting environments. The lower mean correlations between observed and simulated chronologies in the calibration periods (Table S4) but at the same time highest degree of stationarity favor VS-Lite as the preferred tool for the identification of moderate but stable climatic drivers of tree growth.

4.4.4.2 THE EFFECT OF SITE CLIMATIC CONDITIONS AND SPECIES ON NON-STATIONARITY

The three dendroclimatic clusters differed considerably in terms of the occurrence and partly in the degree of non-stationarity. Significant non-stationarity metrics occurred frequently in cold and mixed dendroclimatic clusters, while dry sites dominated in terms of stationary behavior (Figure 3b). The highest degree of stationarity was found for dry sites from the ITRDB database and for cold sites from the regional CZSK database (Figure 5). While tree growth at cold and dry sites responded positively to a single climatic variable, temperature in the former and soil moisture in the latter, sites with a mixed climatic signal represent moderate environments with complex growth responses to both warm and wet conditions (Fritts, 1976). In fact, the prediction of these complex climate–growth responses at mixed sites posed a challenge to all models. Moreover, both studied species differed in the intensity of non-stationarity, with *P. sylvestris* behaving in a less stationary manner (Figure 5). Interestingly, pronounced between-species differences were found only in the regional data set focused on climatically extreme environments (CZKS) but not at continental scale (ITRDB). The different degree of non-stationarity across Central Europe is consistent with typical patterns of climate–growth responses of both species observed under ongoing climate change. It has been shown that chronologies of *P. abies* in Central Europe are particularly sensitive to drought on the one hand and to low temperatures on the other hand at low and high elevation sites, respectively (Hartl-Meier *et al.*, 2014; Mäkinen *et al.*, 2002).

By contrast, the growth of *P. sylvestris* often responds positively to temperature in late winter and early spring (Harvey *et al.*, 2020), but it may also be significantly correlated with summer temperatures and/or soil moisture both at dry and cold sites (Bose *et al.*, 2020; Pärn, 2009; Treml *et al.*, 2022). We assume that this disparity between these two species in the type and strength of the climatic signal reflects the position of the individual sampling sites of the CZSK data set within each species-specific climatic niche. While *P. abies* sites in Central Europe represent the temperature- and drought-limited distribution margins of this species with growth strongly affected by climate, *P. sylvestris* sites occupy local ecological niches which are far from its potential margins at high latitudes or in the Mediterranean (Bose *et al.*, 2020; Sánchez-Salguero *et al.*, 2017). This higher complexity of the growth response of *P. sylvestris* to increasing temperature observed across Central Europe is more difficult to reproduce by any model, resulting in a higher probability of decoupling between simulated and observed chronologies in the independent verification periods.

Surprisingly, between-species differences in the intensity of non-stationarity were significantly less pronounced in the ITRDB. We suggest that the mean non-stationarity of both species might have been shifted due to inconsistencies in sampling strategies used at different sites from the ITRDB. We speculate that most of the *P. sylvestris* ITRDB chronologies might have been sampled for dendroclimatic purposes, that is, at sites and microsites with presumably strong and uniform climatic signals (Hartl *et al.*, 2021; Solomina *et al.*, 2022). By contrast, the sampling strategy was instead focused on dendroecological research questions in the prevailingly old-growth *P. abies* forest stands with strong intra-specific competition and large proportions of suppressed trees (Schurman *et al.*, 2019). This sampling inconsistency might have artificially decreased/increased mean stationarity of *P. abies*/*P. sylvestris* chronologies from the ITRDB database.

4.4.4.3 THE EFFECT OF DATA ORIGIN ON NON-STATIONARITY

The occurrence of significant non-stationarity metrics (Figure 3d) and mean values of slope and R^2 ratios (Figure 4) suggested a stronger non-stationarity in the ITRDB compared with the CZSK data set, mainly for models based on linear correlations. Stronger non-stationarity of ITRDB might arise from inhomogeneous site and tree selection strategies, less precise climatic data (gridded EOBS vs. local station data) or a larger number of sites with a mixed climatic signal (Figure 1), that is, the dendroclimatic cluster characterized by strong non-stationarity. Given the multitude of factors that might reduce stationarity in large-scale networks, we recommend paying closer attention to non-stationarity in studies based on large databases with possible sampling inconsistencies compared with regional data sets from harsh environments.

4.4.4.4 PRACTICAL CONSEQUENCES OF A MULTITUDE OF NON-STATIONARITY DRIVERS

Our results revealed that the detection of climate–growth non-stationarity might be driven or altered by multiple factors and their interaction, including site climatic conditions, species, and the type and temporal resolution of the climate–growth model. Our results are in accordance with currently available empirical evidence (Büntgen *et al.*, 2006; Ljungqvist, Thejll, *et al.*, 2020; Wilmking *et al.*, 2020) showing that, for existing climate–growth models, non-stationarity rather than stationarity is a more common type of tree response to climate in temperate forests. From a methodological point of view, we endorse the use of monthly non-linear process-based models as we identified systematically lower non-stationarity of these models compared with linear approaches with daily temporal resolution. In doing so, we strongly support earlier calls of other scientists for using more complex but widely applicable climate–growth models that might better reflect ecological reality (Eckes-Shephard *et al.*, 2022).

AUTHOR CONTRIBUTIONS

Václav Treml and Jan Tumajer developed the idea of the study; Václav Treml, Vojtěch Čada, Ryszard J. Kaczka, Jiří Mašek, Jan Tumajer, Miroslav Svoboda, Miloš Rydval, and Krešimir Begović sampled and processed dendrochronological data; Lukáš Vlček and Michal Jenicek sampled soils and calibrated the soil moisture model; Jan Tumajer calibrated the dendrochronological models, performed statistical analyses, and interpreted results; Jan Tumajer led the writing of the manuscript with significant contribution of Václav Treml, Miloš Rydval, and Jelena Lange. All coauthors discussed individual steps of the research, contributed to the discussion about the manuscript structure and approved the final version of the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All raw tree-ring width data, including new sites from the CZSK database, are openly available in the ITRDB network at https://www.ncei.noaa.gov/products/paleoclimatology/tree-ring (reference numbers for the CZSK sites: CZEC009, CZEC011-027, SVK007-014) and REMOTE Forest network at https://www.remoteforests.org/. Climatic data for Slovakia and ITRDB sites are openly available from EOBS 22.0. at https://surfobs.climate.copernicus.eu/dataaccess/access_eobs.php. Our interpolation of climatic data for the Czech Republic and simulated soil moisture levels for all sites of the CZSK data set are openly available at Zenodo at http://doi.org/10.5281/zenodo.7140644. To run process-based models of wood formation, we used scripts published by Anchukaitis *et al.* (2020) (https://www.github.com/kanchukaitis/vsm) and Tolwinski-Ward *et al.* (2011) (https://www.ncei.noaa.gov/access/paleo-search/study/9894).

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article or in the Supporting Information subsection (S4) of the Bibliography section at the end of this Thesis.

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DISCUSSION

This Thesis aimed to build on the concurrent knowledge of natural forest dynamics and climatic variability to assess the impacts of environmental change on varying spatiotemporal processes by disentangling the effects of intrinsic and extrinsic drivers of tree growth in Central-Eastern European primary and near-natural forests. More specifically, I was determined on quantifying the interactions between the antecedent and contemporary exogenous drivers of tree growth, and elucidating their impacts on tree-level tradeoffs, population-level growth trends and legacy effects, and landscape-level biomass and carbon dynamics, with the overarching aim of making robust predictions of future developmental pathways, ecosystem processes and functioning under global climate change. In the following subsections I elaborate on the relevance and significance of the presented Results, and conclude with prospective research directions and general suppositions that can be derived from the Results to provide empirical support for nature conservationists and management policy makers.

5.1 GROWTH-CLIMATE ASSOCIATIONS ARE INCREASINGLY MODULATED BY LOCAL SITE CONDITIONS AS INTENSIFYING DROUGHTS BECOME THE LEADING DRIVER OF TREE GROWTH IN EUROPEAN TEMPERATE FORESTS

Latest climate risk assessments based on vegetation and climate modelling indicate that the rising drought-related risk could trigger demographic shifts and cause significant carbon losses in Central Europe (Anderegg *et al.*, 2022). The detrimental impacts of epochal large-scale mortality events have recently been recognized following the extreme summer droughts of 2003 and 2018, which exhibited profound impacts on contemporary forest structure and the forestry sector in Europe (Schuldt *et al.*, 2020). Drought-induced mortality can drastically reduce carbon uptake and push forests beyond the hydraulic tipping points (Anderegg *et al.*, 2022; Ciais *et al.*, 2005; Kannenberg *et al.*, 2020; Schwalm *et al.*, 2017; Zhao & Running, 2010; Zhou *et al.*, 2019), which could ultimately disrupt forest ecosystem processes and functioning. Using dendrochronological methods and tree-ring datasets from extensive networks of permanent study plots capturing the wide range of environmental conditions over unmanaged montane and lowland Central-Eastern European forests, allowed me to identify the general growth-climate associations and scale the implications of changing climatic conditions from tree-level interactions to landscape-scale outcomes.

The growth-climate associations of Norway spruce and silver fir from mixed-species primary forests in the Dinaric mountains demonstrated somewhat contrasting relationships to the generally temperature-driven conifer forests in more continental parts of Europe over the 20th century (*e.g.*, Bijak, 2010; Bošel'a *et al.*, 2018; Büntgen *et al.*, 2007; Lebourgeois, 2007; Parobekova *et al.*, 2016). Unlike the monospecific Norway spruce primary mountain forests in the Western Carpathians, which demonstrated lack of a distinct summer moisture signal and are predominantly driven by summer temperatures (section 4.2, Fig. 5), the Dinaric Mountains conifers are highly dependent on summer moisture availability as the dominant growth-limiting factor (section 4.1, Fig. 4-6) Both species grow here at the edge of their ecological niche in southern-eastern Europe, and although these forests receive abundant annual rainfall, high soil permeability and porous bedrock considerably limit groundwater retention during the growing season, while high summer temperatures exacerbate the effects of limited water availability and increased evapotranspiration. With the climate becoming increasingly warmer and drier, higher competitiveness of silver fir due to morphological advantages (*e.g.*, deep taproot vs shallow vertical rooting system in Norway spruce; Idžojtić, 2009) and higher genetic diversity (Bošel'a *et al.*, 2016; Gazol *et al.*, 2016) could lead to demographic shifts against Norway spruce. This could potentially already be reflected by the onset of growth decline observed in Norway spruce populations over recent decades (section 4.1, Fig. 3). With the continuation of the global trend of rising hotter droughts in the 21st century, intensifying climatic stressors may lead to physiological weakening of trees and heightened susceptibility to the impacts of climatic and non-climatic perturbations in the Dinaric Mountains.

Study of growth-climate associations spanning across a wide range of Norway spruce and Scots pine temperature-limited montane and moisture-limited mesic and xeric sites across Europe demonstrated adverse growth-climate associations within and across the biogeographic regions (sections 4.3 and 4.4). The impacts of accelerated environmental changes introduce a higher complexity of tree growth response to changing climatic conditions, particularly in sites where tree species are developing at the edge of their optimal ecological niche (such as the Scots pine in the CZSK dataset; sections 4.3 and 4.4). These mixed-climatic signals complicate the assessment of the general growth-climate associations, which limit the reproducibility of the (non-)linear growth-climate interactions in Scots pine sites over recent decades. Whereas Norway spruce montane forests generally enhance growth under rising summer temperatures, due to the positive effect of rising temperatures on cell kinetics and wood production (Tranquillini, 1979), large spatial variability in climatic sensitivity observed across the Scots pine highlands and both species' lowlands indicate that growth-climate sensitivity is significantly modulated by the interaction between local site attributes (*i.e.*, topography, soil type), species-specific functional traits (*i.e.*, anatomical resistance, carbon allocation patterns) and methodological approaches to quantifying growth-climate associations (*i.e.*, linear vs non-linear models; daily vs monthly resolution; section 4.4, Fig. 5), but with the general trend of intensifying moisture-growth sensitivity reflected by a distinct growth decline over the last decade (section 4.3, Fig. 3, 6, 8, 9b). Extreme heatwaves and recurrent droughts inhibit metabolic processes needed for sustaining tree growth, leading to hydraulic failure and rapid depletion of carbon storage (McDowell *et al.*, 2008; 2015; 2020), thus reducing annual radial growth. Although higher xylogenetic plasticity and conservative carbon allocation strategies of the isohydric Scots pine might mediate transient drought legacy effects (Körner, 2003; Phillips *et al.*, 2016), perpetually dry conditions caused by more frequent droughts will likely affect future growth trends of both species equally, and may push forest ecosystems beyond hydraulic limits (Peltier & Ogle, 2019; Serra-Maluquer *et al.* 2018), which could ultimately trigger large-scale tree-dieback and ecosystem carbon cycle feedbacks, even in the cold and wet Scots pine montane sites (Cook *et al.*, 2015; Dai, 2011).

Furthermore, significant dependency of tree growth on climatic conditions in the year prior to tree-ring formation was universally observed across the latitudinal and altitudinal gradient (section 4.1, Fig. 4, 5; section 4.2, Fig. 5; section 4.3, Fig. 6, 7), which is a distinct physiological trait observed in conifers throughout the Mediterranean basin (*e.g.*, Fyllas *et al.*, 2017; Macias *et al.*, 2006; Tegel *et al.*, 2014), south-eastern Europe (*e.g.*, Panayotov *et al.*, 2010, Toromani *et al.*, 2011) and the Alpine mountain region (*e.g.*, Carrer *et al.*, 2010; Lebourgeois et al., 2007; 2010). Metabolic processes and cambial activation are highly dependent on carbohydrate storage and soil water reserves prior to the onset of tree growth (Fritts, 1976; Kozlowski, 1992). Prolonged growing season and warmer previous year autumns stimulate active carbon storage by extending the period of photosynthesis (Buermann *et al.*, 2013; Menzel & Fabian, 1999), whereas large snow accumulation during winter replenishes soil water reserves for growth initiation in spring and early summer (Barnett *et al.*, 2005), which are generally the dominant periods of xylem formation and wood production in low- and high-elevation conifer forests, respectively (Gruber *et al.*, 2009; Rossi *et al.*, 2009). Increased respiration losses under the compound impacts of high summer temperatures and low water availability during the previous growing season can inhibit the initiation of tree-ring formation in the following year by impeding carbon assimilation (Bouriaud & Popa, 2009; Kahle, 1996; van der Maaten-Theunnisen *et al.*, 2012). Overall, the observed large spatial variability in growth sensitivity to increasing climatic pressures suggest that the future resilience of the main Central-Eastern European temperate conifer forests will increasingly depend on species-specific functional traits to cope with drought stress, as well as local site properties (Babst *et al.*, 2013) and novel growth constraints (Schurman *et al.*, 2019; Svobodová *et al.*, 2019).

5.2 UTILIZATION OF BLUE INTENSITY PARAMETERS IMPROVES CLIMATE-SIGNAL STRENGTH IN MOUNTAIN FORESTS AND ENHANCES THE GENERAL UNDERSTANDING OF DROUGHT LEGACY EFFECTS IN XYLEM FORMATION

European conifers are generally at a higher risk of hydraulic failure under severe and chronic drought stress than broadleaf species (Adams *et al.*, 2017; McDowell *et al.*, 2016; Peltier *et al.*, 2016), mainly due to the bio-morphological limitations inhibiting rapid acclimation to increasing evapotranspiration demands (*e.g.*, shallow root system in Norway spruce, inability for rapid needle shedding; Jump *et al.*, 2017; Kozlowski *et al.*, 1992). If the future trends of rising annual temperatures and declining soil moisture continue at the current rate (IPCC, 2021), the general trend of rising moisture-growth sensitivity will likely lead to divergent growth-climate associations and increasing frequency of large-scale disturbances, particularly in sites with physiographic attributes that promote rapid soil drying (*i.e.*, steep sandstones in Scots pine Central European forests) or with limited water-retention capacity (*i.e.*, shallow soils atop porous limestone in the Dinarides).

To broaden the existing knowledge of the growth-climate sensitivity of main European temperate conifer species (*i.e.*, Norway spruce, silver fir and Scots pine) under average climatic conditions and during severe droughts, I investigated the behaviour and applicability of BI parameters in the temperature-driven Western Carpathian mountain forests, and the drought-prone environments of Dinaric Mountain primary forests and Central European mountain and lowland nature reserves, through a series of parametric and non-parametric tests. Unlike the dimensionless tree-ring width index (RWI) chronologies, which generally demonstrated a high degree of temporal instability and declining strength of the most important growth-climate associations towards present times in all species (section 4.1, Fig. 6; section 4.2, Fig. 5; section 4.3, Fig. 8), earlywood blue intensity (EWBI) and delta blue intensity (ΔBI) chronologies showed a more stable and generally increasing temporal coherence with the corresponding climatic factors, respectively. Additionally, EWBI and ΔBI, as surrogates for earlywood and latewood cell (*i.e.*, tracheid) size and density, provided a more in-depth understanding of the impacts of severe drought events on individual wood components, which are usually confounded in RWI due to the nature of tree growth or potential other non-climatic factors (Rydval *et al.*, 2015).

EWBI signal originates from wood formed at the start of the growing season (*i.e.*, earlywood), when cell formation is highly dependent on water availability and the amplitude of changing late spring/early summer temperatures. Despite the relatively high elevation of the study sites, earlywood of Norway spruce and silver fir in the Dinarides was strongly dependent on early growing season moisture content and summer season precipitation, further underscoring the importance of water availability on cell production at the start of the growing season, when temperatures for growth are optimal. In the Central European lowlands, which have experienced altered precipitation regimes and declining soil moisture content in recent decades (see Supplementary information S3, Fig. S1), EWBI additionally exhibited a significant negative correlation with high summer temperatures (section 4.3, Fig. 7). Chronically hot and dry conditions in the early growing season reduce stomatal conductance and inhibit synthesis and mobility of carbohydrates (Zweifel *et al.*, 2009), which in turn induces formation of cells with narrower lumen and thicker cell-walls going from earlywood to latewood, thus producing higher earlywood density (Björklund *et al.*, 2017; Cuny *et al.*, 2014). A more pronounced EWBI response to growing season moisture variation observed in Scots pine compared to Norway spruce indicates a heightened sensitivity of xylogenic processes to the effects of shifting moisture constraints, but also could be indicative of higher anatomical plasticity of Scots pine to decreasing moisture content, as denser earlywood translates into greater hydraulic safety margins under summer drought stress.

On the other hand, density of the latewood component is generally a factor of cell-wall thickening processes and late summer/early autumn climatic variation (Björklund *et al.*, 2019; Carrer *et al.*, 2017; Yasue *et al.* 2000). Whereas the latewood blue intensity parameter (*i.e.*, LWBI) demonstrated non-significant relationships with temperature in the Dinaric Mountains (Supplementary information S1, Table S2), adopting the ΔBI parameter as a proxy of latewood density and comparing against climatic factors in the Central European forests demonstrated a strong positive association with summer season temperatures in Norway spruce mountain forests, and generally weaker contrasting temperature-growth relationships across moisture-limited Norway spruce lowland sites and all Scots pine sites (section 4.3, Fig. 8; Supplementary material S3, Fig. S8-S11). The identified opposing impacts of previous year late summer temperatures (negative effect) and moisture availability (positive effect) on latewood density in the following year likely reflect the general benefit of optimal water availability for alleviation of high summer evapotranspiration rates and extending the period of carbohydrate accumulation and latewood production following the summer solstice (Hoch *et al.* 2003; Martin-Benito *et al.*, 2013;Vaganov *et al.* 2006). However, under persistent drought conditions and/or high growing season temperatures, early stomatal closure prevents hydraulic failure and halts cambial activity (Gruber *et al.* 2010; Pichler & Oberhuber, 2007) at the cost of decreased carbon assimilation rates (McDowell *et al.*, 2008; Piovesan *et al.*, 2008; Jones, 2009) and resource allocation to cell-wall thickening (Willey & Helliker, 2012), in turn reducing latewood density and mechanical integrity.

To further explore the observed variability in the detected climate correlations of RWI and BI parameters, and identify potential legacy effects in tree growth during and following severe drought events, pointer year analysis and superposed epoch analysis (SEA) were conducted. Pointer year analysis from the Dinarides showed significant reductions in earlywood density and ring width reductions in the year following decreased moisture availability in both Norway spruce and silver fir, highlighting the sensitivity of early growing season tree growth to previous year conditions (section 4.1, Fig. 7). SEA of mean growth anomalies from the Central European forests highlighted the significant site- and species-specific variability in mean growth reductions during severe droughts, but also complex post-drought recovery strategies between Norway spruce and Scots pine (section 4.3, Fig. 10). Whereas Norway spruce response was generally non-uniform and greatly varied between sites, from an EWBI and ΔBI growth reduction in response to lower-than-optimal temperatures prior to severe droughts to a significant 2–3-year post-drought RW reduction in the lowlands, Scots pine generally exhibited strong RW and ΔBI reductions during severe droughts and strong reductions in cell-wall thickness up to 3 years following a severe drought event. These findings potentially reflect the species-specific singularity in xylogenic plasticity and distinct acclimation strategies under drought stress. The more isohydric Scots pines prioritize hydraulic safety at the expense of growth through rapid downregulation of stomatal conductance (Oberhuber *et al.*, 2015), cessation of cell production, and reduced resource investments in the lignification phase (Eilmann *et al.*, 2009), albeit with higher risks of cavitation and decreased mechanical structural integrity if supported by thinner cell walls (Gričar *et al.*, 2015; Hacke & Sperry, 2001). On the other hand, Norway spruce demonstrated higher structural stability in earlywood under severe drought stress, which indicates that the overall growth performance and, consequently, wood plasticity will increasingly depend on the length and magnitude of chronic drought conditions limiting carbon availability in the latter part of the growing season (*i.e.*, resource mobility and carbohydrate reserves; Castagneri *et al.* 2018). Overall, the large species- and site-specific differences in the magnitude of ΔBI response to moisture conditions suggest increasing localised coping strategies and xylem modifications as frequency of compound drought events increase (Babst *et al.*, 2012; Campelo *et al.*, 2010; Carrer *et al.*, 2010; Știrbu *et al.*, 2022), and again highlights the rising importance of micro-environmental variation on xylogenic processes under global climate change (Mayr, 2007; Oberhuber, 2004; Rehschuh *et al.* 2021).

5.3 INTERPLAY BETWEEN NATURAL FOREST DYNAMICS AND IMPROVING GROWING CONDITIONS DETERMINES THE FUTURE POTENTIAL OF PRIMARY MOUNTAIN FORESTS FOR ENHANCED CARBON UPTAKE

Disturbances, in tandem with environmental controls, play a fundamental role in driving natural forest dynamics, shaping forest structure and species composition, as well as determining biomass accumulation pathways and overall biodiversity (White & Pickett, 1985). In closed-canopy forests, many trees will have recruited in shade and undergone repeated cycles of suppression and releases, whereas others will have recruited in canopy openings following a severe disturbance (Canham *et al.*, 1990), thus shaping the conservativeness of a tree's growth history and, potentially, longevity. Large old trees (hereafter “LOTs”) are generally a rare feature in forest landscapes, mainly due to the negative association between age and size with early growth (*i.e.*, growth-longevity tradeoff), but also heightened sensitivity to abrupt climatic perturbations (Bennet *et al.*, 2015), historical land-use, and/or disturbance regimes (Lindenmayer *et al.*, 2012; Piovesan & Biondi, 2021). Yet LOTs exhibit a disproportionate impact on carbon storage (Clark & Clark, 2000; Keith *et al.*, 2010), provisioning of habitats (Lindenmayer, 2016; Lindenmayer *et al.*, 2014), and shaping micro- and meso-climates (Lindenmayer & Laurance, 2017). Additionally, LOTs are used to highlight areas of high ecological value as indicators of historical ecosystem dynamics and forest naturalness (Di Filippo *et al.*, 2017). Therefore, identifying LOTs and understanding the underlying principles of their distribution and development are fundamental groundwork for protecting and/or restoring natural landscapes (Chiarucci & Piovesan, 2020; Lindenmayer, 2017), but also revisiting classical ecological theories that shaped our understanding of tree growth and forest dynamics under environmental changes (*e.g.*, “the respiration hypothesis”; Odum, 1969).

In a world of accelerating changes in environmental conditions driving tree growth, understanding the concurrent impacts of tree-level tradeoffs and stand-level dynamics on LOT distribution and forest landscape structure is crucial for predicting the consequences of global climate change for biodiversity and carbon storage. In an effort to disentangle the effect sizes of various spatiotemporal factors obscuring the existence of the theorized growth-longevity tradeoff limiting LOT abundance and caping forest biomass development under climate warming, I found concurrent impacts of individual tree age/growth drivers and stand-level dynamics on LOT development in montane primary spruce forests (section 4.2). Whereas life-history traits (*i.e.*, slow growth) and disturbance dynamics (*i.e.*, growth release events) determine the attainment of old age, the effects of recently observed improving baseline growing conditions (*i.e.*, rising temperatures since the 1980s) transcend age/size limitations of tree growth and enhance forest productivity across all age groups (section 4.2, Fig. 6). Ultimately, this suggests that past growth histories do not hamper the growth potential of LOTs to continue accumulating biomass under improving growing conditions.

The implications of LOTs growth continuity under environmental changes are multifold: on one hand, the fact that individual LOTs can reverse the slow-growing strategies established earlier in life and accumulate additional biomass when growing constraints are alleviated, indicates these trees have not yet reached their maximum size, nor lost their growth capacity. Furthermore, LOTs exhibiting ability for continued biomass accumulation under improved growing conditions demonstrate that age- and size-related growth declines are likely not the prevailing cause of tree death, but rather the combined impacts of exogenous mortality drivers (Pretzsch *et al.*, 2020, Sillett *et al.*, 2015). In turn, this could carry broad consequences for forest productivity, carbon storage, and ecosystem dynamics, as LOTs accumulate a disproportionately higher amount of biomass compared to smaller and younger trees (Fauset *et al.*, 2015; Trotsiuk *et al.*, 2016), and have a longer carbon residence time following a mortality event (*i.e.*, as standing dead trees; Shu-miao *et al.*, 2019). Moreover, if LOTs continue responding incrementally to improving growing conditions, rising temperatures could elevate carbon uptake and increase forest biomass, which would certainly benefit carbon storage and could mediate carbon losses under increasing climate-related disturbances across the European mountain biomes (Lindenmayer *et al.*, 2012; Liu *et al.*, 2013; Senf & Seidl, 2021).

If the climate-driven accelerated growth rates explicitly lead to increased mortality and faster carbon turnover rates, we would expect the co-occurring antagonistic impacts of drivers promoting growth (*i.e.*, rising temperatures) and mortality vectors (*i.e.*, disturbances) to push stands toward younger age and reduced productivity (Brienen *et al.*, 2016; McDowell *et al.*, 2020). However, annual background mortality rates have generally remained stable in the Western Carpathians primary mountain spruce forests despite accelerated growth in recent decades (Synek *et al.*, 2020), indicating trees are still dying at the same age, but could be attaining larger sizes before death. Furthermore, post-disturbance environmental conditions that favor higher rates of productivity also improve soil potential to store additional carbon (Mayer *et al.*, 2020), increasing soil organic matter fluxes and ultimately leading to larger carbon gains (Keith *et al.*, 2009). Although the exacerbated effects of intensifying moisture-growth limitations and increasing frequency of climate-induced disturbance events will eventually increase mortality rates, the adverse effects of rising mortality will likely be attenuated by the synchronic post-disturbance tree recruitment and rapid understory growth benefiting from improved growing conditions (*e.g.*, increased light availability and nutrient availability increase due to enhanced deadwood decomposition), which will undoubtedly benefit carbon sequestration (Mikoláš *et al.*, 2021; Pugh *et al.*, 2019; Trotsiuk *et al.*, 2016), and offset potential increases in heterotrophic respiration from dead wood decomposition (Luyssaert *et al.*, 2008). Ultimately, although a projected increase in disturbances and severe climate anomalies might increase contemporary mortality and offset biomass, and consequently carbon, gains on a local scale, Western Carpathian primary mountain spruce forests will likely continue benefiting from the stimulatory effects of rising temperatures, either through an increase in overall growth rates (Pan *et al.*, 2011), or through development of a post-disturbance multilayered canopy structure (Meigs *et al.*, 2017).

5.4 FUTURE RESEARCH PERSPECTIVES

Results of this Thesis highlight the diverse range of impacts induced on tree growth and forest dynamics by global climate change, and provide clear evidence of generally increasing moisture-growth limitations in recent decades across three separate forest landscapes (*i.e.*, the Dinaric Mountain and the Western Carpathian primary mountain forests, and Central European mountain and lowland nature reserves). These findings highlight the urgent need for additional comprehensive multi-species analyses along a range of environmental conditions, as the severity and magnitude of the resulting climatic stressors impose varying effects across species and spatiotemporal scales, but ultimately may drive entire ecosystems beyond their tipping points (Vitasse *et al.*, 2019).

Establishing new extensive permanent sampling plots across European forest landscapes, and continuing the long-term monitoring efforts from unmanaged forest ecosystems, will reduce the uncertainties regarding the impacts of increasing temperatures and changing hydroclimatic patterns on tree species' resilience and forest ecosystem dynamics. Furthermore, our results highlight the importance of accounting for both regional and tree-level drivers when assessing contemporary ecosystem dynamics under climate change. If European temperate forests are expected to continue mitigating the impacts of rising global greenhouse gas emissions, detailed assessment of the spatiotemporal patterns in forest resilience to specific disturbance agents, and mechanistic modelling techniques extended by stratifying stand structural attributes and disturbance legacies as contributing factors to contemporary forest dynamics will undoubtedly improve the concurrent understanding of the complex climate-growth-disturbance interactions.

By combining multiple tree ring parameters, we identified a large variability in species- and site-specific adaptive strategies reflected in xylogenic modifications under extreme drought stress, with an overall heightened sensitivity of seasonal wood anatomical components to abrupt climatic perturbations. Understanding the future tolerance and coping mechanisms of economically and ecologically important species (*e.g.*, Scots pine and Norway spruce) and assessing their capacity for growth continuation and carbon fixation under intensifying chronic growth-inhibiting conditions, will require improved understanding of the plasticity of xylo-morphological processes across a broad range of environmental conditions. Future studies should, thus, aim to combine novel tree ring parameters (*e.g.*, BI parameters or the upcoming high-resolution wood surface light reflectance parameter – SI; Rydval *et al.*, unpublished) with anatomical density records (*i.e.*, quantitative wood anatomy or QWA; von Arx *et al.*, 2016v**)** and/or stable isotopes analysis (Gessler *et al.*, 2014) from an altitudinal and latitudinal range of species' natural distributions, in order to provide a better insight into drought-induced eco-physiological mechanisms under different environmental conditions. This will lead to improved understanding of climate legacy effects in inter- and intra-annual growth variance and could provide a robust interpretation of the more nuanced metabolic processes behind wood formation under climate stress. Finally, utilization of BI parameters in dendroecological studies to assess the impacts of non-climatic factors (*e.g.*, past management activities or bark beetle outbreaks) may advance the utilization of such parameters for empirical application, as density fluctuations and intra-annual growth variability are often the first signs of forthcoming forest decline (Cailleret *et al.*, 2019), and could thus help guide future management strategies under global climate change.

5.5 MANAGEMENT IMPLICATIONS

Information about responses to intensifying climatic constraints ranging from tissue-level to stand-level, and interpreting how they relate to regional and landscape-level tradeoffs, are not only important for understanding the changing effects of exogenous drivers on forest development, but also for developing adequate management planning (Nabuurs *et al.*, 2017). Global change forces will likely drive future declines in European temperate forest landscapes in the absence of adaptive management strategies, which could result in severe economic and ecological losses (Hanenwinkel *et al.*, 2013; Mina *et al.*, 2022). However, the complexity of interactions between disturbances (*e.g.*, nested effects of windthrow and bark beetle outbreaks with summer droughts), different spatiotemporal scales of disturbance effects on forest ecosystems, and the inherent sensitivity of forest ecosystems and disturbances to changing climate regimes complicate the presupposition of managing for future resilience and sustainability, particularly if management strategies aim to achieve short-term goals (Mori, 2011). This Thesis provides empirical information on keystone ecological components at various hierarchical levels that can aid forest conservationist and managers to identify and retain (*e.g.*, Western Carpathians) or restore (*i.e.*, Central European lowlands) landscape structural components that will ensure the long-term ecological integrity under global warming.

In the Western Carpathian and the Dinaric mountains, primary spruce forests are generally fragmented over large mountain ranges and constitute a mosaic landscape of disturbance-driven forests, where maintaining landscape heterogeneity is essential for preserving paramount ecosystem functions, such as carbon sequestration, nutrient regulation, and protecting wildlife habitats and biodiversity species (Kameniar *et al.*, 2021; Langbehn *et al.*, 2021; Mikoláš *et al.*, 2021). As demonstrated earlier in our study (section 4.2), LOTs exhibit a disproportionate impact on forest feedbacks in terms of carbon cycling, biomass dynamics, microclimatic buffering, and habitat provisioning, relative to their paucity in the landscape. Thus, identifying and protecting LOTs is arguably the most effective strategy for accumulating atmospheric carbon and, simultaneously, benefitting other important ecosystem services. Activities that promote small- to large-scale deforestation of buffer zones and protected areas that could interfere with self-regulating processes (*e.g.*, salvage logging) should be prohibited or at least minimized, to ensure the preservation of LOT habitats and allow for conservation of biodiversity.

In the more drought-prone mixed-species Dinaric primary mountain forests, the effects of intensifying soil moisture constraints could lead to demographic shifts and alter forest species composition, as Norway spruce further declines under increasing perturbations (section 4.1). Rise in mortality could lead to high amounts of variable coarse woody debris on the forest floor, but also high structural heterogeneity across the regional scale, with cascading effects on biodiversity, edaphic conditions, and biogeochemical cycles, which may translate into higher disturbance-mediated ecosystem resilience. Thus, forest managers and conservationists will require a deeper understanding of past ecosystem variability before determining the spatial scale of areas where passive/active management could allow for the continuation of natural processes to promote desired ecosystem services (Kulakowski *et al.*, 2017; Vacchiano *et al.*, 2016). Therefore, management strategies should weigh the economic and ecological benefits of post-disturbance activities, promote physical soil and water conservation interventions in areas with high erosion, and generally aim at restorative functions that will identify new localities with old-growth features (*e.g.*, secondary forests) and incorporate such areas into protected landscapes, which could improve the inter-connectivity between forests of high ecological value and promote disturbance-induced complexity, structural diversity and, consequently, high ecological resilience under global climate change.

Findings from the Central European lowland nature reserves suggest a complex scenario of spatiotemporally heterogenous and species-specific contrasting responses to future heatwaves and droughts. Large altitudinal and latitudinal variability in the responses of Norway spruce and Scots pine populations to average climate conditions and extreme climatic events emphasize the importance of the amplification effects of topographic gradients and local site conditions for future species/forest resilience. Thus, enhancing forest ecosystem resilience will require localized assessments of the current state of demographic processes and promote management activities that preserve or reintroduce structural, compositional, and functional attributes that could minimize large-scale disturbance-induced structural perturbations. However, even if the disturbance patterns cause abrupt and unpredictable demographic shifts, ensuring large enough conservation areas that allow for a range of disturbances to sustain structural characteristic, and leaving behind some proportion of live and dead biomass at tree, stand, and landscape scales, will likely support biodiversity and future ecological resilience, and should thus be prioritized. Bearing in mind that reduced competition due to rising neighborhood mortality increases resource availability, which could subsequently enhance radial growth and post-drought recovery of younger subcanopy trees (Au *et al.*, 2020), implies that the large adverse short-term impacts of reduced carbon stocks could eventually be mediated by the long-term positive effects on ecosystem functioning. Spatiotemporally irregular cutting activities with varying intensities could be introduced to ensure retention of critical forest structures (Čada *et al.*, 2020; Gustafsson *et al.*, 2012), whereas natural regeneration may be assisted at the intra-specific level by modifying the functional and genetic diversity with more drought-resistant varieties to improve the adaptive capacity of forest populations to future environmental stress (Bussotti *et al.*, 2015). Generally, future innovative experimental approaches testing the potential for long-term adaptation under the umbrella of the non-equilibrium nature of forest dynamics, and scaling management strategies across hierarchical levels should be supported across the environmental gradient (Regos *et al.*, 2016; Vilà-Cabrera *et al.*, 2018).

CONCLUSION

This Thesis aimed to explore the magnitude and scope of past and contemporary impacts of external factors (*i.e.*, climate and natural disturbances) on tree growth dynamics in European unmanaged forests. By utilizing comprehensive tree-ring datasets from primary and near-natural mountain and lowland forests in Central-Eastern and Southeastern Europe, the results of the Thesis provide a deeper insight into how global climate changes shape the structural characteristics of present-day forests and modulate the broad range of spatiotemporally diverse ecosystem processes and functions. Assessing tree-level responses to short-term and long-term climatic and non-climatic perturbations from multiple tree-ring parameters allowed me to robustly link tree-level physiological mechanisms with ecosystem-level biogeographic patterns, and describe the extent of growth variation among trees, within species and sites with adverse environmental conditions, and across forest landscapes.

Dendroclimatological assessments of the prevailing growth-climate associations across the altitudinal and latitudinal gradient revealed that the interpretation of the climate-growth relationships are increasingly dependent on multi-factorial interactions, mainly micro-environmental conditions and species-specific traits, and the spatiotemporal resolution of climate-growth sensitivity analysis. Growing season temperature was widely recognized as the predominant climatic driver of tree growth across the network, but the effects of the associated temperature-growth sensitivity ranged from positive impacts on forest productivity in the cold and high-mountainous Western Carpathian mountains, to growth-inhibiting impacts of high summer season temperatures, in tandem with severe moisture constraints, in the more drought-prone Dinaric Mountains and Central European nature forest reserves. Considering that the shifting hydroclimatic patterns and intensifying heatwaves in Central Europe have already evoked distinct growth declines across conifer forests in recent decades, suggests that future development of European temperate forest landscapes will increasingly depend on local adaptation strategies for preserving forest ecosystem functioning. Furthermore, observing the general trend of incoherent and nonlinear growth sensitivity with the dominant climatic drivers in environments with complex and mixed-signal responses, indicate that the long-term performance and future development of these forests will increasingly depend on micro-environmental conditions.

Dendroecological evaluation of manifold processes underlying the attainment of high age (*i.e.*, longevity) in the Western Carpathian primary mountain spruce forests, and determining how these processes interact with regional drivers to shape contemporary forest dynamics, demonstrated the fundamental role of slow growth early in life and growth release events later in life for a multi-centennial lifespan in primary mountain spruce forests. Moreover, the clear interdependence of the observed trend of enhanced growth with rising temperatures in recent decades, shows that the effects of improving baseline environmental conditions transcend the latent age/size limitations, and suggests trees are not bound by past growth histories to add on additional carbon. Although faster growth may accentuate the growth-mortality tradeoffs, the landscape consequences of enhanced biomass accumulation could mediate carbon losses under intensifying climate-driven disturbances and promote legacy sink effects of primary spruce forests for decades to come.

With the predicted continuation of the global trend of rising atmospheric temperatures throughout the 21st century, along with more frequent occurrence of severe droughts, uncertainties regarding future ecosystem resilience and functioning along broad environmental gradients depend on how extreme climatic years manifest on tree physiological processes, which are closely tied with species' adaptation potential and, consequently, forest ecosystem functioning. On that note, non-parametric tests were invoked to disentangle the leading modes of climate response in tree-ring width and individual components of wood formation during severe drought years. Distinct growth reductions and discrete legacy effects are most pronounced in the low-elevation forests, and together with the observed declining growth trends in the 21st century, suggest that the predicted increase in frequency and duration of summer droughts will likely drive future growth declines across the region through increased evapotranspiration demands, depletion of stored carbohydrates and, ultimately, decreased resistance to extrinsic mortality factors. However, the identified distinct antagonistic responses to shifting climatic conditions and severe droughts both intra- and inter-species, indicates future species' capacity and anatomical plasticity is a function of both micro-climate and geomorphological conditions. Finally, this Thesis highlights the advantage of utilizing the BI parameters as robust proxies of short-term drought impacts and long-term trends of antecedent and contemporary climatic drivers on tree growth from moisture-limited environments, and calls for additional studies that will incorporate mechanistic methodological approaches that will better reflect the ecological reality and multi-parameter assessments that will allow for robust predictions of future tree resilience under global climate change.

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ELECTRONICAL SUPPORTING INFORMATION

This appendix contains the supporting information for each research paper.

Chapter 4.1: CLIMATE-GROWTH RELATIONSHIPS OF NORWAY SPRUCE AND SILVER FIR IN PRIMARY FORESTS OF THE CROATIAN DINARIC MOUNTAINS

Supporting Information S1

Chapter 4.2: LARGE OLD TREES INCREASE GROWTH UNDER SHIFTING CLIMATIC CONSTRAINTS: ALIGNING TREE LONGEVITY AND INDIVIDUAL GROWTH DYNAMICS IN PRIMARY MOUNTAIN SPRUCE FORESTS

Supporting Information S2

Chapter 4.3: SPATIOTEMPORAL CHANGES IN DROUGHT SENSITIVITY CAPTURED BY MULTIPLE TREE-RING PARAMETERS OF CENTRAL EUROPEAN CONIFERS

Supporting Information S3

Chapter 4.4: ECOLOGICAL AND METHODOLOGICAL DRIVERS OF NON-STATIONARITY IN TREE GROWTH RESPONSE TO CLIMATE

Supporting Information S4