Czech University of Life Sciences Prague

Faculty of Forestry and Wood Sciences

A DENDROECOLOGICAL PERSPECTIVE ON TREE LIFE HISTORY ACROSS A GRADIENT OF PRIMARY TEMPERATE FORESTS IN CENTRAL, EAST, AND SOUTHEAST EUROPE

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Objectives of thesis

Tree life history strategies are crucial determinants of forest community structure and dynamics. Knowledge of tree life history traits is thus critical for a more comprehensive understanding of forest ecosystem tendencies. Furthermore, quantifying these developmental characteristics and how they relate to dominant drivers may serve as an important basis for projections of future forest states. Using dendroecological and supporting data collected on up to 1000 permanent sampling plots, the main aim of this thesis is to analyze the variability in some of the key life history traits such as longevity and canopy accession of the dominant tree species across primary temperate mountain forests of Central, East, and Southeast Europe. Additionally, the aim is to examine and assess the relationships between tree life history traits and their drivers. The specific objectives of this thesis were:

1) To quantify the life span variability among dominant tree species and analyze the dominant drivers of their life spans. Additionally, to assess the landscape variability of old tree densities.

2) To analyze the variability of canopy accession patterns across dominant tree species and to investigate how these patterns are influenced by disturbance history, climate, and topography.

3) To investigate growth releases in dominant tree species and examine the species-specific relationships between the growth and duration of growth releases and multiple factors, including disturbance severity, climate conditions during release, topography, tree age and size, as well as temporal trends.

Methodology

To address the objectives of this thesis, data were collected in the scope of a large-scale network of permanent sampling plots located in primary temperate mountain forests of the Balkan Mountains, Carpathians, and Dinarides. Plots were set up using a stratified random design covering an elevational gradient from broadleaf-dominated and mixed forests at lower elevations to conifer-dominated forests at higher elevations. Data collection encompassed documenting physiographic site information, dendrometric data and collecting tree increment cores. Tree increment cores were processed using standard dendrochronological techniques. Ring widths were measured and cross-dated and were subsequently used to calculate the life-history-related parameters and to reconstruct the plot-level disturbance histories. The interspecific variability in life-history-related parameters was ultimately assessed using generalized linear mixed effect models in combination with post-hoc tests, while the trait drivers were analyzed using generalized linear mixed effect models.

The proposed extent of the thesis

100 NS

Keywords

Disturbance; Life span; Canopy accession; Radial growth; Irradiance; Shade tolerance; Growth release; Suppression; *Abies alba*; *Acer pseudoplatanus*; *Fagus sylvatica*; *Picea abies*

Recommended information sources

Baker, P.J., Bunyavejchewin, S., 2006. Suppression, release and canopy recruitment in five tree species from a seasonal tropical forest in western Thailand. J. Trop. Ecol. 22, 521–529. https://doi.org/10.1017/s0266467406003312

Bigler, C., Veblen, T.T., 2009. Increased early growth rates decrease longevities of conifers in subalpine forests. Oikos 118, 1130–1138. https://doi.org/10.1111/j.1600-0706.2009.17592.x

Brienen, R.J.W., Zuidema, P.A., 2006. Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. J. Ecol. 94, 481–493. https://doi.org/10.1111/j.1365-2745.2005.01080.x

Di Filippo, A., Pederson, N., Baliva, M., Brunetti, M., Dinella, A., Kitamura, K., Knapp, H.D., Schirone, B., Piovesan, G., 2015. The longevity of broadleaf deciduous trees in Northern Hemisphere temperate forests: insights from tree-ring series. Front. Ecol. Evol. 3, 1–15. https://doi.org/10.3389/fevo.2015.00046

Leuschner, C., Meier, I.C., 2018. The ecology of Central European tree species: Trait spectra, functional trade-offs, and ecological classification of adult trees. Perspect. Plant Ecol. Evol. Syst. 33, 89–103. https://doi.org/10.1016/j.ppees.2018.05.003

Lindenmayer, D.B., Laurance, W.F., 2017. The ecology, distribution, conservation and management of large old trees. Biol. Rev. 92, 1434–1458. https://doi.org/10.1111/brv.12290

Nagel, T.A., Svoboda, M., Kobal, M., 2014. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. Ecol. Appl. 24, 663–679. https://doi.org/10.1890/13-0632.1

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547.

Salguero-Gómez, R., Jones, O.R., Jongejans, E., Blomberg, S.P., Hodgson, D.J., Mbeau-Ache, C., Zuidema, P.A., De Kroon, H., Buckley, Y.M., 2016. Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. Proc. Natl. Acad. Sci. U. S. A. 113, 230–235. https://doi.org/10.1073/pnas.1506215112

Valladares, F., Niinemets, Ü., 2008. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. Annu. Rev. Ecol. Evol. Syst. 39, 237–257. https://doi.org/10.1146/annurev.ecolsys.39.110707.173506

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Declaration of independence

I hereby declare that this Ph.D. Thesis, titled “A dendroecological perspective on tree life history across a gradient of primary temperate forests in Central, East, and Southeast Europe”, 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.

September 1st, 2024, Prague

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ABSTRACT

Assessing the survival patterns of trees is crucial for gaining a deeper understanding of tree life history strategies, which play a key role in shaping forest structure and function. In light of widespread shifts in environmental dynamics, documenting the current range of life history traits and their interactions with the environment is essential for predicting novel ecosystem states. However, lifelong tree development is often confounded by the effects of human land use. As a result, adequate studies of tree life histories governed by natural dynamics, free from forest management interventions, can only be conducted in restricted, remote areas that have either never been directly impacted by land use or have fully recovered their ecosystem structure and function. Additionally, studying various tree life history traits is further complicated by the long life cycles of trees. To address this, dendroecological techniques were used to investigate variability in some of the key life history traits, including longevity and canopy accession, as well as how these traits respond to various internal and environmental development drivers. Analyses were based on over 20,000 increment cores collected from the four dominant tree species across primary forests in the Balkan Peninsula and the Carpathians. This thesis offers valuable insights into the ecological dynamics of temperate European mountain forests.

Firstly, the variability in life span amongst four dominant tree species (Norway spruce, *Picea abies* (L.) H. Karst.; silver fir, *Abies alba* Mill.; European beech, *Fagus sylvatica* L.; and sycamore maple, *Acer pseudoplatanus* L.) across primary forests of the Balkan Mountains, the Carpathians, and the Dinarides was assessed along with their drivers (Section 4.2, 5.1, and 6.1). Individuals of all four species surpassed 400 years in age, however, only beech trees surpassed 500 years with the oldest individual dated to 578 years. There were significant differences in life span between the four analysed species with a general ranking beech > fir > spruce > maple. These differences imply there is a pronounced variation in longevity between these species, which may contribute to the coexistence of tree species in temperate forests. Additionally, landscapes subjected to more severe disturbances were less likely to sustain old trees, while trees that endured multiple cycles of suppression and release, along with periods of pronounced slow growth, were more likely to achieve old age. Apart from the weak and negative impact of mean vegetation season temperature on the life span of fir and maple, no other analyzed environmental factor significantly affected the probability of attaining old age.

Secondly, tree canopy accession patterns of the four aforementioned species across the primary temperate mountain forests of the Balkan Mountains, the Carpathians, and the Dinaric Alps and how they are affected by disturbance histories, topography, and climate were investigated (Section 4.3, 5.2, and 6.2). High intraspecific variability in canopy attainment patterns was evident across all four species, yet significant differences also existed between them. Individual trees of all four species survived at least 100 years of initial suppression. Fir, and especially beech, endured longer periods of initial suppression, attained the canopy later on average, exhibited more growth releases, and had a higher proportion of trees attaining the canopy after initially suppressed growth compared to spruce and maple. The latter two species relied more on faster growth rates and non-suppressed conditions for successful canopy ascension, suggesting a competitive advantage in the absence of suppression. These findings indicate that the shade tolerance of beech and fir surpasses that of maple and spruce. Next to that, differences were also apparent in canopy accession of spruce from higher-elevation spruce-dominated forests and spruce from lower-elevation mixed forests. Namely, the higher-elevation spruce endured shorter periods of initial suppression, and exhibited marginally fewer growth releases, with a greater proportion of trees reaching the canopy with no growth suppression relative to spruce from mixed forests. Modeling results indicated that disturbance history-related factors are the primary drivers of canopy accession in these closed-canopy forests. Disturbances influence canopy accession by regulating forest light regimes, which in turn govern competitive dynamics and species composition.

Finally, the investigation focused on growth rates and durations of growth releases of beech and spruce across the mountain forests of the Carpathians and how releases relate to several internal and environmental factors (Section 4.4, 5.3, and 6.3). Growth rates during releases for both species exhibited a marginally increasing trend over the past century, contributing to stable canopy recruitment rates. Disturbance severity emerged as the primary external driver of average growth during release for both species, though it was relatively more influential for beech. In contrast, average growth response showed no significant correlation with the release-long averages of included climatic variables for either species. The predominantly negative response of spruce to age at release onset, compared to the primarily positive response of beech growth to DBH (diameter at breast height) at the onset of release, suggests that spruce's reactive capacity might be more adversely affected by the duration of prior suppression than beech. Despite the lack of a

clear climatic signal when analyzing multi-annual averages, a marginal yet significant negative effect of potential irradiance on beech growth was observed, implying that beech growth releases might be negatively impacted by reduced water availability, particularly on drier south-facing slopes. Unlike growth rates, the durations of growth releases were largely insensitive to the included environmental drivers and showed a strong negative relationship with increasing DBH.

In this thesis, I document marked variability of some key life history traits amongst the dominant tree species across temperate mountain forests of Europe. Furthermore, disturbance regimes are demonstrated to play a major role in controlling tree life histories, implying disturbances are an important driver of compositional dynamics across these closed-canopy forests. These insights may provide valuable baseline information for shaping close-to-nature management systems that aim to emulate natural disturbance patterns, fostering a wide array of developmental pathways to support diverse species across the shade tolerance gradient in European temperate forests. Additionally, I report substantial densities and multi-centennial ages of old trees across analyzed landscapes. Given their significant role in long-term carbon storage and microhabitat provision, the considerable conservation value of these primary forests is strongly underscored.

Keywords: Disturbance; Life span; Canopy accession; Radial growth; Irradiance; Shade tolerance; Growth release; Suppression; *Abies alba*; *Acer pseudoplatanus*; *Fagus sylvatica*; *Picea abies*

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1. INTRODUCTION

The variation in how and when species typically grow, reproduce, and die represents the species' life history strategies (Franco and Silvertown, 1996; Salguero-Gómez et al., 2016). The patterns and trends associated with these strategies are crucial for our understanding of ecosystem dynamics. For predicting novel ecosystem states resulting from ubiquitously shifting environmental drivers, it is imperative to document the current ranges of life history dimensions and how they interact with the environment. Forests hold great importance for global carbon storage and sequestration, biodiversity, hydrological and nutrient cycling, as well as supporting a plethora of societal values (Bonan, 2008). Studying survival strategies of trees as a keystone life form of forest ecosystems is therefore a prerequisite for developing climate policies and managerial tools aiming to optimize the provision of associated ecosystem services.

Adequate studies of tree development under reference conditions governed by natural disturbances may, however, only be conducted in limited remote areas that evaded direct effects of human intervention or had sufficient time to recover the ecosystem structure and function (Nagel et al., 2014). Namely, the variability of ecosystem characteristics crucial for the evolution of native communities, such as complex age and size structures at different spatial scales and abundance of deadwood in various decay stages, is generally missing from managed forests on comparable sites (Mikoláš et al., 2019). Under traditional silvicultural regimes, the natural diversity in tree developmental pathways is generally restricted, whereby species composition, tree growth, and stand age structures are regulated for yield (Aszalós et al., 2022; Bauhus et al., 2009; Keren et al., 2017). Consequently, managed forests are unsuitable for analyzing tree life history attributes such as longevity or canopy accession patterns. Due to a long history of land-use practices, appropriate reference conditions for developing new management regimes or adapting existing ones are nowadays rare across temperate Europe. Yet, they can still be found in primary forests and old-growth remnants in some mountainous regions, predominantly in Central, East, and Southeast Europe, where forests are mostly dominated by European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.), and Norway spruce (*Picea abies* (L.) H. Karst.) (Nagel et al., 2014).

Natural disturbances are an integral component of forests, much like other ecosystems. Broadly considered as discrete events altering the structure and function of an ecosystem at different spatial scales, they are one of the key drivers of ecosystem development

(Pickett and White, 1985; Turner, 2010). There is renewed interest in understanding natural disturbance processes and how disturbances interact with different tree species to ultimately drive long term forest community dynamics, especially in the light of ongoing environmental change. If shifts in climatic drivers result in more severe disturbance events (Seidl et al., 2017), there is a need to understand how resilient natural forests are to these modified disturbance regimes. This in turn requires knowledge on how tree life history characteristics modify responses to disturbance events and regimes. Such baseline ecological understanding may then be the basis for management systems accounting for the complexity of old-growth stands, particularly with the aim of providing a multitude of ecosystem services and increased resilience (Aszalós et al., 2022; Bauhus et al., 2009; Bengtsson et al., 2000).

Studying and quantifying lifelong tree development presents a complex endeavor due to the intricate interplay of confounding factors affecting forest development and the long life spans of trees. However, this undertaking is highly motivated by the inherent values of forests and uncertainties concerning their responses to future external perturbations. The variability in tree life history patterns and their interaction with the environment underpin the value of unmanaged forest landscapes and the necessity for their conservation. Moreover, implications following the developmental tendencies of the presented species may serve as a theoretical basis for adapting the management approaches in forest landscapes of temperate Europe.

2. AIMS AND OBJECTIVES

Understanding the typical species' responses to major developmental catalysts is instrumental for predicting future ecosystem states and dynamics amid ongoing environmental shifts and further adapting the associated conservation and management practices. Data collected on up to 1000 permanent sampling plots set up in the primary forests of the Carpathian Arc and the Balkan Peninsula was used to study the variability in some of the key life history traits such as longevity and canopy accession among dominant tree species. Patterns of longevity and transition to the dominant stand layer have marked effects on forest community dynamics and important implications for carbon storage. A further aim was to assess how these traits respond to some of the dominant internal and environmental drivers, whereby the evaluated relationships hold substantial significance for forest resilience capacities.

Specific objectives of this thesis were:

- To quantify the life span variability among dominant tree species and analyze the dominant drivers of their life spans. Additionally, to assess the landscape variability of old tree densities.
- To analyze the variability of canopy accession patterns across dominant tree species and to investigate how these patterns are influenced by disturbance history, climate, and topography.
- To investigate growth releases in dominant tree species and examine the species-specific relationships between the growth and duration of growth releases and multiple factors including disturbance severity, climate conditions during release, topography, tree age and size, as well as related temporal trends.

3. LITERATURE REVIEW

3.1 LIFE HISTORY STRATEGIES

3.1.1 Introduction to life history theory and its relevance

Identifying prevalent dimensions of ecological variability among species and where it stems from is one of the core objectives in plant ecology (Westoby et al., 2002). Organisms display a marked variability in how they develop, how and when they grow, at what size and age they might mature, how often they reproduce, how many offspring they produce, and how long may they live. These size-, age-, and developmental stage-specific pathways of an organism's growth, survival, reproduction, and life span determine its life history. Life history theory aims to understand how the process of natural selection shapes organisms to successful reproduction, accounting for intrinsic and extrinsic factors that influence survival and reproduction (Fabian and Flatt, 2012; Stearns, 2000). To study the optimization of survival and reproduction in species, it is important to study the specific fitness attributes or life history traits such as growth rates, survival rates, reproductive effort, and life span. As individuals have limited resources to invest in their development, there are trade-offs between different traits. For example, investing in growth is generally in trade-off with investing in defense mechanisms (Mole, 1994). The spectrum of how species sustain a population is thus also inherently linked to environmental drivers (Westoby, 1998), and life history strategies therefore play an important role in shaping community structure and dynamics (West et al., 2009).

Knowledge of tree life histories is thus further essential for framing sustainable forest management practices. Research of interspecific differences in tree life-history traits may yield valuable insight into ecosystem functioning and subsequently provide fundamental guidelines for practitioners. Analyses across gradients of ecological conditions defining species' habitats are needed to provide a comprehensive overview of their life history characteristics. This is particularly important because variations in plant life history and functional traits at both within- and between-species levels have significant ecological effects. Namely, environmental conditions impose strong selective pressures and are crucial in shaping life cycles (Liu et al., 2017). Providing context by trying to elucidate the patterns and trends related to great variation in species abundances and performance in time and space has thus been a long-standing goal of ecological research (Adler et al., 2014).

3.1.2 Life history traits and trade-offs

The concept of traits is commonly used in ecology, whereby a trait is considered a proxy for organismal performance. Across different research fields and subfields, various definitions of traits and trait-based concepts are used. In the scope of this thesis, a trait is understood as “any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization” following the definition of Violle et al. (2007). Further, this work generally refers to life history traits and less so to functional traits, whereas the former are indicators of schedules of survival, growth, and reproduction (Salguero-Gómez et al., 2016), while the latter are generally traits with indirect effects on fitness through its effects on survival, growth, and reproduction (Violle et al., 2007). Both concepts are nonetheless related, whereas variability in functional traits was demonstrated to be closely correlated to plant life histories (Adler et al., 2014). Sets of correlated traits may reflect fundamental trade-offs as well as general life strategies of plants, such that species occurrence is based on their trait spectra (Stahl et al., 2013). For example, increased investment in the formation of thick bark and the synthesis of defensive chemicals can contribute to a longer tree life span. However, this also results in fewer resources being available for growth, leading to lower growth rates. A contrasting life strategy in another plant would therefore include rapid growth instead of investment in defense mechanisms, but the likely consequence is a rapid decline in the number of individuals in the cohort upon reaching maturity (Loehle, 1988). The evolution of life histories may thus also be viewed as an optimization problem, whereby the question is what trait-specific values maximize survival and reproductive success. In advancing this knowledge, it is important to understand the boundary conditions: 1) the response of survival and reproductive success to various intrinsic and environmental factors, and 2) how trade-offs or other constraints influence how life history traits may evolve (Stearns, 2000).

3.1.3 Fast-slow continuum hypothesis

Earlier research in the field confirmed the so-called fast-slow continuum hypothesis describing the evolution of life histories on several animal groups (e.g. Charnov and Berrigan, 1991; Harvey and Zammuto, 1985). It was later also confirmed on a variety of different perennial plants (Franco and Silvertown, 1996; Salguero-Gómez et al., 2016). According to the hypothesis, species can be arranged on a scale from those enduring high adult mortality rates on one end to those undergoing relatively low adult mortality on the other. Species with higher adult mortality tend to have shorter life spans, higher fecundity, and faster development rates compared to those with lower adult mortality (Franco and Silvertown, 1996). Much evidence has also been presented in the scientific literature confirming the compromise between growth and reproduction in plants (Geber, 2006; Obeso, 2002). The direct correlation between reproduction-related demographic traits (such as the net reproductive rate or the intrinsic rate of natural increase) and longevity as well as age at the onset of reproduction is however less clear. Namely, the constant increase in size throughout a tree's life cycle driving the increase in fecundity may offset for the negative effect of mortality on fitness (Franco and Silvertown, 1996). Salguero-Gómez et al., (2016) have later also shown that more than 50% of variability in plant life history strategies can be explained by two axes: the fast-slow continuum, with short-lived, fast-growing species at one end and long-lived, slow-growing species at the other, and a reproductive strategy axis, ranging from highly prolific species to those with low reproductive capacity.

3.1.4 Growth-differentiation balance hypothesis

The resource allocation patterns have also been reflected in the growth-differentiation balance (GDB) hypothesis (Herms and Mattson, 1992). Plant activity at the cellular level can be categorized into two processes: growth, which includes cell division and enlargement, and differentiation, involving chemical and morphological changes that lead to cell maturation and specialization. GDB hypothesis of plant defense thus posits that there is a trade-off between growth and defense as both the phenologically driven biomass increase and herbivory pressure driven increase in defense use the same resource pool (Glynn et al., 2007; Lerdau et al., 1994). Plants thus face the following predicament: an individual has to grow fast enough to stay competitive, yet also maintain the necessary defenses to withstand the pressure of pathogens and herbivores (Herms and Mattson, 1992). At the tree level, increased investment in the compounds such as tannins, phenolics, monoterpenes, and resins or into structural elements such as fibres, lignins, dense wood, or thick bark, generally constitutes and enhances the defense mechanisms against pathogens, insect attacks, or browsing by other herbivorous species and reduces the risk of breakage (Coley et al., 1985; Larson, 2001; Lerdau et al., 1994).

The hypothesis implies that in the environments with high resource availability as in large gaps or nutrient-rich and moist sites, growth receives a high priority in resource allocation since it is a highly resource-demanding process (Kleczewski et al., 2010). Therefore, individuals with fast growth and reduced secondary metabolism presumably prevail since they benefit from amplified resource acquisition and increased competitiveness at the expense of reduced stress tolerance and increased mortality due to herbivores, pathogens, or other agents of environmental stress (Bigler, 2016). At low levels of resource availability, growth rates are restricted more intensely than net assimilation rates, and resource allocation to secondary metabolism receives a higher priority. Individuals with slower growth rates but high secondary metabolism, therefore, dominate in such environments (Bigler, 2016; Glynn et al., 2007; Kleczewski et al., 2010). However, resource availability can be highly variable even within relatively small areas, such as the availability of light near the forest floor in closed-canopy forest ecosystems. Consequently, the relative success of species with different life strategies is highly dependent on the community structure.

Fast-growing trees under favorable light conditions therefore have increased short-term survival probabilities, yet their expected longevity may be lower due to long-term effects of reduced investment in defense mechanisms as well as the increased risk of stem breakage (Bigler and Veblen, 2009). Opposed to fast early growth rates, species developed several other strategies to reach adult age. Shade-tolerant species generally developed mechanisms of more efficient light use, particularly by higher leaf area ratio (LAR), that is the ratio of leaf area to plant mass (Givnish, 1988). Additionally, suppressed trees of fir or some other shade-tolerant species, for instance, have the ability to cessate both apical and radial growth, which allows them to redistribute the assimilates and enables them to survive through periods of low net assimilation rates (Yasuda et al., 2018). Another example of adaptation to low-light conditions is stem-layering, as observed on seedlings of sugar maple (*Acer saccharum* Marsh.). Older suppressed seedlings may thus sprout adventitious roots along the prostrate sections of the stem, reducing the demand to invest resources in older parts of the stem and maintaining a more favorable leaf area to height ratio (Woods, 2008). The differences in growth prioritization additionally relate to interspecific variability in longevity (Brienen et al., 2020; Di Filippo et al., 2015).

3.1.5 Phenotypic plasticity

A given genotype has the capacity to exhibit varying phenotypes in response to gradients of environmental conditions. This phenomenon is referred to as phenotypic plasticity

(Sultan, 2000). The inter- and intra-specific variability of plant traits is thus not exclusively defined by genetic variability among individuals and populations but is also dependent on resource availability and environmental stress. However, the reaction norm, or the gradient of genotype reactions across different environments, is genetically imposed (Gratani, 2014). Plastic responses of plants range across a wide array of traits related to their physiology, morphology, anatomy, as well as developmental and reproductive pathways. Phenotypic plasticity thus enables individuals of the same genotype to successfully develop and reproduce in variable microsites, as well as it enables individuals to adjust to temporally variable environmental drivers such as light, temperature, and moisture availability at diurnal, seasonal, or longer-term time scales (Sultan, 2000). For instance, individuals of shade-tolerant species that commonly establish in the shaded understories of closed-canopy forests are able to substantially adjust their physiology, anatomy, and morphology in response to abrupt increases in irradiance following formation of a canopy opening (Valladares et al., 2002).

Individual plasticity has important implications for ecological patterns at higher levels such as stress tolerance at population and species levels, species' biogeographies, or adaptive capacities to environmental shifts. Species with genotypes exhibiting low plasticity capacities are typically limited to narrower, specialist ecological niches, while species characterized by genotypes that display high plasticity are commonly ecological generalists (Sultan, 2000). Traits of a genotype or a higher organizational unit may, however, differ in their amounts of plasticity (Acasuso-Rivero et al., 2019). This is mainly because phenotypic plasticity is generally expressed at a sub-individual level, that is through individual meristems, leaves, branches, stems, and roots. The interactions of different interconnected modules can then further increase or decrease the capacity for a plastic response along the environmental gradients (De Kroon et al., 2005). Besides adaptive capacity, phenotypic responses to environmental cues may be characterized by several further factors. For instance, timing, duration, reversibility, or promptness of reaction can also importantly contribute to fitness (Schneider, 2022).

3.2 LONGEVITY AND SENESCENCE

3.2.1 Relevance of tree longevity

Analyses of longevity, one of the key life history traits, of the prevalent tree species within old-growth temperate forests in Europe constitute an important part of this dissertation thesis. Quantifying tree age, potential longevity, and how different environmental factors affect these metrics can importantly contribute to the understanding of growth processes that lead to diverse forest structures (Di Filippo et al., 2017). Many descriptions of different relations between longevity and various other traits can be found in the scientific literature. The theory implying that when site factors reduce wood growth, trees tend to reach longer life spans, was presented many decades ago (Schulman, 1954). This pattern was since observed and confirmed for many plant and specifically tree species (Bigler, 2016; Black et al., 2008; Brienen et al., 2020; Brutovská et al., 2013; Büntgen et al., 2019; Castagneri et al., 2013; Di Filippo et al., 2015, 2012; Johnson and Abrams, 2009; Piovesan et al., 2005; Rötheli et al., 2012). One of the most apparent examples in temperate forests is *Thuja occidentalis* L., which typically rarely reaches 400 years of age, yet individuals older than 1600 years have been found in extreme sites (Larson, 2001).

Documenting the longevity potential of tree species as one of the crucial measures determining species' life strategy has important implications for close-to-nature forest management due to having significant effects on the dynamics of forest stands. Tree longevity is closely linked to forest demography whereby tree longevity is analogous to forest mortality (Di Filippo et al., 2015; Stephenson et al., 2011). Tree longevity patterns further importantly contribute to trends of carbon sequestration and carbon residence times and thus have far-reaching environmental and societal consequences. Namely, long-term carbon storage is highly dependent on carbon residence times and therefore tree longevity (Büntgen et al., 2019; Körner, 2017; Martin-Benito et al., 2021). Furthermore, trees that attain ages close to their potential longevity foster a variety of morphological features that serve as microhabitats for a plethora of other organisms and are thus crucial for supporting forest biodiversity (Fritz and Heilmann-Clausen, 2010; Kozák et al., 2023; Lindenmayer and Laurance, 2017).

There are several reasons why a tree would strive to reach a long life span. For instance, long-lived trees may endure through periods of adverse environmental conditions and exploit the windows of opportunity when conditions improve (Petit and Hampe, 2006). Furthermore, long-lived trees may benefit from longer reproduction time and consequently likely from higher reproductive output, thus increasing their fitness (Lanner, 2002). Reproduction is also distributed over a longer period of time, raising the chances of offspring being able to develop in periods characterized by more favorable conditions and to compensate for the losses in periods of less favorable conditions (Petit and Hampe, 2006). The longer life spans are however often related to longer periods before attaining reproductive maturation (Valen, 1975). Due to various external factors of mortality, such as infestations by pathogens, extreme climatic events, sustained strong shading by surrounding trees, and other disturbance events, trees are thus at a high risk of dying before being able to reproduce (Bigler, 2016). Only a very small proportion of individuals, therefore get to attain ages close to potential longevity for the species (Cannon et al., 2022). Additionally, the maximum age varies considerably in relation to environmental features, even within the same species (Di Filippo et al., 2015; Lindenmayer and Laurance, 2017).

3.2.2 Tree longevity and carbon residence times

Using biosphere and particularly forest carbon sequestration as a mean to mitigate the greenhouse effect is widely considered and discussed (Canadell and Schulze, 2014). Namely, plants fix CO_2 in the process of photosynthesis and store it in their body parts (Körner, 2017). As plants are mortal, the carbon they store escapes their bodies upon their mortality and decomposition and ultimately returns to the atmosphere before the cycle repeats in case of regrowth. Higher carbon turnover or faster growth does not necessarily correspond with higher carbon storage in an ecosystem (Keeling and Phillips, 2007). To calculate the size of a carbon pool in an ecosystem one must subtract the net carbon input from net carbon output and multiply it with carbon residence time. That is, the average age of carbon from the time of sequestration to its release. Carbon pool in a forest can thus grow with a demographic shift toward a bigger abundance of older age classes and higher mean longevity (Körner, 2017). Primary forests are a prime example of large carbon pools, resulting from relatively long carbon residence times. Albeit, these can be largely modulated by shifts in disturbance regimes as well as shifts in other growth drivers (Martin-Benito et al., 2021). For instance, faster tree growth in response to novel environmental conditions has been shown to be compensated by reduced tree longevity. Potential growth rate increases would thus not necessarily result in increased carbon pools in aboveground forest biomass (Büntgen et al., 2019; Keeling and Phillips, 2007).

3.2.3 Old trees and biodiversity

Large old trees play several critical ecological roles and are through various functional pathways also important for supporting biodiversity. Specifically, they provide a wide range of microhabitats that can serve as shelter, dwellings, foraging sites, and breeding grounds for various animals. Additionally, they can act as substrates for other plants, such as bryophytes, epiphytes, and mistletoe, as well as fungi and lichens (Kozák et al., 2023; Lindenmayer and Laurance, 2017). Some most typical of these features for instance include cavities, various injuries alongside exposed wood, dendrotelms, and fruiting bodies of fungi. Presence and abundance of most of these features are simultaneously positively correlated with the size and age of the tree, as bigger trees are generally more susceptible to physical damage, while more microhabitats may also develop in a longer life span (Asbeck et al., 2019; Kõrkjas et al., 2021; Kozák et al., 2023). Tree age and size are generally correlated, thus large trees are generally not young. Anyhow, the largest trees are not necessarily the oldest (Issartel and Coiffard, 2011), whereas the presence of certain types of microhabitats is linked more closely to age rather than size of a tree. For instance, the occurrence of burrs and cankers caused by different pathogens was more dependent on age than on size across the Carpathian mountain forests, as well as presence of exposed sapwood and insect galleries which can potentially facilitate colonization of further xylophagous insects (Kozák et al., 2023). In general old trees often develop characteristic morphological traits such as a more pronounced stem taper, more pronounced stem eccentricities, and, in some species, more rugged bark and distinct color shades of bark (Handegard et al., 2021). Large old trees may also develop features that young, similarly sized trees lack, such as deep bark fissures, which can be crucial for facilitating the colonization of their surfaces by certain lichen or bryophyte species (Gloor et al., 2024; Lindenmayer et al., 2014).

3.2.4 Intrinsic and extrinsic determinants of tree longevity

Trade-offs between growth rate, tree size, and life span are well described in the existing scientific literature, nevertheless, certain aspects are still not understood well. Increases in size are generally associated with ageing, but it was long unclear whether the decreases in growth coupled with higher mortality rates are driven predominantly by size or age (Koch et al., 2004; Ryan and Yoder, 1997; Silvertown et al., 2001). Age-related growth declines were in the past decades then shown to be primarily a function of increasing size and not cellular senescence (Marziliano et al., 2019; Mencuccini et al., 2007, 2005). More recent studies pointed out that accelerated growth is related to faster ontogeny and demonstrated that the time of death in trees is primarily determined by their size. Faster-growing individuals reach critical dimensions relatively sooner, which often results in shorter life spans compared to slower-growing trees (Bigler and Veblen, 2009; Büntgen et al., 2019). In particular, increases in overall size present challenges due to the higher metabolic costs required to maintain a larger mass of living tissues. Increased height also presents constraints in transporting water and minerals to the highest parts of the tree and transporting assimilates from leaves to roots (Groover, 2017; Koch et al., 2004).

In trees, the perpetual growth can lead to development of large-bodied individuals, which can produce a large number of reproductive structures, while the great size (especially height) can also be beneficial for pollen and seed dispersal. Therefore there is a potential benefit of delaying senescence even at a large body size (Groover, 2017). By attaining large stature, however, exposure to dominant disturbance drivers increases, raising the risk of mortality with growing body mass (Bigler, 2016; Di Filippo et al., 2015). The largest trees are therefore not necessarily the oldest, particularly within the same species (Mu et al., 2023; Piovesan and Biondi, 2021). Nevertheless, extremely big trees may also be extremely old. For instance, individuals of *Sequoia sempervirens* (D.Don) Endl. and *Sequoiadendron giganteum* (Lindl.) J.Buchh. can exceed 90 m in height and live for more than 2000 years (Sillett et al., 2015). However, longevity in trees is generally negatively correlated with metabolic rate (Issartel and Coiffard, 2011), in accordance with the long-standing rate of living theory (Pearl, 1928).

The relatively unproductive sites are known to harbor the oldest individuals of any species (Schulman, 1954). Areas characterized by reduced growing seasons and/or low fertility in general are therefore more likely to support particularly old individuals. The extremely resource-limited environment is also characteristic of the habitats of the oldest documented nonclonal tree individuals, belonging to *Pinus longaeva* D. K. Bailey, which can exceed 5,000 years in age (Salzer and Baisan, 2013). Another apparent example of such ecosystems are cliff forests, where trees older than 1000 years were found both in Northern America as well as Europe (Camarero and Ortega-Martínez, 2019; Larson et al., 2000). Using radiocarbon dating, an individual of *Juniperus phoenicea* L., estimated to be over 1,790 years old, was identified on the cliffs of the Ardèche canyon in Southeast France (Mathaux et al., 2016). Similarly, the oldest individuals of *Pinus heldreichii* H. Christ, some of which exceed a millennium in age and are among the oldest living trees in Europe, also grow in extreme sites near the timberline, characterized by rocky soils (Piovesan et al., 2019b). In contrast to shade-tolerant trees, whose growth is often primarily limited by competition, trees on extreme sites typically display a growth pattern characterized by relatively wide tree rings during the juvenile stage, followed by a prolonged period of very narrow rings (Biondi and Qeadan, 2009; Piovesan et al., 2019b). The negative correlation between longevity and resource availability within species is generally apparent for species covering relatively wide niches, whereby the oldest individuals are generally found closer to species' biogeographical limits, such as at high elevation (Di Filippo et al., 2015, 2012; Rötheli et al., 2012).

Furthermore, tree mortality is mostly a result of external factors, rather than of internal ageing (Brutovská et al., 2013). Tree interaction with extant abiotic and biotic environmental factors is thus highly influential on life span. In most environments, drought is an episodic event and is a primary agent of abiotic stress for trees. It can lead to mortality either directly through hydraulic failure or indirectly through carbon starvation, as a tree may close its stomata to minimize water loss, which also reduces CO_2 diffusion (McDowell et al., 2013). Carbon starvation, or a weakened physiological state in general also promotes susceptibility to negative impacts of biotic factors, predominantly insects and pathogens (McDowell et al., 2008). The likelihood of the effects of biotic stress being detrimental for a tree raises in time with the tree growing older (Das et al., 2016). Mortality is often caused by the accumulated effects of abiotic and biotic stress combined. The oldest trees are often found in areas with infrequent disturbance events that kill many trees, typically growing outside intense storm zones (Di Filippo et al., 2015).

Metabolism and growth rates may also be regulated by light availability (Kobe et al., 1995). In closed-canopy forests light is a crucial factor driving tree survival and growth (Valladares and Niinemets, 2008). Individuals of particularly shade tolerant species may thus attain old ages by surviving protracted periods of time shaded exhibiting slow growth rates before accessing the dominant canopy layer (Nagel et al., 2014). In temperate primary forests, trees are characterized by highly variable growth patterns governed primarily by the light exposure history. The correlation between size and age may thus be low (Piovesan and Biondi, 2021). In the study of Di Filippo et al. (2015), a clear anticorrelation between growth rates and longevity was apparent from analyses of a large database of broadleaf deciduous temperate trees growing in closed-canopy old-growth forests in the Northern Hemisphere. Most studies on longevity patterns in closed-canopy forests have identified a strong correlation between maximum tree ages and slow juvenile growth rates (e.g. Begović et al., 2023; Bigler, 2016; Bigler and Veblen, 2009; Büntgen et al., 2019). Büntgen et al. (2019) further concluded that amongst sampled trees exclusively individuals characterized by slow juvenile growth reached old ages. The time spent growing suppressed in the understory, or growing relatively slowly, with relatively low aboveground biomass increment, can constitute a significant portion of a tree's total life span. This results in a lower overall biomass accumulation and thus a smaller size.

The premise is that the canopy residence time, and not tree age per se, modulates the trajectory of tree-level aboveground biomass increment (Trotsiuk et al., 2016). Castagneri et al. (2013), however found that even if there was a negative correlation between fast juvenile growth and longevity, high ages of analyzed spruce trees were more closely related to low growth rates during adult and mature stages. Alternatively, some other studies have not found any evidence of a trade-off between early growth and longevity (Cailleret et al., 2017; Ireland et al., 2014).

3.2.5 Tree longevity potential and senescence

It has been proposed that tree life span might potentially be unlimited (Ally et al., 2010; Peñuelas and Munné-Bosch, 2010), yet some general principles of the behavior determining mortality were presented in the scientific literature both for plants and animals. Firstly, longevity is typically inversely correlated with plant metabolism, whereby plant metabolism encompasses respiration and photosynthesis (Issartel and Coiffard, 2011). As a tree ages, its genome function continuously changes which can lead to physiological deterioration or senescence (Baudisch et al., 2013; Pérez-Llorca and Munné-Bosch, 2021). Senescence precedes a decline in biological activity and decline in organismal vitality (Bonsall, 2006). Senescence often starts after an organism transits from vegetative to reproductive phase, when replicative senescence in meristems, age-specific loss in genomic information, size-specific reductions in phenotypic plasticity cause a regression of bodily function, tree vitality and viability, fertility, and body mass of above-optimally sized individuals. Namely, trees are under selection pressure to optimize their body size in a way that their age-, as well as size-specific probability of mortality, is minimized and conversely fertility maximized (Dani and Kodandaramaiah, 2018). The ultimate effect of senescence-related processes is therefore increased probability of mortality (Silvertown et al., 2001). All plants senesce at the cellular and organ level therefore immortality is attainable only through clonal reproduction or germ line (Munné-Bosch, 2018).

Senescence at suborganismal levels may, however, be favorable in many cases. For example, leaf senescence in response to drought stress may help to reduce water losses and ameliorate the water balance of the plant (Munné-Bosch and Alegre, 2004). Similarly, seasonal senescent processes in ephemeral organs (such as fine roots, leaves, or petals) are crucial for nutrient resorption and remobilization (Wojciechowska et al., 2020). A single tree additionally behaves as a population of modules, with each module potentially aging individually (Brutovská et al., 2013). Moreover, trees are characterized by relatively slow rates of mutational changes, slowing down mutational meltdown as the base of senescence (Burian et al., 2016). For example, a sample of *Ginkgo biloba* L. trees up to 600 years old, despite experiencing reduced xylem production, still showed no signs of senescence in the vascular cambium. Furthermore, the expression of disease-resistance genes and synthesis of protective secondary metabolites remained high with advancing age, along with undiminished leaf photosynthetic efficiencies and seed germination rates (Wang et al., 2020). Senescent changes are thus not always apparent in trees. In a research of 290 angiosperm species, 93% of the species have not shown any senescence patterns at the organismal level. Even amongst phanerophytes (i.e. woody perennials) specifically, 81% displayed no senescence (Baudisch et al., 2013). As only an exceptionally low percentage of trees reach very old age, assessing senescence in old trees presents a significant challenge (Munné-Bosch, 2018). Namely, even the oldest trees of some long-living species are often very vital, exhibiting ample growth and adaptability to environmental changes (Piovesan et al., 2019b; Sillett et al., 2015)

3.2.6 Longevity in temperate forests of Europe

Regarding the maximum life span of trees in many temperate forests, 300-400 years can be considered as a baseline threshold (Di Filippo et al., 2015). Other studies suggest that beech and silver fir trees in mixed forests of Central Europe may reach the ages of up to 450 years, while sycamore maple (*Acer pseudoplatanus* L) and Norway spruce may reach the ages of up to 300 years (Leuschner and Meier, 2018). A large density of old beech trees (over 240 years old) was reported in the Sonian forest, lying 10 km south of Brussels, on a site characterized by favorable climate and site conditions. Most of these trees still exhibit relatively high growth rates (4,75 mm year^{-1}), indicating the species' ability to reach long life spans (Vandekerkhove et al., 2018). Nonetheless, much older trees were found in old-growth forests around Europe. The oldest beech tree in high Central Apennines, for example, was 559 years old, while in the high elevational belt of Eastern Alps the oldest beech tree was 520 years old (Di Filippo et al., 2017). The absolutely oldest beech trees were found in the Pollino Massif, in southern Italy, wherein the measured ages of two trees were 620 and 622 years, respectively (Piovesan et al., 2019a). For example, the oldest beech tree identified in a similar study in the Perućica Forest Reserve in the Dinaric Mountains of Bosnia and Herzegovina was 523 years old, while the oldest sycamore maple tree was 350 years old and the oldest silver fir tree was 345 years old (Nagel et al., 2014). Another study conducted in four old-growth forests reserves along the Dinarides, also reported high ages of oldest beech, fir, and spruce trees, with the oldest documented fir tree (487 years) surpassing the ages of the oldest documented beech (486 years) and the oldest documented spruce (454 years) (Motta et al., 2024). In the subalpine vegetational belt in Swiss Alps, the oldest spruce trees ranged from 238-322 years, while according to the model, the expected maximum longevity for the individuals reaching the canopy was 263-386 years (Bigler and Veblen, 2009). That is still notably shorter than the maximum age found for Norway spruce in a Fennoscandian boreal forest in southern Norway, with reports of multiple trees exceeding 400 years in age, and the oldest individual dated at 529 years. None of these reported trees were found in particularly harsh environments, nor did they exhibit unusual morphological traits such as multiple stems, krummholz, clonal growth, miniature size, or similar (Castagneri et al., 2013).

3.3 CANOPY ACCESSION

3.3.1 Relevance of canopy accession patterns

Canopy recruitment is a vital element of forest resilience. However, as environmental drivers shift, the regenerative capacity of forests remains uncertain (Johnstone et al., 2016; Saulnier et al., 2020). More comprehensive knowledge of canopy accession patterns and interactions with their drivers is thus warranted. In temperate forest ecosystems, the dynamics of tree growth and progression through different life stages depend largely on light availability (Givnish, 1988). Canopy layer buffers light transmission, whereby low irradiance in the subcanopy may become largely limiting for trees (Gravel et al., 2010; Lieffers et al., 1999). Canopy structure and light conditions, however, fluctuate in space and time. Different species thus develop a variety of strategies to cope with the range of occurring conditions while attempting to attain the canopy and gain competitive advantage (Canham et al., 1990; King, 2003; Walters and Reich, 1996). As morphological and physiological adaptations to survive in a low-light environment are generally discordant with adaptations to survive in a high-light environment, no plant species may function optimally across the whole light gradient (Valladares and Niinemets, 2008). The complexity of the light regime may be importantly linked to the complexity of the community structure (Canham et al., 1994, 1990). Additionally, the light regimes in forests are largely governed by disturbance regimes, whereby the scale, intensity, and frequency of particular events may largely vary in space and time (D'Amato and Orwig, 2008; Frelich and Lorimer, 1991). Namely, canopy disturbance events remove portions of the dominant canopy and release the subcanopy of light suppression. Understanding how trees respond to these dynamics coupled with other environmental drivers and how they ultimately progress from the understorey to the dominant canopy layer provides an important baseline for projections of future forest structure and function.

3.3.2 Canopy accession and shade tolerance

Most individuals of a given tree species in closed-canopy forests fail to reproduce in the course of their lifetime, therefore having zero fitness. Only a small minority of trees that reach the canopy is able to reproduce (Landis and Peart, 2005; Omelko et al., 2018). This is mainly due to limited light in the subcanopy (Gravel et al., 2010; Kobe et al., 1995). Patterns of canopy accession are thus related to shade tolerance, that is the minimum light required for an individual to survive (Valladares and Niinemets, 2008). Multiple pathways for achieving shade tolerance in plants have been identified. According to the carbon gain hypothesis, shade-tolerant plants maximize the capture of light and its utilization for photosynthesis while minimizing the costs of respiration (Givnish, 1988; Walters and Reich, 1996). Alternatively, plants may boost their survival probability by enhanced persistence through increased investment in storage and defense (Kitajima, 1994). In line with both of these is the growth-survival trade-off hypothesis, positing that survival in low light and growth in high light are negatively correlated (Kobe et al., 1995; Salguero-Gómez et al., 2016). To cope with low light conditions plants have developed a plethora of different adaptations in terms of their physiology and morphology. For instance, shade tolerance is associated with low light compensation point, low dark respiration rate, low nitrogen content per area and mass, low leaf clumping, high wood density, low root-shoot ratio, high leaf area ratio, or relatively long potential life spans (Valladares and Niinemets, 2008). As shade tolerance is related to many different traits while also being non stationary with ontogeny it does not refer to one absolute measure stable in space and time (Leuschner and Meier, 2018; Valladares et al., 2016). Additionally, shade tolerance is generally in trade-off with tolerance to other stress factors such as drought, waterlogging, or cold. Polytolerance to these stressors is therefore rare (Laanisto and Niinemets, 2015; Niinemets and Valladares, 2006; Pavanetto et al., 2023; Stahl et al., 2013). This may also be reflected in intraspecific variability in shade tolerance capacities. Climatic conditions may thus modulate how different populations of the same species typically respond to the light gradients (Wright et al., 1998).

Canopy accession strategies differ markedly between species across the shade tolerance spectrum. On one end of the spectrum, shade-intolerant species typically exhibit high mortality rates when growth is slow (e.g. in low light), implying that mainly only the fastest-growing individuals elude protracted periods of suppression and can compete for space in the dominant canopy (Kobe et al., 1995). For these species, fast early growth is thus crucial in generating and maintaining the size advantage over their competition during canopy ascension (Landis and Peart, 2005). Alternatively, more conservative resource allocation strategies enable shade-tolerant species to endure low light conditions for prolonged periods with minimal growth rates and consequently exhibit lower mortality rates (Lin et al., 2002; Wright et al., 2000). In temperate forests, for instance, shade-tolerant species may remain suppressed for more than 100 years (Martin-Benito et al., 2020; Trotsiuk et al., 2016). They generally also exhibit a greater growth response to an upsurge in light in low-light conditions compared to shade-intolerant species. Nonetheless, their maximum growth in high-light conditions is mostly outpaced by the shade-intolerant species (Kobe et al., 1995; Wright et al., 1998), which, by shorter passage times through smaller size classes, generally ascend to the canopy faster (Brienen and Zuidema, 2006). Shade-intolerant trees establish in canopy gaps more often, exhibiting comparatively fewer growth releases before accessing the canopy (Janda et al., 2021; Nagel et al., 2014). Alternatively, growth patterns of shade-tolerant species are often characterized by greater variability in time, whereby trees may exhibit multiple releases from suppression prior to canopy accession (Baker and Bunyavejchewin, 2006; Brienen and Zuidema, 2006; Di Filippo et al., 2017; Martin-Benito et al., 2020; Nagel et al., 2014; Wright et al., 2000).

3.3.3 Drivers of canopy accession

Canopy accession patterns are besides interspecific variability in shade tolerance also governed by environment. Disturbances regulate the understorey light availability in space and time and may thus also regulate the patterns of canopy accession (Feldmann et al., 2018; Lorimer and Frelich, 1989; Saulnier et al., 2020; Whitmore, 1989). More shade-intolerant species, for instance, need larger canopy openings with more light to establish than shade-tolerant species (e.g. Nagel et al., 2010; Petritan et al., 2007) and are therefore more abundant under conditions of more intense disturbance regimes (Janda et al., 2021; Martin-Benito et al., 2020). Next to disturbances, other environmental factors such as topography and climate can also control the patterns of canopy accession, particularly as shade tolerance depends on the availability of other resources spanning ecological gradients (Valladares and Niinemets, 2008). For example, trees of the same species tend to be less shade tolerant in a comparatively drier environment, whereby in moister conditions, juveniles exhibit longer suppressions, more and stronger releases, as well as a more variable pattern of canopy accession (Brienen et al., 2010). Similarly, light conditions and competition for light may change with rising elevation, as trees frequently have more open canopies in higher-elevation forests (Coomes and Allen, 2007a; Rajsnerová et al., 2015). Additionally, topography affects irradiance, temperature, and soil moisture, where north-facing slopes in the northern hemisphere receive less solar radiation than southern slopes (McCune and Keon, 2002), and are in turn colder, with comparatively higher soil moisture.

In addition, canopy accession patterns in closed-canopy forests are largely driven by tree plasticity in adjusting growth rates through prompt physiological, anatomical, and morphological adaptations to abrupt environmental shifts, particularly to novel canopy openings (Annighöfer, 2018; Annighöfer et al., 2017; Čater, 2021). These adaptations may, for instance, include leaves with thicker lamina, increased photoprotective compounds, new foliage with adjusted anatomical structure (Wyka et al., 2007), root mass fraction increase at the expense of leaf mass fraction, and increased investment in branch growth (Annighöfer, 2018). However, the growth reaction of a released tree is not dependent solely on the surge in the irradiance levels.

Forest microclimate, namely, is significantly different from climate beyond the canopy cover; whereby the canopy cover dampens temperature and humidity fluctuations beneath it by reducing wind speed and filtering sunlight (De Frenne et al., 2021; Thom et al., 2020; Zellweger et al., 2020). Released trees have to therefore cope with more pronounced seasonal and diurnal temperature extremes compared to suppressed and sheltered understory (Vinod et al., 2022), as well as with potentially increased water deficit (Izworska et al., 2022). Alternatively, intense competition for light of the understory trees and associated reduced availability of resources could thus result in higher sensitivity of suppressed trees to climatic stress (Rollinson et al., 2021). Canopy removal could thus also result in decreased competition for soil moisture, potentially benefitting the water availability of surviving trees (Schuster and Oberhuber, 2013).

Many slowly changing environmental variables affect long-term trends in tree growth that might be apparent on multiannual or multidecadal timescales only (Anderson-Teixeira et al., 2021). Next to shifting climate and disturbance regimes (Senf et al., 2019), rising atmospheric CO_2 concentrations (Walker et al., 2021), and pollutant depositions (Marchand et al., 2023; Solberg et al., 2009) are amongst drivers of tree growth change that have been documented to drive a long term response of tree growth. It is however less known to what degree growth releases might have shifted in the recent period and whether and how the response vigour of trees is changing.

Furthermore, the magnitude of the growth release may also be contingent on the size of the tree (Stan and Daniels, 2010), wherein tree growth (expressed in ring widths) generally increases with increasing crown size but starts to decrease after the ratio between crown projection size and tree volume peaks due to rising costs of nutrient and water conductivity (Mencuccini et al., 2005; Pretzsch, 2020). Particularly for shade-tolerant species, size is not always a good indicator of tree age (e.g. Issartel & Coiffard 2011; Di Filippo et al. 2012; Castagneri et al. 2013; Bigler 2016; Piovesan & Biondi 2020; Begović et al. 2022), the relationship between tree size and growth during a release might thus differ from the relationship between tree age and growth during a release. Besides the first few years, age does generally not exhibit strong control over tree growth (Mencuccini et al., 2007). Nonetheless, growth-size relationship is often not homologous to growth-age relationship even when size and age are closely correlated, whereby growth is more typically positively related to size and more negatively to age (Matsushita et al., 2015). Additionally, the age at the onset of a release is generally largely determined by the duration of the prior suppression period (Orwig and Abrams, 1994), whereby under conditions of resource limitation (such as in deep shade), the non-structural carbon reserves may decline in time, potentially decreasing the growth potential or ultimately causing tree death (Petrovska et al., 2021). Age at the onset of the release event could thus exhibit indirect control over the magnitude and duration of a growth release. However, our understanding of how understory individuals of different species respond to gradients of growth drivers following an abrupt increase in light remains incomplete. Analyses of growth releases in European temperate primary forests as an important element of tree canopy accession and forest resilience capacity were thus also incorporated into this thesis.

3.3.4 Canopy accession patterns and shade tolerance of dominant species in European temperate mountain forests

Of the four dominant species in European temperate mountain forests, beech and fir are recognized as highly shade tolerant amongst European tree species (Ellenberg et al., 1991). Maple and spruce are regarded as more intermediate, while Niinemets and Valladares (2006) rank the capacity of spruce closely behind fir and beech. Leuschner and Meier (2018) describe beech as a late-successional broadleaved tree, with minimum light demand of the adult trees lower than other focal species, comparable with fir only. They describe fir and spruce as late-successional conifers, while maple is described as a mid-successional broadleaved tree. In contrast with the other three species, maple is generally referred to as a gap specialist species (Petritan et al., 2009), with lower average survival times in the subcanopy in comparison to beech, for example (Petrovska et al., 2022). Lower shade tolerance of maple in comparison to beech or fir was also indicated in the study of Nagel et al. (2014), whereby maple was found to access the canopy primarily through gaps, exhibited fast growth rates, and had a lower ability to survive in the shade in contrast with beech or fir. Additionally, fir was found to exhibit longer periods of suppression and more suppression-release cycles on average than beech, implying it might be more shade tolerant. Nevertheless, beech and maple were found to generally exhibit superior acclimation to increased light levels in comparison to the two coniferous species, presumably due to annually changing foliage. Fir, in particular, is characterized by more slowly adapting assimilating apparatus (Čater, 2021).

3.4 PRIMARY FORESTS

3.4.1 Definitions and distribution of remaining primary forests in Europe

Lifetime tree development including growth patterns and longevity are confounded by various forest management practices (Di Filippo et al., 2017). The typical interventions may differ significantly between management systems, however, their applications steer forests to a range of states and pathways more or less divergent from their default states. This is generally achieved through implementing sets of silvicultural operations aiming to change one or several key variables such as tree species composition, stand density, age structure, stand edge structure, or other site attributes that shift the ecosystem dynamics (e.g. Aszalós et al., 2022; Bauhus et al., 2009; Duncker et al., 2012; Gamborg and Larsen, 2003; Matthews, 1989). Natural variability in progression through different life stages and potential longevity can thus only be adequately studied in forests where management practices have never impacted ecosystem dynamics or where the ecosystem has had sufficient time to recover (Nagel et al., 2014). There are various terms in the literature depicting such forest ecosystems, including primary, pristine, primeval, virgin, old-growth, or least-disturbed (e.g. Di Filippo et al., 2017; Vandekerkhove et al., 2022), which are, however, not all synonymous. In scope of this work I primarily refer to primary forests.

According to Food and Agriculture Organization of the United Nations, primary forests are naturally regenerated forest ecosystems of native tree species, where there are no apparent indications of human activities and ecological processes are not significantly disturbed (*Global Forest Resources Assessment 2020: Main report*, 2020). Human land use practices have significantly transformed Europe's landscapes from mid-Holocene onwards, including forests (Kaplan et al., 2009). Mainly due to deforestation and forest exploitation, a large majority of the primary forests have thus been altered (Kaplan et al., 2009; Sabatini et al., 2021, 2018). As a result, extant forests considered undisturbed by man present only 2.2% of the entire area of European forest ecosystems (FOREST EUROPE, 2020), whereby the known areas of primary forests are even smaller (0.7% of forest area in Europe), of which less than half are strictly protected (Sabatini et al., 2018). Some of these forests thus continued to have been logged even in recent times (e.g. Mikoláš et al., 2019; Potapov et al., 2017; Sabatini et al., 2021). Additionally, the remaining primary forests in Europe are mostly small, fragmented, and largely limited to remote mountainous areas and the boreal north. Primary remnants of many forest types are, therefore, exceptionally rare or do not exist in such form anymore (Mikoláš et al., 2019; Sabatini et al., 2018). It is also important to note that a comprehensive field-verified mapping of European primary forests has not yet been conducted, which further hinders protection of remaining fragments that have not yet been protected as predicted by the European Union Biodiversity Strategy for 2030 (Barredo et al., 2021; "EU biodiversity strategy for 2030 : bringing nature back into our lives," 2021; Hirschmugl et al., 2023).

3.4.2 Values and relevance of primary forests

Primary forests hold a multitude of values, including serving as some of the last remnants most closely representing the notion of wilderness and pristine landscapes on the continent (Schnitzler, 2014). They hold high biomass carbon densities, therefore, their conservation is paramount in mitigating carbon emissions to the atmosphere. Primary forests of the temperate zone studied here are particularly valuable in this regard, as due to relatively high rates of carbon sequestration and relatively slow decomposition rates, they may support exceptionally high carbon stocks (Keith et al., 2009; Ralhan et al., 2023). The absence of systematic biomass removal on these sites also allows accumulation of deadwood in the form of snags and coarse woody debris in a range of decay stages. Deadwood is besides storing carbon crucial in sustaining a large variety of native biodiversity (Garbarino et al., 2015; Sturtevant et al., 1997). Most notably, this influences saproxylic species, which directly or indirectly depend on presence of deadwood (Ferenčík et al., 2022; Kozák et al., 2021), nonetheless deadwood may also provide important resources for non-saproxylic taxa (Seibold et al., 2015). Alternatively, managed forests typically support significantly lower densities of both deadwood but also large-diameter trees, and are thus, in many cases, insufficient for supporting taxa dependent on mature forest conditions (Asbeck et al., 2022; Nagel et al., 2017a). Large old trees are another characteristic element of primary forests (Begović et al., 2023; Lindenmayer and Laurance, 2017). They are keystone ecological structures storing large amounts of carbon, and influencing abundance and distribution of conspecifics as well as numerous other species through habitat provision in addition to shaping the light environment and microclimate (Keith et al., 2010; Lindenmayer et al., 2014; Lindenmayer and Laurance, 2017). Furthermore, in these landscapes, trees of wide age and size ranges (ranging from seedlings to large and/or old trees) are distributed in diverse patterns of horizontal and vertical structures primarily governed by the history of local disturbances (Coomes and Allen, 2007b; Franklin et al., 2002; Meigs et al., 2017; Rodrigo et al., 2022). This is in contrast with the majority of managed forest landscapes in Europe, which are typically more homogenized in structure. Such structural homogeneity tends to diminish the habitat quality for many forest-dwelling species and weakens the resilience of these ecosystems to environmental perturbations (Aszalós et al., 2022).

3.5 DISTURBANCES

3.5.1 Definition, components, and relevance of disturbances

Disturbances are defined as more or less discrete events driven by biotic and/or abiotic drivers that modify the structure and function of an ecosystem at different spatial scales (Pickett and White, 1985). These events may vary markedly in intensity, severity, size, and frequency. Intensity generally refers to the physical energy released in the course of the event and is typically expressed per area and per time, whereas it refers to the agent and not the effect on the organism or on the ecosystem. Severity is closely related to intensity, whereby a more intense event is usually also more severe. However, the severity of a disturbance event expresses the extent of the impact on the organism in contrast with the released energy. The size of a disturbance event stands for the spatial extent of the impacted area, whereas disturbance frequency stands for the average (mean or median) number of disturbance events occurring at an average point of a specific time period (Turner et al., 1998). The long-term dynamics of disturbances in a particular ecosystem represent the disturbance regime of the respective region (Turner, 2010). Historical range in variation of a disturbance regime (Landres et al., 1999) is vital in shaping community structure and dynamics as it selects for the set of life history traits crucial in sustaining population viability through sufficient post-disturbance recovery (Johnstone et al., 2016; Turner and Seidl, 2023). Disturbance legacies may set the tone of forest structure and function dynamics even decades to centuries after the event takes place (Rodrigo et al., 2022; Turner, 2010). These legacies include material (individuals, seeds, residual matter) as well information (stored as spectrum of traits in the surviving individuals) (Johnstone et al., 2016). Post disturbance succession may differ markedly between areas affected by events of different spatial scales, severities and frequencies. For example, larger scale events characterized by higher severity may often drive colonization from surrounding habitats, create novel substrates and typically generate more variability in successional patterns compared to smaller events. Alternatively, succession after smaller disturbances is typically more predictable (Turner et al., 1998).

Disturbance regimes, however, change in response to shifting climatic drivers. In Europe, as in many other parts of Earth, intensifying trends in disturbance regimes have been reported on the continental scale, however, trends vary among regions (Altman et al., 2024; Seidl et al., 2017, 2014; Senf et al., 2018; Senf and Seidl, 2021a). To draw inferences about future vegetation feedback to modified disturbance regimes, comprehensive knowledge of the typical response of vegetation to historical disturbances is needed. This, in turn, demands quantification of the historical range of variation in disturbance regimes for a focal region.

3.5.2 Disturbance agents

Direct and subsequent legacy effects of disturbances caused by different agents may differ markedly. Namely, various agents may disproportionately alter different layers of forest ecosystems, that is the tree canopy layer, the understorey, and the soil (Roberts, 2004). The distribution of dominant disturbance agents is therefore a crucial element shaping the intra-biome or intra-landscape variability in disturbance activity (Seidl et al., 2020)

Fire, for example, typically occurs in two forms. Surface or cool fire may remove variable proportions of the forest understorey, but generally minimally alter the soil and do not damage the forest canopy layer. Alternatively, hot fires (burning in the understorey and in tree crowns), characteristically remove large portions of the understorey and may also remove variable portions of the forest overstorey. Hot fires generally also alter soil parameters more profoundly than cool fires. However, even the most severe forest fires in most cases leave a significant part of the soil organic layer unburnt. Herbivory (referring to browsing specifically) tends to have a similar effect as cool fires, whereby variable portions of the understorey may be consumed whilst the tree canopies and soil are generally directly unaffected. Floods, similarly to browsing or cool fires, generally have a variable effect on forest understorey, albeit with the exception of trees removed by the current, they typically do not remove portions of the forest overstorey (De Frenne, 2023; Roberts, 2004). Floods, however, have a profound impact on the forest floor and soil. Beyond causing material displacement, deposition, and erosion, the ensuing waterlogging plays a significant role in soil formation and tree growth (Camarero and Ortega-Martínez, 2021; Hupp and Osterkamp, 2013). Landslides in contrast with the previously listed agents, may by removing portions of soil to bedrock, completely alter all three layers of the forest ecosystems. However, they generally affect relatively smaller areas and are largely predisposed by topography. Droughts, on the other hand, may affect large landscapes simultaneously, killing a variable proportion of canopy trees and understorey vegetation in the process.

The last group of forest disturbance agents summarized here, represented by ice, snow, wind, pathogens, and gradations of insects, directly affects primarily the tree canopy layer, whereby the short-term effects on forest understorey and forest floor with soil are minimal (De Frenne, 2023; Roberts, 2004).

Winds causing disturbance and tree mortality may be caused by different atmospheric processes. They can be cyclone-induced or may alternatively be thunderstorm-related, whereby the relative importance of wind origin for disturbance regimes may be region-specific (Nagel et al., 2017b; Pettit et al., 2021). Winds generally cause disturbance by snapping or uprooting the canopy trees, at variable spatial scales and severities. Winds are a ubiquitous determinant of stand dynamics across temperate forests. However, the prevalence of wind-caused disturbances in forests and their impact may vary significantly between regions (Kulakowski et al., 2017).

Alternatively, pronounced insect outbreaks that cause widespread tree mortality are generally more related to landscapes with specific tree species particularly susceptible to attacks by certain leaf defoliators or bark beetles. The extent of these events is crucially linked with the species-specific population dynamics of the attacking insects, driven by many biotic and abiotic factors. For instance, tree host abundance and connectivity between tree hosts are often crucial (Biedermann et al., 2019). Next to that, insect gradations are largely dependent on weather conditions, which regulate survival and reproduction of these insects but may also affect the susceptibility of trees to attack (Hlásny et al., 2021; Marini et al., 2017). Trees may then be damaged and ultimately killed as a consequence of damage caused by the organisms feeding on their biomass. Affected trees may thus be left standing for protracted periods of time even after they die; however, their canopy buffering diminishes as soon as the dead foliage sheds.

Snow typically causes most damage when a lot of wet, heavy snow falls in late spring or autumn, when broadleaved species have their leaves. Under heavy loads of snow, trees may then get uprooted, though snapped or bent stems also commonly occur. Snow-related disturbances can also happen in the winter. Particularly, under conditions when wet snow freezes on branches, trees are due to additional load and increased drag more susceptible to wind damage (Nagel et al., 2017b).

Ice accumulation on trees may have similar effects as wet snow load, whereby trees may suffer minor to severe branch damage or may alternatively get snapped or uprooted (Roženbergar et al., 2020). Damage patterns, like those caused by several other disturbance agents, can vary significantly between events and across landscapes affected by a specific event. This variability is notably due to differences in ice accretion, as well as differences in susceptibility to damage among species and individuals of varying sizes (Klopcic et al., 2020). Besides the direct effect of these canopy disturbances which may remove portions of the dominant canopy, these events significantly enhance light availability in the understorey and disrupt the canopy buffering of microclimate (De Frenne, 2023). Additionally, these agents (wind, insect infestations, snow, and ice) can similarly as severe droughts affect large areas on the landscape scale (Nagel et al., 2017b). As canopy disturbance events driven primarily by ice, snow, wind, pathogens, and gradations of pests prevail in temperate mountain forests of Europe (Kulakowski et al., 2017; Nagel et al., 2017b), the focus of this thesis is primarily on the effects of these disturbances.

3.5.3 Disturbance regimes in temperate mountain forests of Central, East, and Southeast Europe

The disturbance patterns of the focal regions are generally well described in the literature. As in other temperate forests, mixed-severity disturbance regimes prevail in the forests of the Carpathians (Čada et al., 2020; Frankovič et al., 2020; Meigs et al., 2017; Svoboda et al., 2014; Trotsiuk et al., 2014) and the Balkan Peninsula (Nagel et al., 2017b, 2014), with disturbance events ranging from frequent tree fall gaps to less frequent events covering larger regions (up to several hundred square kilometers in case of ice storms). Windstorms and bark beetle (particularly *Ips typographus* L.) outbreaks are the main disturbance agents in higher-elevation spruce-dominated stands, while windstorms alongside heavy snow and ice storms (particularly in the Dinaric Mountains) are the main disturbance agents in the mixed beech stands.

The most severe events that may cause near-stand replacement on tens of hectares are generally caused by windstorms, bark beetle outbreaks, or a combination of different agents acting in succession (Čada et al., 2020; Frankovič et al., 2020; Kulakowski et al., 2017; Nagel et al., 2017b; Pettit et al., 2021; Synek et al., 2020). The return interval of such events may be very long (several centuries), making its precise quantification difficult. Ice storms and heavy snow may generally affect even larger areas of several hundred square kilometers, whereas they typically cause intermediate severity damage (Nagel et al., 2017b). Moderate-scale (>10 ha patch) and moderate severity (with 25-75% canopy area disturbed) events are also common, and account for more than half of the total disturbed area in some of the observed regions. Their return intervals, ranging from one to several centuries, are generally shorter than the life spans of the prevalent tree species (Čada et al., 2020; Frankovič et al., 2020; Nagel et al., 2017b). In contrast, studies from certain landscapes, such as the mid-elevation beech-dominated forests in the Ukrainian Carpathians, report that the processes and stand dynamics in the area were mostly driven by a small-scale disturbance regime and that events of moderate- and high-severity and spatial scale left only minimal traces on contemporary forest structure and species composition (Hobi et al., 2015).

Droughts were not considered a common mortality agent in the region in the past centuries. However, drier-than-average conditions have been shown to significantly correlate with higher canopy removal rates (Schurman et al., 2018). Furthermore, there are cases of reported beech, fir, and spruce mortality after pronounced periods of drought in the Dinaric mountains, which generally occurred after protracted periods of extremely low precipitation and very high temperatures even in areas with relatively high average annual precipitation (approaching 1900 mm). Additionally, drought spells can physiologically weaken trees, significantly increasing the susceptibility of stands to other agents, particularly secondary pests like bark beetles in coniferous forests (Nagel et al., 2017b). In the following period these growing populations of bark beetles may then further infest even the trees and parts of stands in the proximity of initially stressed trees that were not significantly affected by the initial drought (Korolyova et al., 2022). Similarly, as drought-induced mortality, wildfires are generally rare in most temperate mountain forest of Central, Eastern, and Southeastern Europe. Nevertheless, certain forest types are importantly shaped by fire, such as pine-dominated forest types in the Dinaric Alps or in the mountain ranges of Bulgaria (Nagel et al., 2017b; Panayotov et al., 2017). In Bulgarian mountains, fires are relatively common even in the spruce-dominated forests, where the size of affected forest stands may range up to several thousand hectares (Panayotov et al., 2017). Fire events are relatively uncommon in the mixed-beech and beech-dominated stands in the focal region (Lestienne et al., 2023; Nagel et al., 2017b). Additionally, it has been demonstrated that the pronounced historical recruitment of beech and decline in spruce in eastern Carpathians coincides with a pronounced drop in fire frequency around 4000 years before present (Lestienne et al., 2023). Besides fires caused by different human activities, lightnings are considered the predominant natural cause for fires (Nagel et al., 2017b).

3.5.4Projected trends in disturbance regimes governing European forests

Disturbance caused by many agents such as fire, wind, drought, pest and pathogen outbreaks, or floods are forced by climate. A shift in disturbance activity with changing climate is thus inevitable (Seidl et al., 2020). Disturbances could change in their frequency, severities, as well as size, potentially changing the forest structure and function. For instance, more frequent and more severe disturbances would likely lead to younger and more open forest landscapes (McDowell et al., 2020). Additionally, disturbance regime shifts may also result in tree species composition shifts (Liang et al., 2023) However, these changes are unlikely to be universal across space and time.

The natural disturbance impacts significantly increased in the last decades around Europe, whereby mortality caused by various biotic factors exhibited the fastest rate of increase (Patacca et al., 2023). Additionally, several trends of future forest disturbance regimes have been projected at the continental scale. In case of warmer and wetter conditions, disturbances caused by wind and pathogens are likely to increase while warmer and drier conditions are likely to drive a rise in drought events, fire, and insect-related disturbance activity (Seidl et al., 2017), whereby particularly conditions warmer and drier than average were in the past consistently associated with elevated disturbance activity in temperate forests (Schurman et al., 2018; Seidl et al., 2020; Sommerfeld et al., 2018). In contrast with disturbances caused by most other agents, disturbances from ice and snow are more likely to decrease under warmer conditions as the temperatures increase (Seidl et al., 2017).

European forests were found to be widely resilient to past disturbances. Namely, the areas where the disturbance rate exceeds the rate of forest recovery were reported to present solely 6% of the total forest cover (Seidl and Turner, 2022). However, further intensification in disturbance regimes coupled with an intensification of other environmental stress agents could have significant negative effects on the forest resilience capacity (Saulnier et al., 2020; Senf and Seidl, 2021b). Increasing disturbance activity could also lead to alternative pathways of post-disturbance reorganization, where either the structure, composition, or both fail to recover and instead shift (Seidl and Turner, 2022). The rate, timing, and place of these changes, is however linked to a lot of uncertainty (Turner and Seidl, 2023)

3.6 DENDROCHRONOLOGY AND DENDROECOLOGY

Woody species in areas of pronounced seasonality, such as in mid to high latitudes, but also in tropics and subtropics where dry and wet seasons regularly change, form distinct annual growth rings, commonly referred to as tree rings in the case of trees (Rathgeber et al., 2016; Speer, 2010). Since many intrinsic and extrinsic factors drive plant growth, the sequences of these annual rings (i.e. ring series) are unique archives that may serve as a proxy for the environment (such as climate, competition, or disturbances) and internal factors (such as ontogenetic or genetic factors) that determine the radial growth of a particular individual. Dendrochronology is a discipline that most notably uses the woody tissue of species with annually resolved radial growth rings to mark time and record environmental variability (Baillie, 1992; Bräker, 2002; Speer, 2012). The origins of dendrochronology date back at least to the times of Ancient Greece and the suggestion of Theophrastus (in 322 B.C.) that trees develop growth rings (Studhalter, 1956). Dendrochronology, however, established itself as an independent scientific discipline relatively recently, particularly from the early 1900s onward, when several principles, concepts, and procedures that continue to frame dendrochronological approaches today were introduced (Douglass, 1941, 1909).

The most prominent principle of dendrochronology is the cross-dating principle, which assumes that tree ring sequences from individuals governed by the same growth drivers will generally exhibit a common pattern over time. This principle is applied in the procedure of cross-dating which uses the variability in tree ring series to determine the exact year of each ring's development (Douglass, 1941; Fritts and Swetnam, 1989). Namely, under conditions of limited energy supply, such as under low light intensity due to competitive suppression, certain species may partially or fully cessate their secondary growth, whereby only partial growth rings are formed, or rings are fully absent in certain years (e.g. Bormann, 2016; Yasuda et al., 2018). Simple ring counts are, thus often not sufficient to date ring chronologies reliably. The cross-dating principle is linked to the limiting factor principle, which, based on Liebig's law of the minimum, states that growth (i.e. tree ring parameter variability) is regulated primarily by the most limiting factor. These are connected to further concepts and principles, such as the principle of uniformitarianism, the principle of aggregate tree growth model, the concept of autocorrelation, the concept of ecological amplitude, the principle of replication, and the concept of standardization which are the basis for most of the dendrochronological research, regardless of the addressed questions (Fritts and Swetnam, 1989; Speer, 2012). Using dendrochronological approaches has, due to wide applicability, branched out to a variety of fields, including archaeology, climatology, geomorphology, hydrology, and ecology (Bräker, 2002; McCarroll and Loader, 2022). Within ecology, dendrochronological techniques can be used to describe a multitude of different ecological phenomena, whereby the field at the intersection of ecology and dendrochronology is commonly referred to as dendroecology (Fritts and Swetnam, 1989).

Dendrochronology presents an effective set of tools to reconstruct tree life history traits such as life spans and radial growth patterns as well as their potential drivers, even for individuals that might have established several centuries or even millennia ago (e.g. Castagneri et al., 2013; Nagel et al., 2014; Piovesan et al., 2019a; Schulman, 1954). Using these techniques, consequently largely expands possibilities for tracking lifetime growth patterns of trees compared to repeated census methods (Bakker et al., 1996). Additionally, analyses of tree rings combined with instrumental environmental data (such as climate or atmospheric deposition data) may reveal much about the ecological niches of tree species and their populations, as well as how tree growth responds to shifts in driving factors (Anderson-Teixeira et al., 2021; Babst et al., 2019; Buechling et al., 2017; Marchand et al., 2023; Schurman et al., 2019).

Furthermore, tree ring series can also be used to date and reconstruct disturbance histories at different scales. This can, for instance, be achieved by dating apparent marks in tree ring sequences such as fire scars in case of low fires (Abrams et al., 1998; Mcewan et al., 2014) or rockfall scars (Stoffel and Perret, 2006). Next to that, disturbances can also be reconstructed in forests where disturbances may not leave traceable scars on the surviving trees but may affect their growth patterns, such as driving sustained growth decreases in response to outbreaks of leaf defoliators (Speer et al., 2001) or distinct juvenile growth patterns related to canopy opening creation (Lorimer and Frelich, 1989). Techniques to reconstruct past canopy dynamics can most notably be applied in closed-canopy forests where trees may either establish in the canopy openings or under suppression, whereby suppressed conditions are reflected in suppressed radial growth. Since trees can attain the dominant canopy either through continuous rapid growth after establishing in tree fall gaps or through one or more competitive releases leading to abrupt growth increases, disturbance histories can be reconstructed by analyzing the spatial and temporal synchronicity of these two individual growth patterns across a population (Fraver and White, 2005; Frelich and Lorimer, 1991; Lorimer and Frelich, 1989).

These techniques do not enable to distinguish between different agents causing specific disturbance events in the past. Given that disturbance events caused by agents such as wind, insect outbreaks, ice, snow, or a combination of these can vary widely in severity and scale, it is impossible to identify the specific agent responsible for a particular disturbance event using only dendroecological methods for reconstruction. However, reconstructions of canopy cover dynamics, regardless of the agent causing it, may still be of great value, particularly as the proportion of removed canopy is likely more important for growth of surviving trees following a disturbance event. Dendroecology thus also presents tools to investigate interactions between tree development and disturbances. Nevertheless, tree growth and carbon sequestration are highly complex processes, whereas the interplay of several environmental and internal drivers with temporally variable effects may obfuscate insights into processes discerned from tree ring patterns (Anderson-Teixeira et al., 2021).

4. METHODS

In this chapter, research design, data collection approaches, and utilized methods of data analyses applied in all the constituent parts of this thesis are described. First, in section *4.1 Study area and general approaches used across studies*, I outline the research areas and core procedures of data collection, data processing, and data preparation common across all three sub-topics. In sections *4.2 Tree life span in temperate primary forests of Europe*, *4.3 Canopy accession across temperate primary forests of Europe*, and *4.4 Growth rates and durations of growth releases of beech and spruce and their drivers* the approaches used in separate studies are described. Each of these studies was aimed at addressing one of the specific objectives listed in chapter *2. Aims and objectives*.

4.1 STUDY AREA AND GENERAL APPROACHES USED ACROSS STUDIES

4.1.1 Study region

This work was based specifically on European temperate primary forests. A large majority of extant remnants of primary forest in the European temperate zone is limited to the mountainous regions of Central, Eastern, and Southeastern regions of the continent (Sabatini et al., 2021, 2018), where past direct impacts of human land use were absent or at least minimal. More specifically, the study sites are located across the ranges of the Carpathians (in Slovakia, Ukraine, and Romania), Dinarides (in Croatia, Bosnia and Herzegovina, and Albania), and the Balkan Mountains in Bulgaria.

Lower and mid-elevation forest stands across the whole study region are dominated by European beech with a variable admixture of other broadleaves such as sycamore maple, Norway maple (*Acer platanoides* L.), European ash (*Fraxinus excelsior* L.), Scots elm (*Ulmus glabra* Huds.), Bosnian maple (*Acer obtusatum* Waldst. et Kit. ex Willd.) and manna ash (*Fraxinus ornus* L.) in the Dinaric mountains as well as several other minor species. Above 800-900 m in elevation, silver fir and Norway spruce are common and, in many study sites, significant in admixture alongside several other broadleaved species listed earlier. In the Carpathians, above around 1200 m, forests are dominated by spruce with a minor admixture of fir, stone pine (*Pinus cembra* L.), rowan (*Sorbus aucuparia* L.), and European larch (*Larix decidua* Mill.), as well as other sporadically present species. Some of the highest research plots are at around 1700 m in elevation, whereas forest stands there are still relatively dense and can be considered as closed-canopy. High-elevation sparser forests close to the timberline were thus not included.

Carpathian Mountains are the second most extensive mountain system in Europe covering more than 200 000 km^2 and span eight countries: Austria, Czech Republic, Slovakia, Poland, Hungary, Ukraine, Romania, and Serbia. The Carpathians harbor the largest share and the most extensive remnants of primary forests in temperate Europe (Kameniar et al., 2023; Mikoláš et al., 2019; Sabatini et al., 2018), with majority of the sites located in Slovakia, Poland, Ukraine, and Romania. The sites span a relatively high elevational gradient from approximately 600-1700 m above sea level and also cover a diverse geological gradient spanning between various types of sedimentary and metamorphous bedrock (Begović et al., 2023). The annual precipitation values range from around 600 mm at low elevations to around 2400 mm at the highest peaks in High Tatra Mountains in Slovakia, but in most sites it ranges from 900-1200 mm. Average annual temperatures range from 13˚C at lower elevations to around 0.5˚C at the highest elevations (Saulnier et al., 2020; Schurman et al., 2024).

Dinarides are the most extensive mountainous area on the Balkan Peninsula spanning from the Julian Alps in the north along the east coast of the Adriatic Sea to Šar and Korab massif. They span across the borders of eight countries: Italy, Slovenia, Croatia, Bosnia and Herzegovina, Montenegro, Serbia, Kosovo, and Albania. It is a relatively young mountain range, built mostly of limestone and dolomite deposits. Much of the surface is characterized by rugged karst terrain, which likely contributed to the absence of substantial direct human impacts in many remote, higher-elevation sites. Dinarides are located between temperate continental and Mediterranean climate zones, whereby the high elevation sites receive relatively high amounts of average annual rainfall between 2000-3000 mm, at an average annual temperature 2-6˚C (Begović et al., 2020).

Balkan mountain range is located in the southeast of the Balkan Peninsula from Bulgarian-Serbian border in the west to Black Sea in the east. Similarly as in Carpathians, bedrock is rather diverse. Comparable to the Carpathians and the Dinarides, beech-dominated forests prevail in mid-elevation zones, while the share of conifers is greater at higher elevation. Due to steep and inaccessible terrain many sites remained unmanaged. Relatively large remnants of well-preserved forests can thus still be located in the Balkan Mountains, particularly so in the Central Balkan National Park. The sites included in our study are beech-dominated with a minor admixture of fir. The average annual precipitation of these sites is around 700 mm, and the average annual temperature is around 8˚C (Table S4).

Most of the included sites are formally protected (in scope of national parks, natural parks, forest reserves, whereby many of the beech sites are also listed as UNESCO World Heritage sites among "Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe"). There are many formal definitions of primary forests alongside the use of several other terms describing forests with high naturalness. Here, primary forests are referred to as forest ecosystems with no signs of direct human impact, and where forest structure and composition are primarily driven by natural disturbances. Notably, these forests do not necessarily have to be in the old-growth development stage (Kozák et al., 2018; Mikoláš et al., 2019). The sites used for ultimate data collection were located and verified in multiple steps. Available prior inventories of primary forest (Veen et al., 2010), historical maps, archival data, and help from local experts were first used to locate the potential study sites. The sites were then further surveyed on the field for various indicators of forest naturalness, such as natural species composition, pit and mound microtopography, presence of large trees, diverse age, horizontal, and vertical structures, as well as presence of coarse woody debris in various stages of decay. Forests with signs of past logging activity, previously grazed sites, or sites in vicinity of grazed sites (ca. 500 m) were subsequently avoided (Kozák et al., 2018; Mikoláš et al., 2019)

4.1.2 Data collection approaches

All three studies use different subsets of data collected within the REMOTE Primary Forests research network (https://www.remoteforests.org). Further information on specific subsets of plots included in each of the three studies is provided in sections *4.2.1*, *4.2.2*, *4.3.1*, and *4.4.1*. REMOTE (REsearch on MOuntain TEmperate primary forests) is a long-term dendroecological forest inventory project, aiming to monitor select extant primary forests of temperate Europe in both protected and isolated unprotected areas (Schurman et al., 2024) The network of circular permanent sampling plots (PSPs) was established between 2010-2019, with the sampling protocols undergoing slight changes over time.

Plots were randomly located within a regular grid laid over each stand. The grid size was 1-2 ha in higher elevation spruce forests in Carpathians and 10 ha in mixed beech forests. In the older surveys, 500 m^2 or 1000 m^2 plots were randomly located in the interior of every cell (0.25 or 0.5 ha) in spruce forests, where up to 25 released living individuals were cored for further dendrochronological analyses. Five additional suppressed trees were cored to establish the open canopy recruitment threshold.

From 2014 onwards, nested plots (1500 m^2 or 2000 m^2) were set up in the mixed beech forests. A point was randomly generated in the 0.5-3.4 ha interior of each grid cell, and a pair of nested research plots was set up on both sides along the contour line, with plot centers 80 m apart (Figure 1). In 2014, all living trees with DBH (diameter at breast height) ≥ 10 cm were cored in the inner 200 m^2 circle on all the plots, while all released trees with DBH ≥ 10 cm, all suppressed trees with DBH ≥ 15 cm, and three randomly selected suppressed trees with DBH between 10 and 15 cm were cored on the remaining part of the 1000 m^2 circle on the 2000 m^2 plots. Additionally, up to 12 released trees with DBH ≥ 10 cm were cored within the outside 2000 m^2 circle alongside all the trees with DBH ≥ 60 cm. From 2015 onwards, all living trees with DBH ≥ 10 cm were cored in the inner 200 m^2 circle on the 1500 m^2 plots. All the trees with DBH ≥ 20 cm plus 25% of randomly selected released trees with DBH between 10 and 20 cm were cored outside the 200 m^2 plot in the second 1000 m^2 circle. In the outermost circle inside the 1500 m^2 all the trees with DBH ≥ 60 cm were cored.

All the tree cores were taken perpendicularly to the slope contour line and cored approximately 1 m from the ground to avoid reaction wood. The DBH of all the trees ≥ 10 cm was measured alongside their relative position to the plot center. Additionally, the crown projection areas of 5-15 trees on the plot, later used in disturbance parameter calculations, were documented. Tree species and canopy status (suppressed or released; trees were considered to be released when their crowns were forming the top canopy layer and receiving ≥ 50% of full light) were also recorded.

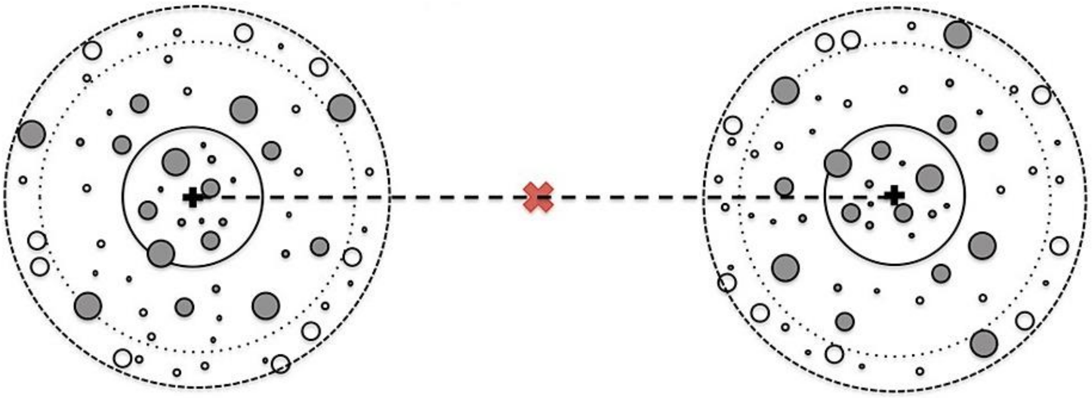

Figure 1. Example of the nested plot structure in mixed forests. The red cross represents the randomly generated navigation point used to locate the pair of circular sample plots. The plot center is 40 m away from the navigation point.

4.1.3 Tree ring processing

All increment cores (each representing a single tree) were air-dried, glued on wooden boards, and sanded with progressively finer grit sanding paper or microtome-surfaced using steel microtome blades until the tree rings were clearly discernable. Ring-width series were measured using a Lintab sliding-stage measuring system coupled with TSAP-Win software (Rinntech, Heidelberg, Germany; http://www.rinntech.de) and cross-dated using marker years (Yamaguchi, 1991) and correlation analysis with CDendro software (Larsson, 2015). For all the tree ring series with a missing pith, the number of missing rings and distance to the center was estimated depending on the curvature and growth rates of the innermost rings (Duncan, 1989).

4.1.4 Disturbance history reconstructions

Radial growth patterns of increment cores were analyzed for evidence of past disturbance events within each plot. Quantitative reconstructions of disturbance histories for different regions of the larger dataset used here have been published previously (Čada et al., 2020; Frankovič et al., 2020; Janda et al., 2019, 2017; Meigs et al., 2017; Nagel et al., 2017b; Schurman et al., 2019, 2018; Standovár and Kenderes, 2003; Svoboda et al., 2014; Trotsiuk et al., 2014), and provide detailed descriptions of dendroecological methods. We therefore only briefly summarize the methods used to reconstruct disturbance below. We used the original approach of Lorimer and Frelich (1989), in which each core is screened for (1) abrupt, sustained increases in radial growth (i.e releases) and (2) rapid early growth rates (i.e. gap-recruited trees), both of which provide indirect evidence of mortality of a former canopy tree. Following Lorimer and Frelich (1989), we only included release events before trees reached a diameter threshold, such that only mortality events that provided access to the canopy were counted. The diameter threshold was based on comparisons of diameters of currently suppressed versus released trees in the plot data. Multiple releases were allowed as long as they occurred before the diameter threshold. The severity of disturbance was based on the relative canopy area removed on each plot calculated from the current crown area of trees containing evidence of past disturbance; this approach makes the assumption that the sum of the current crown areas of such trees is representative of the proportion of the plot disturbed in the past (Lorimer and Frelich, 1989). Further details of calculating specific parameters used in the three studies are described in sections: *4.2.3 Data analysis*, *4.3.2.1 Tree ring analysis*, and *4.4.3 Growth release detection and disturbance severity calculations*.

4.2 TREE LIFE SPAN IN TEMPERATE PRIMARY FORESTS OF EUROPE

4.2.1 Study area and site selection

This study was conducted in primary temperate mountain forests of the Carpathian Mountains and the Balkan Peninsula, spanning from beech-dominated and mixed forests (hereafter referred to as beech-dominated) at lower elevations to spruce-dominated forests at higher elevations. These two regions contain the largest remnants of primary forests in the temperate zone of Europe (Sabatini et al., 2018, Janda et al., 2019; Mikoláš et al., 2019; Nagel et al., 2014). Primary forests were characterized as unmanaged forests with natural stand composition, diverse horizontal, vertical, and age structure, and a significant amount and diversity of downed and standing dead trees in different stages of decomposition; most stands were typically in an old-growth stage of development, but early seral stages developing after more severe natural disturbances were also present in these primary forest sites (Mikoláš et al., 2019). The dataset used for this study is a part of the REMOTE network (for more details see www.remoteforests.org), which is focused on surveying remaining tracts of primary forest landscapes in Europe and long-term study of their dynamics. The plot network has a hierarchical sampling scheme, with plots located within stands, and multiple stands organized in larger landscapes. For the purposes of this study, we split the dataset into 11 landscapes, based on geographic location and forest type. They include seven beech-dominated landscapes (i.e. Albania, Bulgaria, Croatia, Central Slovakia beech, Eastern Slovakia beech, Northern Romania beech, and Southern Romania beech) and four spruce-dominated landscapes (i.e. Central Slovakia spruce, Ukraine spruce, Northern Romania spruce, and Southern Romania spruce). The landscapes comprise a total of 35 spruce-dominated stands, and 33 beech-dominated stands (Figure 2; Table S1.)

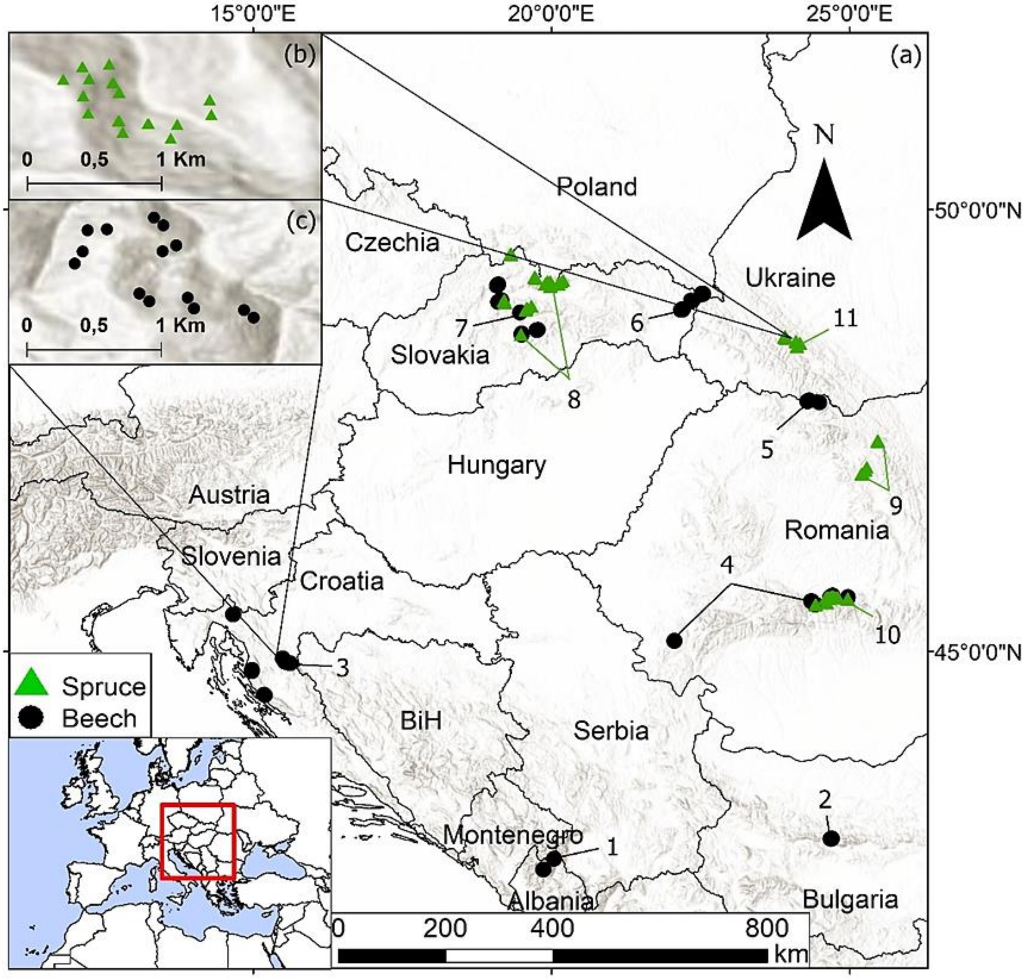

Figure 2. The hierarchical design and spatial distribution of study plots. The map shows the distribution of spruce stands and beech-dominated stands across the study region (a), including insets of plot locations within (b) spruce and (c) beech-dominated stands. The numbers mark the forest landscapes: 1 – Albania, 2 – Bulgaria, 3 – Croatia, 4 – South Romania beech, 5 – North Romania beech, 6 – East Slovakia, 7 – Central Slovakia beech, 8 – Central Slovakia spruce, 9 – North Romania spruce, 10 – South Romania spruce, and 11 – Ukraine

Norway spruce comprised 99% of all trees in spruce-dominated stands, and was occasionally mixed with fir, *Pinus cembra*, and *Sorbus aucuparia*. In beech-dominated stands, beech accounted for 75% of all trees on average, followed by fir (14%), spruce (7%), and maple (2%); other less common species were sporadically present, such as *Acer platanoides*, *Acer obtusatum*, *Ulmus glabra*, *Fraxinus excelsior*, and *Fraxinus ornus*.

4.2.2 Data collection

Data was collected between 2010–2018, in a network of circular permanent sampling plots established within each primary forest stand (Table S1). A more detailed description of the field sampling protocol is described in section 4.1.2 Data collection approaches. Ultimately, analyses included data from 437 beech plots and 534 spruce plots. In beech stands, a mean of 33.9 increment cores/plot was collected, and in spruce stands, a mean of 24.1 increment cores/plot. Data from 13 plots affected by recent stand-replacing disturbances were excluded from further analyses.

4.2.3 Data analysis

In total, 20,600 increment cores were processed using standard dendrochronological procedures. Each tree was represented by a single core. A more detailed description of the applied approaches is described in section 4.3 Tree ring processing. All cores that had more than 20 estimated rings missing or were of poor quality and therefore did not allow tree rings to be measured and crossdated reliably were excluded. In total, 3500 cores were omitted from further analyses (320 fir, 74 maple, 2790 beech, and 316 spruce cores), which resulted in a decrease in the overall mean diameter of cored trees for each species (from 31.4 cm to 28.0 cm for fir, 37.1 cm to 34.4 cm for maple, 36.4 mm to 31.6 cm for beech, and 36.6 cm to 36.4 cm for spruce).

Disturbance histories were reconstructed based on approaches described in section 4.1.4 Disturbance history reconstructions. Disturbance parameters and lifetime growth patterns of trees were then used to derive several variables that may influence longevity. These included the timing and severity (i.e. percent plot canopy area killed) of the reconstructed maximum severity disturbance event on each plot (Meigs et al., 2017) (hereafter referred to as disturbance severity and disturbance year), as well as the number of release events per core. To assess the influence of growth rates on longevity, we used the average growth rate of the first 50 years following Bigler (2016) (hereafter referred to as early growth). As such, we excluded all cores that had less than 50 rings measured or estimated. We also included metrics of the minimum and maximum 10-year average growth periods for each tree ring series following Orwig and Abrams (1994) (hereafter referred to as minimum and maximum growth), as well as the number of releases detected throughout the series.

Several different environmental variables were also compiled to test their influence of longevity. Raw values of slope steepness for each plot were used, while values of slope aspect were transformed into northness following the formula: northness = cosine [(aspect in degrees * π)/180)] (Janda et al., 2019). To avoid problems with multicollinearity, altitude was excluded because it was strongly correlated with temperature ($r = -0.752$). Mean temperature of the vegetation season for each plot was calculated for the period from the 1st of May until the 31st of October, by downscaling the Worldclim gridded data (Fick and Hijmans, 2017) for the period 1970–2000; this was done by building a linear model of temperature versus the product of altitude, longitude, and latitude. Given that we use the 1970-2000 period, which is likely not representative of the temperatures experienced during early life stages of old trees, our temperature variable is more of an index of relative temperature across the study region. Finally, there are several broad-scale differences between the Balkan and Carpathian study sites that may influence tree growth and longevity, including higher annual precipitation and temperature in the Balkan region, as well as differences in bedrock (Kozák et al., 2018); raw values of latitude for each plot were therefore included to further explore if there are differences in life span across the region.

To estimate life span within a species, we simply use the 90^{th} percentile of age distributions for each species from pooled data across the entire study (Nagel et al., 2014). To compare life span among species, we used a negative binomial generalized linear mixed model (GLMM) with the ages of trees ≥ the species-specific 90th percentile (hereafter referred to as the oldest trees) as the response variable and species as the explanatory variable. A four-level random effects structure was applied to account for the potential effects of geographical variability: a plot nested within a pair of plots (in beech-dominated regions), a pair of plots nested within a stand, and a stand nested within a landscape. Wald tests were performed to assess statistical significance. We used Tukey pairwise comparisons to test for differences among individual species.

To identify the most influential drivers of life span, a binomial GLMM was fit for each species. To facilitate interpretation, the 90^{th} percentile ages were converted to a binary variable, such that the age status of a given tree age was either ≥ species-specific 90th percentile or < species-specific 90th percentile. Age status was used as a response variable and disturbance history, growth rate, and environmental variables were included as fixed effects. In the spruce GLMM, forest type (spruce or beech-dominated) was used as an additional fixed factor that may cause potential differences in longevity of spruce growing in these two forest types. The mean values and ranges of all the variables included in these models are listed per species in Appendix S3. In the maple model, some variables were strongly correlated (i.e. early growth with maximum and minimum growth, latitude with the average temperature of the vegetation season, and disturbance year with disturbance severity). To avoid multicollinearity issues, we assembled a simpler model excluding disturbance year, early growth, number of releases, and latitude from the model. None of the final models showed problems associated with multicollinearity (all variance inflation factors were < 3.00) (Zuur et al., 2009). We used the same random-effects structure as described above. We calculated marginal determination coefficients (R^2_m) and conditional determination coefficients (R^2_c) for each GLMM to assess the relative contribution of fixed effects and all effects, respectively (Nakagawa et al., 2017).

All the analyses were performed in R language version 3.5.1 (R Core Team, 2019) using the following libraries: 'glmmTMB' (Brooks et al., 2017) to run the models, 'car' (Fox and Weisberg, 2019) for analysis-of-variance calculation, 'emmeans' (Lenth, 2019) to perform Tukey pairwise comparisons, 'DHARMa' (Hartig, 2020) to perform residual diagnostics, 'performance' (Lüdecke et al., 2020) to calculate VIF values, 'MuMIn' (Barton, 2019) to calculate the determination coefficients, and 'ggplot2' (Wickham, 2016) for plotting.

4.3 CANOPY ACCESSION ACROSS TEMPERATE PRIMARY FORESTS OF EUROPE

4.3.1 Study area and data collection

The data for this study were collected in primary forests of the Carpathian mountains and the Balkan Peninsula (Figure 3), where the most extensive tracts of European primary temperate forests are found (Sabatini et al. 2018, 2021; Mikoláš et al. 2019). Primary forest sites were unmanaged with diverse horizontal, vertical, and age structures, containing significant amounts of standing and downed deadwood in different decomposition stages. The majority of the studied stands were in an old-growth stage of development, with stands in early seral stages developing after natural disturbances also present (Mikoláš et al., 2019). The study sites span from mixed and beech-dominated forests (hereafter “mixed beech forests”) to spruce-dominated forests (hereafter “spruce forests”) at higher elevations. Norway spruce was a highly dominant species in the spruce forests ($\overline{\text{BA}}$ (basal area) = 95%), with sporadically admixed fir, stone pine (*Pinus cembra* L.), and rowan (*Sorbus aucuparia* L.). Beech was the most prevalent species in most of the mixed beech stands ($\overline{\text{BA}}$ = 74%), followed by fir ($\overline{\text{BA}}$ = 16%), spruce ($\overline{\text{BA}}$ = 5%), and maple ($\overline{\text{BA}}$ = 4%); other less common species such as Norway maple (*Acer platanoides* L.), Bosnian maple (*Acer obtusatum* Waldst. et Kit. ex Willd.), Scots elm (*Ulmus glabra* Huds.), and European ash (*Fraxinus excelsior* L.) were sporadically present.

The disturbance regime across the study region is complex, ranging from frequent tree fall gaps to rare stand-replacing disturbances covering tens to hundreds of hectares with return intervals of several centuries (Čada et al., 2020; Frankovič et al., 2020; Meigs et al., 2017; Nagel et al., 2017b). The regime includes a number of different disturbance agents, such as wind from summer and winter storms, bark beetle outbreaks in spruce-dominated stands, ice storms, and heavy snow (Čada et al., 2016; Frankovič et al., 2020; Nagel et al., 2017b; Pettit et al., 2021).

The extensive dataset used in this study is a part of the REMOTE network (for further information, see www.remoteforests.org) of sampling plots, aiming to study the long-term dynamics of European primary forests. The sampling design is hierarchical, with multiple plots within a stand. For this study, we used data from 488 plots from 38 mixed beech stands and 405 plots from 33 spruce stands collected between 2011-2019 (Table S4). On each circular plot, we recorded dendrometric and ecological information of all trees $\geq$ 10 cm DBH and collected increment core samples from a subsample of living trees. A more detailed description of data collection protocols can be found in the introductory section *4.1.2 Field sampling methods*.

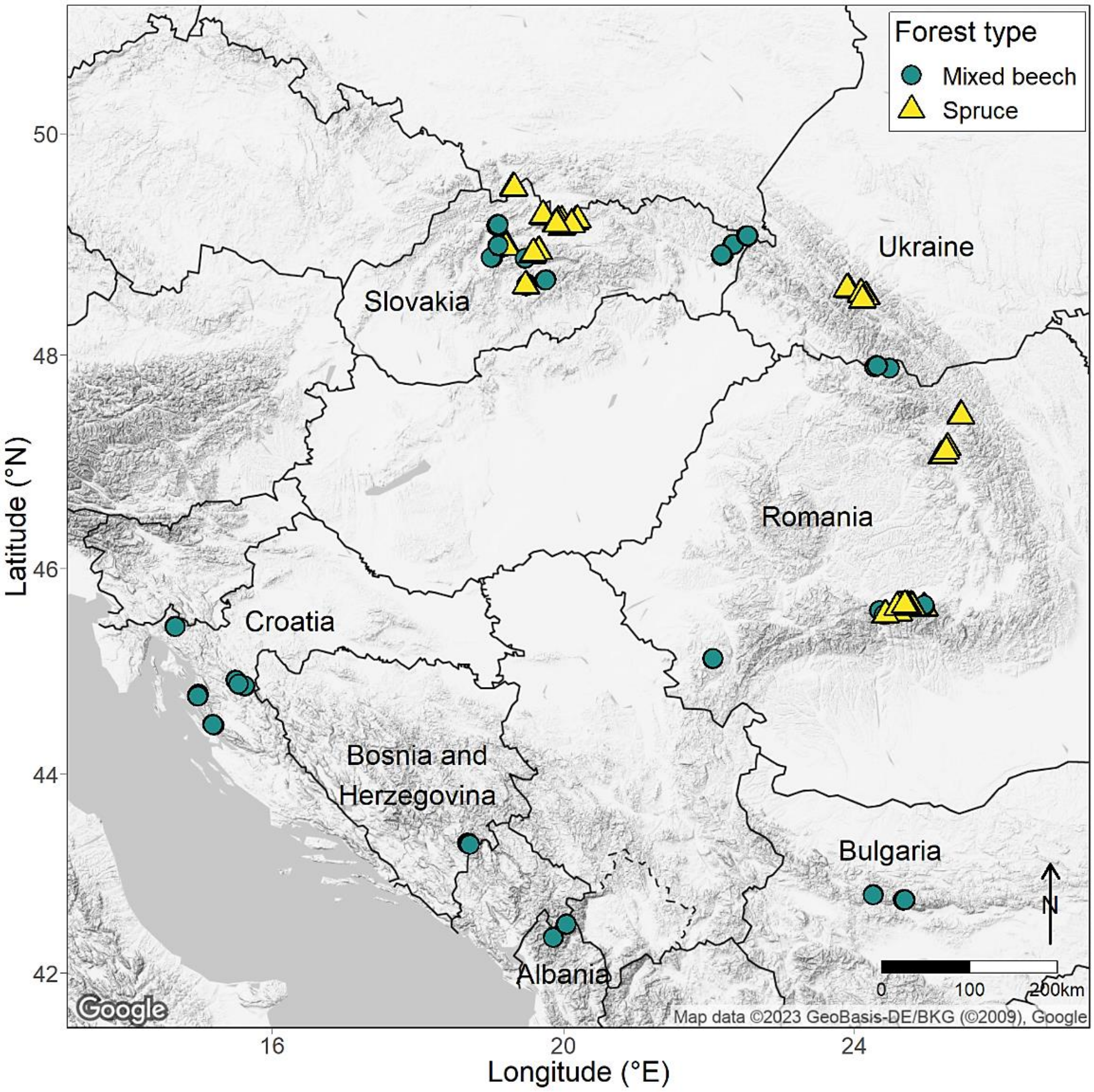

Figure 3. Distribution of mixed beech and spruce stands across the study region

4.3.2 Data analysis

4.3.2.1 Tree ring analysis

Increment cores were processed using standard approaches described in the section 4.3 Tree ring processing. All the samples with more than 30 missing rings or that missed the pith by more than 30 mm were excluded. In total, we used 15405 increment cores (each from a unique tree).

Increment cores were screened for distinct growth patterns characterizing tree's accession to the canopy, such as rapid early growth or release events following periods of suppression. The approaches described here have been applied on smaller subsets of the REMOTE dataset (e.g. Trotsiuk et al. 2014; Frankovič et al. 2020; Janda et al. 2019; Čada et al. 2020). To identify rapid early growth (i.e. establishment in open canopy conditions), we first derived species-specific rapid growth thresholds (Table S5). The thresholds were calculated as optimal cut-points denoting the average annual growth rates from age 5 to 14 years between trees suppressed beneath the forest canopy and the trees located in canopy openings (Lorimer and Frelich, 1989), based on minimising the absolute difference of specificity and sensitivity. Trees with an early growth rate that attained or surpassed the species-specific threshold were considered to have established in the open canopy.

Similarly, we also defined a canopy accession DBH threshold (DBHc) which indicated when trees reached the canopy. The DBHc was calculated as the optimal cut-point separating trees of different canopy status (suppressed or released) based on their DBH measured from the plot census data (Čada et al., 2020; Schurman et al., 2018). The canopy accession DBH threshold was calculated at 251 mm (Table S5).

The absolute increase method was used to identify periods of growth release, indicating formation of a canopy opening above previously suppressed trees (Fraver and White, 2005). First, 10-year running means of radial growth were compiled throughout all chronologies. The growth release events were then identified as continuous events when the difference between two successive 10-year running means (absolute increase) was above or equal to 1.25 standard deviations from the mean difference. To avoid including short term growth fluctuations likely induced by drivers other than canopy disturbance, growth releases were considered only for events that lasted at least seven years (Čada et al., 2020; Fraver et al., 2009; Schurman et al., 2018). Multiple release events were allowed as long as they occurred before attaining the canopy (DBHc).

Using the information on early growth rates and releases, we categorized the trees that attained DBHc into the following canopy accession modes: 1) Open canopy recruited trees, no subsequent release (all the trees that did not exhibit any releases), 2) Open canopy recruited trees, subsequently suppressed and released, 3) Initially suppressed, subsequently released trees. For all trees that attained DBHc we also calculated time needed to reach the canopy (DBHc). DBH was then reconstructed for every growth ring throughout each tree ring series to extract tree age at DBHc. The double sum of tree ring widths was corrected for the potential discrepancy with the measured DBH. The reconstructed DBH was therefore derived as:

$$DBHrj = 2 \times \sum_{i=1}^{j} rw_i \times \left(\frac{DBHf}{2 \times \sum_{i=1}^{n} rw_i} \right) \tag{1}$$

where $DBHr_j$ is the reconstructed DBH at tree ring j, rw_i is the ring width of i-th ring, $DBHf$ is the field-measured DBH, and n is the outermost ring. Time to reach the canopy was defined as tree age when $DBHr_j$ attained or surpassed DBHc. The number of releases was calculated as the sum of all the release events detected before the tree reached DBHc to reflect the number of suppression-release cycles. For all trees of non-open canopy origin that were subsequently released, we also calculated the time to first release as quantification of initial suppression. The first year corresponding to the first tree ring on each core was considered the start of the suppression period, while the last year before the onset of the first release event was considered as the end of the initial suppression period. For the analyses considering canopy accession modes, time to reach the canopy, and the number of releases, only trees with the DBH ≥ DBHc were included. To compare growth potentials between the species, we extracted the average growth rates of the 10-year running mean minimum (hereafter "minimum growth"), and 10-year running mean maximum ring width growth (hereafter "maximum growth"), as well as 10-year running mean minimum basal area increment (hereafter "minimum BAI") and 10-year running mean maximum basal area increment (hereafter "maximum BAI") before trees attained DBHc. Minimum and maximum growth values were corrected for potential discrepancies between the field measured DBH and the double sum of tree ring widths by the same factor as in the calculation of $DBHr_j$.

To investigate the drivers of growth metrics before trees access the canopy, we used the reconstructed canopy disturbance history (i.e. chronologies of proportions of plot canopy area disturbed) as a proxy for historical changes in plot level light conditions. Disturbance histories based on regional subsets of the presented dataset have been published previously (Čada et al., 2020; Frankovič et al., 2020; Janda et al., 2019, 2017; Kameniar et al., 2023; Schurman et al., 2018; Svoboda et al., 2014; Trotsiuk et al., 2014) (see also Section *4.1.4 Disturbance history reconstruction*).

Following the original method of Lorimer and Frelich (1989), tree-level evidence of disturbance, namely abrupt growth rate increases (growth releases) and fast initial growth rates (open canopy establishment), indicating recent mortality of a canopy tree, was converted to canopy area disturbed. Under the assumption that the contemporary crown sizes of canopy trees are representative of the share of the plot disturbed in the past

(Lorimer and Frelich, 1989), the disturbance severity was derived as the proportion of the canopy removed in a certain period based on the contemporary canopy sizes of the trees carrying the disturbance signal. The crown width of each tree was based on the relationship between the DBHs and the measured crown areas. Linear mixed models were employed to predict the current crown areas of broadleaves ($R^2_c = 0.692$, $R^2_m = 0.544$, RMSE = 1.642 m) and conifers ($R^2_c = 0.718$, $R^2_m = 0.516$, RMSE = 0.888 m) separately. Tree canopy areas were then coupled to the year of the release events. To account for variations in tree core availability, each plot was resampled by compiling 1000 subsamples of size m = 12 (a minimum common number of available tree records per plot).

The proportion of canopy area disturbed on each plot for each subsample was calculated for each year as a sum of the current crown areas of the reacting trees (exhibiting a growth release or open canopy recruitment) divided by the total crown area of all the sampled trees. The average of all subsamples calculated at annual resolution then represented the plot level chronology. Due to the potentially prolonged disturbance impacts and non-instantaneous growth response, the plot-level disturbance histories were smoothed with a kernel density function to lessen the uncertainty in the disturbance peak detection. We calculated the density for the 30-year moving window with a bandwidth of five. Peaks of smoothed values were then identified as the years with the maximum proportion of canopy removed, for which the curve was ascending for at least five years before the peak. The severity of a particular event was then calculated as a sum of the canopy area removed between five years before and after the peak (Fraver and White, 2005). We only included the events with at least 10% of the canopy removed.

The identified historical plot-level disturbance events were then used to extract several disturbance variables potentially influencing canopy accession. In short, we used plot-level disturbance histories to extract the maximum disturbance severity occurring between ten years before the first ring in a given tree ring series and the year of canopy accession, as well as the timing of this event for each tree (expressed in years after the ten years before the initial growth ring of a tree). A 10-year extension of the focal period was considered to include the early development period before trees attained the coring height (i.e. 1 m) and were likely affected by local disturbances. As potential drivers of the number of suppression-release cycles, we calculated the cumulative disturbance severity of all the events above 10% of canopy removal (hereafter “cumulative disturbance severity”) for the period between ten years before the first ring in the chronology and the year of canopy accession. We additionally calculated the number of such disturbance events before the canopy was attained.

4.3.2.2 Environmental variables

Since attaining the canopy is a long-term process that may surpass the temporal coverage of reliable and available climate data, the de Martonne aridity index (dMI) (de Martonne, 1926; Pellicone et al., 2019) was used to account for the climatic variability between study sites. The dMI was calculated based on yearly temperature averages and precipitation totals obtained from a gridded CRU-TS4.04 dataset, with a 0.5° spatial resolution (Harris et al., 2020), for the period of 1901 until one year before the field survey for each plot (2010-2018) in the dataset:

$$dMI = \frac{P}{T + 10} \tag{2}$$

where P is the annual precipitation and T is the annual average temperature on the plot. The average value for the entire period was then calculated and used in subsequent modelling. The values ranged from 36.31-89.77, with higher values signifying more humid conditions (Table S3).

To account for the effects of topography-associated variability in potential irradiance levels, we calculated the potential annual direct incident radiation (PDIR) for each plot, using equation 3 as presented in McCune and Keon (2002):

$$PDIR = 0.339 + 0.808 \times \cos(L)\cos(S) - 0.196 \times \sin(L)\sin(S) + 0.607 \times \cos(A)\sin(S) \tag{3}$$

where $PDIR$ is potential direct incident radiation in MJ $\mathrm{cm}^{-2}\ \mathrm{yr}^{-1}$, L is latitude, S is slope, and A is the folded aspect (folded about the north-south line with values ranging from 0-180°). The values ranged from 0.33-1.01 MJ $\mathrm{cm}^{-2}\ \mathrm{yr}^{-1}$ (Table S6).

4.3.2.3 Statistical analysis

To compare canopy accession growth patterns among the focal species, as well as between the two forest types including spruce, we first compiled a series of generalized linear mixed models (GLMMs). These models were thus linked with objectives a) and b). We used the single metrics (canopy accession modes, time to first release, time to reach DBHc (i.e. time to reach the canopy), and the number of releases) as the response variables in the respective models, with species identity (beech, fir, maple, spruce from mixed beech forests, and spruce from spruce forests) as the explanatory variable. Canopy accession modes were converted to a binary variable where all the open canopy established trees with no subsequent releases (assigned 1) were distinguished from trees that exhibited growth release(s) (assigned 0); we used a Bernoulli GLMM with the binary canopy accession variable as the response. We applied negative binomial GLMMs with the time to first release, time to reach DBHc, and the number of releases response variables. Gamma GLMMs with a log link were applied to model growth potentials prior to canopy accession (minimum growth, maximum growth, minimum BAI, and maximum BAI, respectively). A nested random effect structure reflecting the sampling design and potential geographic variability was also applied, with plots nested within a stand. A series of Wald χ^2 tests was used to evaluate the statistical significance of fixed-effect parameters in GLMMs (Bolker et al., 2009). After significant overall tests ($p < 0.05$), pairwise comparisons among individual levels of fixed effects were performed using Tukey-type adjusted p-values (Hothorn et al., 2008).

We were able to reconstruct the disturbance histories for the entire canopy accession period for a subset of trees only, which we applied to the second series of GLMMs fit to examine the potential drivers of radial growth patterns before canopy accession. This series of models was thus linked with objective c). Canopy accession modes, time to first release, time to reach DBHc, and the number of release events were used as response variables. Species, dMI, and PDIR were used as explanatory variables in all four models. The severity of the maximum event and its timing were additional explanatory variables in the models with canopy accession mode, duration of the initial suppression, and time to reach DBHc as response variables, while we used the cumulative disturbance severity and the number of disturbance events as additional explanatory variables in the model with number of release events as the response variable (Table S3). All the numerical explanatory variables were centered and scaled prior to fitting the models. We used the same error distribution families and random effect structure as in the models with the same response variable described above. Final models did not show any signs of multicollinearity between the covariates (all VIF values < 2; Zuur et al. 2009). To assess the relative importance of fixed and fixed with random effects in the models, marginal (R^2_m) and conditional (R^2_c) determination coefficients were calculated for all four models (Nakagawa et al., 2017).

4.3.3 R libraries

The analyses were performed in R version 4.0.4 (R Core Team, 2021) using the following libraries: cutpointr (Thiele and Hirschfeld, 2021) for calculating optimal cutpoints of early growth and DBHc thresholds, glmmTMB (Brooks et al., 2017) for statistical modeling, car (Fox and Weisberg, 2019) for ANOVA calculations, emmeans (Lenth, 2022) for calculating pairwise comparisons, DHARMa (Hartig, 2021) to inspect residual diagnostics, performance (Lüdecke et al., 2020) for VIF values and determination coefficients calculations, as well as ggplot2 (Wickham, 2016), ggmap (Kahle and Wickham, 2013), visreg (Breheny and Burchett, 2017), cowplot (Wilke, 2020), and viridis (Garnier et al., 2021) for plotting.

4.4 GROWTH RATES AND DURATIONS OF GROWTH RELEASES OF BEECH AND SPRUCE AND THEIR DRIVERS

4.4.1 Study area and field sampling

We conducted the study using an extensive network of circular permanent sampling plots (hereafter referred to as PSPs) set up across primary temperate mountain forests across Carpathians, spanning portions of Slovakia, Ukraine, and Romania (Figure 4). The primary forests were considered as forests without apparent direct human impacts, with diverse vertical, horizontal, and age structures, and characterized by significant abundance and diversity of downed and standing deadwood in different decomposition stages (Mikoláš et al., 2019). The study area ranges from lower-elevation mixed and beech-dominated forests in the montane zone to higher-elevation spruce-dominated forests in the subalpine zone. European beech is the most prevalent species of mixed and beech-dominated forests with a variable admixture of mainly silver fir (*Abies alba* Mill.), sycamore maple (*Acer pseudoplatanus* L.), and Norway spruce. Norway spruce is the prevailing species in spruce-dominated forests, with a minor admixture of other species, most notably rowan (*Sorbus aucuparia* L.), beech, silver fir, sycamore maple, and stone pine (*Pinus cembra* L.).

The PSPs are a part of the REMOTE network (www.remoteforests.org) of research plots, placed along various environmental gradients and aimed at surveying the long-term development of European primary temperate forests. The sampling design of the network is hierarchical, with PSPs nested within stands. Altogether 297 plots were set up in 23 mixed beech stands and 544 plots in 38 spruce stands. For all the trees ≥ 10 cm diameter at breast height (DBH) within the plots basic ecological and dendrometric data were documented. Additionally, core samples were collected from a subset of living trees. More than 5300 beech cores from mixed beech forests and more than 11800 spruce cores from spruce dominated forests were collected ultimately. Further details of field sampling procedures are described in the introductory section *4.1.2 Field sampling methods*.

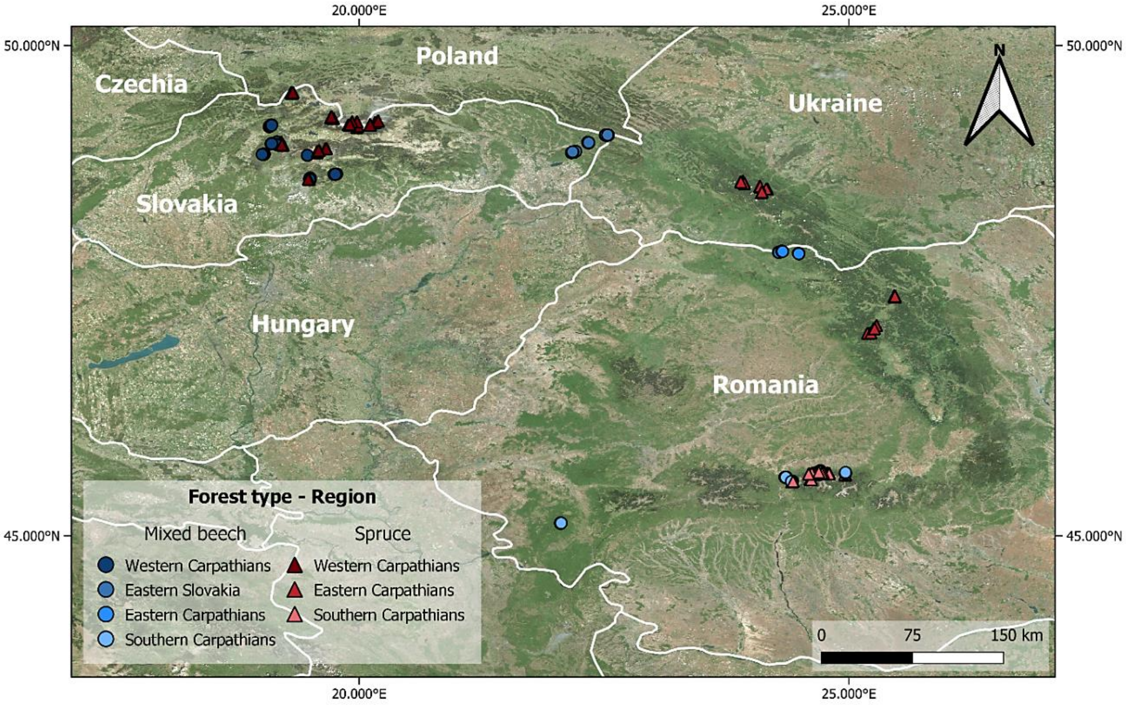

Figure 4. Spatial distribution of study stands. The distribution of mixed-beech (blue circles) and spruce (red triangles) stands across the study area.

4.4.2 Tree ring data preparation

17110 (5305 beech and 11805 spruce) increment cores representing individual trees were processed using standard procedures listed in the section 4.3 Tree ring processing. We further excluded the samples with more than 30 missing rings or those that missed the pith by more than 30 mm.

4.4.3 Growth release detection and disturbance severity calculations

To detect the periods of growth release the absolute increase method was implemented (Fraver and White, 2005), whereby mean 10-year radial growth prior to year n is iteratively compared to mean 10-year radial growth following year n. The release event was then identified as the years when the difference between the following 10-year mean increment and the preceding 10-year mean increment was equal to or exceeded the 1.25 times the standard deviation of the growth differences from the whole dataset. The threshold was species-specific. Events that were identified as releases had to sustain increased growth for at least seven consecutive years in order to avoid inclusion of any short-term fluctuations that happened as result of processes other than canopy release (Fraver et al., 2009), and the release period was considered to continue as far as the following 10-year mean increment was higher than the 10-year mean increment preceding the release onset. A canopy accession DBH threshold was further calculated to exclude all the growth increases that happened after the tree had attained the canopy already. The threshold was calculated as the optimal cutpoint distinguishing between the suppressed and released trees based on their field measured DBH (Čada et al., 2020), minimizing the absolute difference of sensitivity and specificity. The canopy accession threshold was determined at 251 mm (sensitivity = 0.92, specificity = 0.92, AUC = 0.98). Multiple release events per core were then allowed as long as they occurred before attaining the canopy accession DBH threshold. Mean value of tree ring widths during the identified periods of growth release with the onset after 1900 was then calculated for further analyses of the growth rates during growth releases.

Additionally, tree ring series were screened for patterns of rapid early growth indicating an open canopy recruitment for subsequent canopy disturbance history reconstruction. The approach was similar to calculating the canopy accession DBH threshold. The thresholds were calculated as optimal cutpoints distinguishing 10-year growth rate averages between age 5 to 14 years of suppressed trees from trees sampled in canopy openings (Lorimer and Frelich, 1989). Trees were then considered to have established in the open canopy if they attained or surpassed the species-specific threshold, otherwise they were considered to have established under suppression.

Plot-level disturbance histories were derived based on tree-level evidence of disturbance (growth releases and open canopy recruitment), indicating a recent mortality of a canopy tree, which was converted to disturbed canopy area (Lorimer and Frelich, 1989). The procedures applied here have been used on subsets of the REMOTE database before (Čada et al., 2020; Frankovič et al., 2020; Kameniar et al., 2023; Schurman et al., 2018; Svoboda et al., 2014; Trotsiuk et al., 2014) (See also Section *4.1.4 Disturbance history reconstruction*). The severity of the specific disturbance event was based on the current canopy sizes of trees with growth release or open canopy recruitment signal. The underlying assumption of the approach is that the current crown sizes of canopy trees are representative of the share of the plot canopy disturbed in the past (Lorimer and Frelich, 1989). The relationship between the DBHs and measured crown widths served to derive the crown area of all trees. Two linear mixed models were applied to predict the crown areas of broadlaves ($R^2_m = 0.544$, $R^2_c = 0.692$, RMSE = 1.642 m) and conifers ($R^2_m = 0.516$, $R^2_c = 0.718$, RMSE = 0.888 m). The derived canopy areas were then linked to the year of the release event. Plots were resampled by 1000 subsamples of size m = 8 (equal to maximum common number of available tree records per plot). Further the tree-level disturbance signals were summed for each year and converted to proportion of disturbed canopy area on the plot for each year in each subsample. Plot-level chronology was then calculated as the average of all the subsamples for each plot at an annual resolution. Plot-level disturbance histories were smoothed with kernel density function (30-year moving window with a bandwidth of five) to minimize the uncertainty of peak detection. Peaks were then identified for the years with the maximum proportion of removed canopy, for which the curve trend was positive for at least five years before the peak. We only considered events with severity ≥ 10%. Each specific release was linked to the nearest plot-level disturbance event and releases within ± 15 years from the peak year were considered contributing.

4.4.4 Climate data

The CRU TS4.05 (0.5°) gridded monthly climate data (mean temperatures and precipitation sums) (Harris et al., 2020) covering the period 1901-2020 was used in this study. We extracted both monthly mean temperature and precipitation datasets of 15 grid points covering the sampling areas.

For analyzing the growth release drivers average annual temperatures were calculated for the duration of each identified release event based on the data derived from the grid point closest to the PSP of the respective tree. To account for variability in joint effects of precipitation and temperature, average value of Ellenberg quotient (EQ) was additionally calculated for the duration of each identified release following the formula as defined in Ellenberg (1988):

$$EQ = Tjul \times 1000/Pan \tag{4}$$

EQ stands for Ellenberg quotient [°C*1000/mm], Tjul stands for average temperature in July [˚C], and Pan stands for average annual precipitation [mm].

4.4.5 Potential irradiance

Topographical features are an important determinant of potential irradiance. To factor in the topography-related differences and associated differences in potential irradiance, we computed potential direct incident radiation (PDIR) for each plot, using Eq. 3 as demonstrated in McCune & Keon (2002). For the formula applied and the variables used in the calculation refer to description in *4.3.3.2 Environmental variables*.

4.4.6 Analyses of growth release drivers

642 releases from 611 beech trees and 916 releases from 902 spruce trees starting after 1900 were ultimately analysed (Table S9). A series of generalized linear mixed models (GLMMs) was applied to analyze potential drivers of average growth increments during growth releases and their durations for beech and spruce, respectively. Disturbance severity, average annual temperature during release event, average EQ during release event, PDIR, cambial age at the release onset, DBH at release onset, and prior growth were used in the models as explanatory variables, while in the average growth models calendar year at release onset was included as an additional predictor to study potential temporal trends in average growth during releases (Figure 5). Calendar year was not included in the release duration models due to exclusion of all the unfinished release events from the analyses and their seemingly dropping duration at the end of the focal time period, and thus avoiding potentially spuriously derived trends. Gamma GLLMs with log link were used to model average growth during releases while GLMMs with negative binomial error distribution were applied to model duration of release events. As a single tree can exhibit multiple releases, tree identifier was included in the random effect structure of all the models, nested within a plot which was nested within a stand. Due to high correlation between average annual temperature and EQ for both beech ($r(640) = .933$, $p < .001$) and spruce data ($r(914) = .832$, $p < .001$), and moderate correlation between age at release onset and DBH at release onset for beech ($r(640) = .584$, $p < .001$) and spruce data ($r(914) = .639$, $p < .001$), separate sets of models were

run with either average annual temperature during release event or EQ and age at release onset or DBH at release onset alongside the variables listed earlier. All the explanatory variables were centered and scaled prior to model fitting. Signs of multicollinearity were not apparent in any of the models with all VIF values <2 (Zuur et al., 2009). Models were subsequently ranked based on Akaike Information Criterion (AIC) values, whereby the most parsimonious among the candidate models for both response variables and both species was identified as the model with the lowest AIC. The final beech average growth model assumed the following formula:

$$\begin{aligned}\mathrm{Incr_{mean}} = {} & \beta_0 + \beta_1 \times (\text{Disturbance severity}) + \beta_2 \times (\text{EQ}) + \beta_3 \times (\text{PDIR}) + \beta_4 \times (\text{DBH}) + \\ & + \beta_5 \times (\text{Calendar year}) + \mathrm{b}(\text{Stand ID/Plot ID/Tree ID}) + \epsilon \end{aligned} \tag{5}$$

$\mathrm{Incr_{mean}}$ stands for response variable depicting average radial increment during release, β_0 is the intercept, β_1 to β_5 are the coefficients of the explanatory variables, b(Stand/Plot ID/Tree ID) represents the nested random intercepts for stand ID, plot ID, and tree ID, whereas ϵ represents the error term. Age at release onset was included in the final spruce average growth model instead of DBH at release onset. The final duration models for both species assumed a similar structure whereby the calendar year at release onset was not included in the models. Marginal (R^2_m) and conditional (R^2_c) determination coefficients were further calculated for all models following Nakagawa et al. 2017. Additionally, as indicators of the contribution of individual variables in the models, semipartial R^2_m values were calculated based on commonality analysis (Ray-Mukherjee et al., 2014).

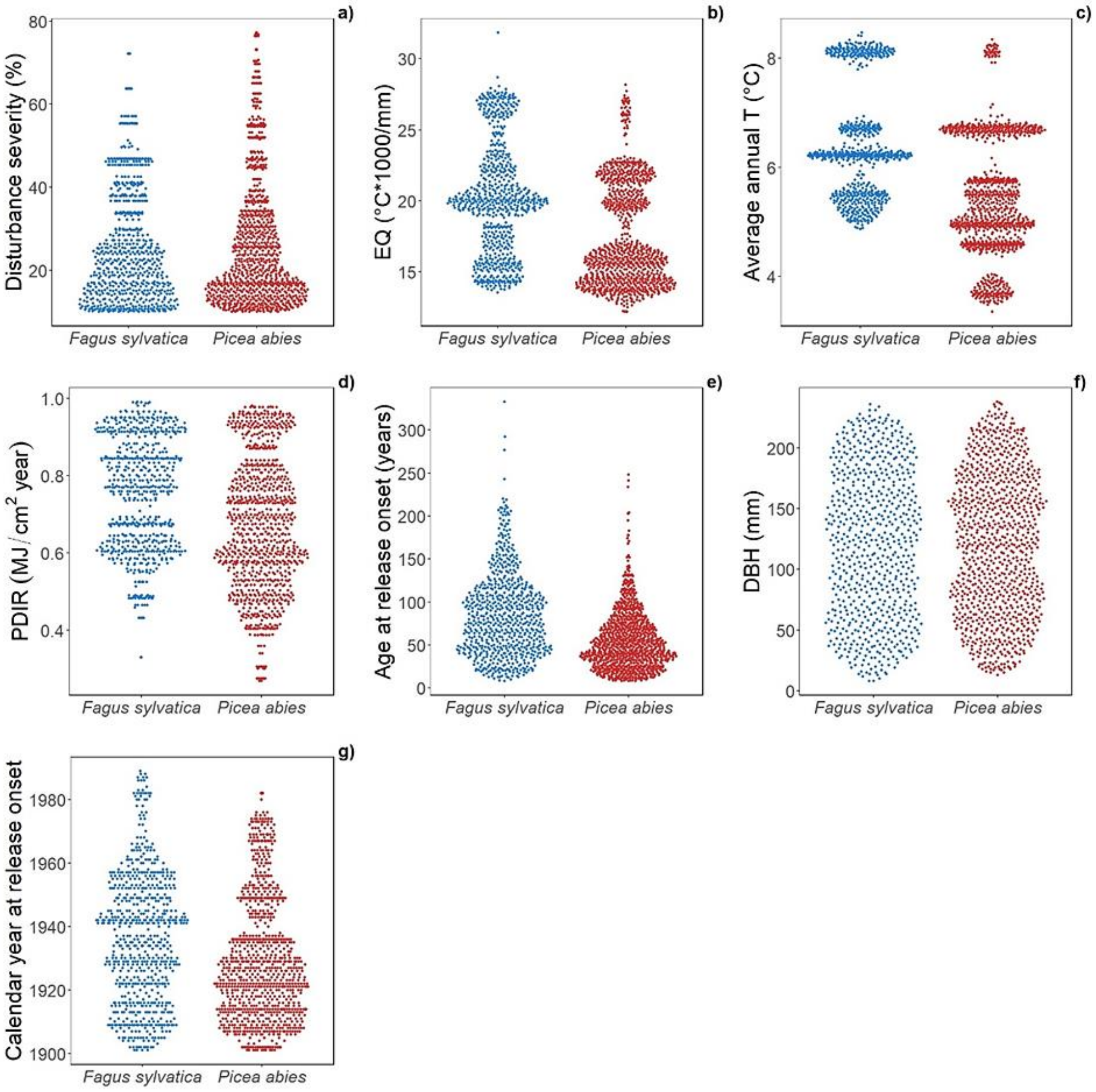

Figure 5. Distribution of identified releases across variables used in the mixed models: disturbance severity (a), Ellenberg quotient (b), average annual temperature during release (c), Potential direct incident radiation (d), age at release onset (e), DBH at release onset (f), and calendar year at release onset (g) for beech and spruce, respectively. The small colored dots represent individual release events.

All the analyses were performed in R version 4.0.4 (R Core Team, 2021) using glmmTMB (Brooks et al., 2017) for statistical modeling, DHARMa (Hartig, 2021) for inspection of residual diagnostics, performance (Lüdecke et al., 2020) for calculations of VIF values, MuMIn (Barton, 2019) for calculations of determination coefficients, as well as effects (Fox and Weisberg, 2018), ggplot2 (Wickham, 2016), and cowplot (Wilke, 2020) for creating the figures.

5. RESULTS

Similar to sections *4.2*, *4.3*, and *4.4* in the methods chapter, sections *5.1 Tree life span in temperate primary forests of Europe,* 5*.2. Canopy accession across temperate primary forests of Europe*, and *5.3 Growth rates and durations of growth releases of beech and spruce and their drivers* are each focused at addressing one of the specific objectives listed in the *2. Aims and objectives*. The results presented in *5.1* follow from methodological procedures described in *4.2*, results in *5.2* follow from procedures disseminated in *4.3*, while results in *5.3* are associated with the approaches listed in *4.4*.

5.1 TREE LIFE SPAN IN TEMPERATE PRIMARY FORESTS OF EUROPE

5.1.1 Interspecific differences in life span

The ages of the oldest trees decreased from beech (291 – 578 years), silver fir (218 – 456 years), spruce (218 – 449 years), to maple (192 – 412 years) (Figure 6, S1). The GLMM showed significant differences in mean age of the oldest individuals among the four tree species ($\chi^2 = 280.41$, $p < 0.001$). The oldest beech trees were significantly older than all the other three species. The oldest fir trees were significantly older than spruce trees, while the differences between the oldest maple and spruce trees, and maple and fir trees, were not statistically significant (Appendix S3).

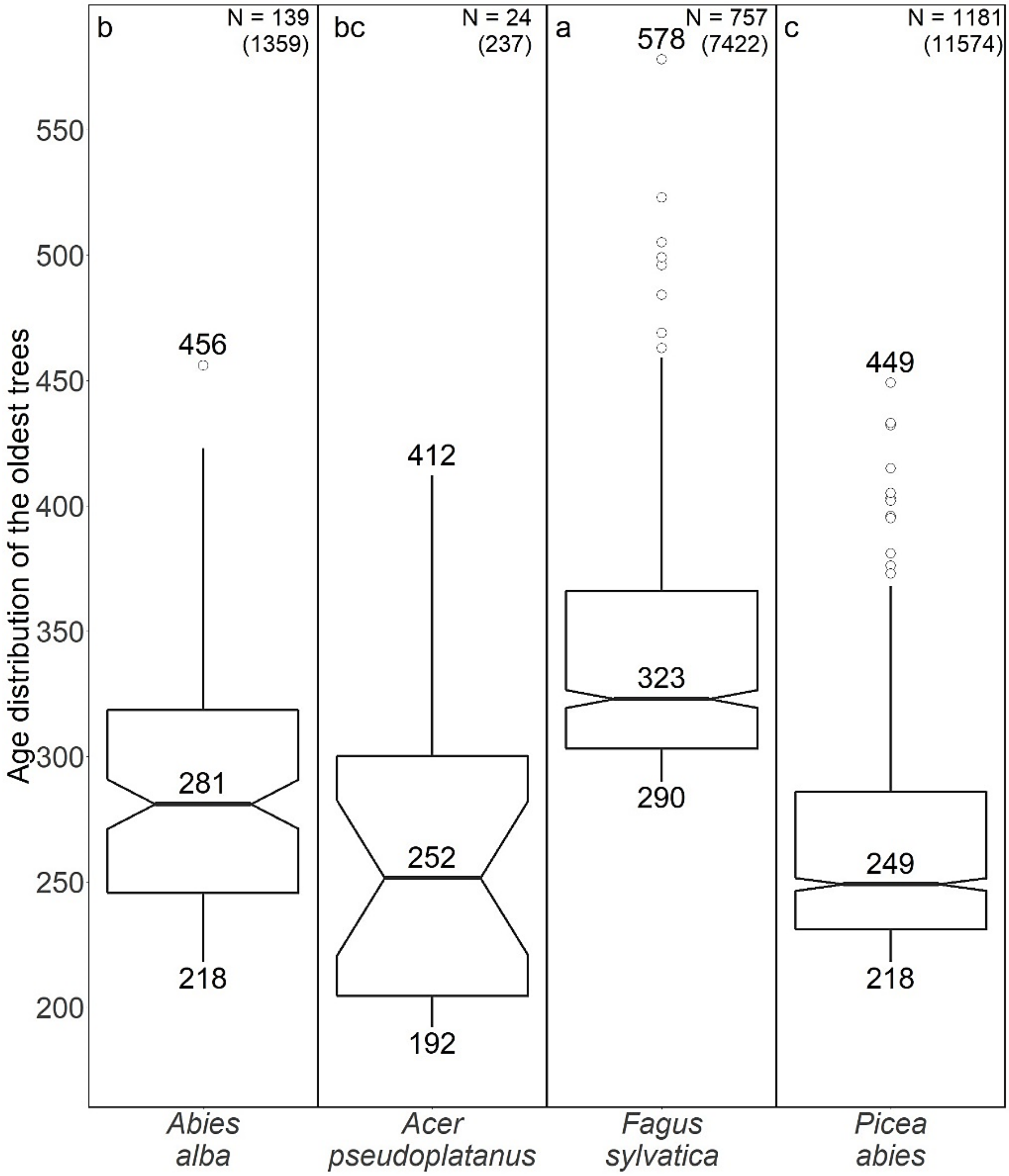

Figure 6. Age distribution of the oldest trees (≥ species-specific 90th percentile of age) of four dominant species pooled across all study sites. Boxes represent the interquartile range, with the median age of the oldest trees represented with a horizontal line within each box, and notches represent 95% confidence intervals of the median. The lower whisker of each box extends to the species-specific 90th percentile of age, while upper whiskers extend 1.5 times the interquartile range, and points show outliers. Numbers in the upper right corners indicate the number of trees above the species-specific 90th percentile, including the total numbers of all trees per species in parentheses. The letters in the upper left corner of each plot indicate significant differences among species ($p < 0.05$) based on Tukey's pairwise comparisons.

5.1.2 Drivers of tree life span

The influence of disturbance related variables on reaching the 90th percentile ages varied among the four tree species (Table 1; Figure S2, S3). Maximum severity of plot-level disturbance had a significant negative effect on life span (i.e. the plot-level presence of trees above the 90th percentile age thresholds) for spruce and maple, while the calendar year of this maximum severity event had a significant negative influence on beech and spruce (i.e. plots with more recent maximum severity events had less trees reaching old age (Figure S2, S3). Neither of the two disturbance variables were significant in the fir model. The number of releases had a significant positive effect on life span in all models.

Growth rate variables had strong and consistent effects on life span among the species (Table 1; Figure S4, S5, S6). Minimum ten-year average growth showed a significant negative influence for each species, while early growth rate had a significant negative influence on life span for beech and fir, but not spruce. Maximum growth was not significant in any of the models.

The models did not show strong evidence of environmental control on tree life spans. Both the plot level (northness and slope) and large-scale drivers (latitude and temperature of the vegetation season) were insignificant for most species-level models. The only exception was the model for fir and maple, in which temperature of the vegetation season had a weak but significant negative effect on life spans (Table 1, Table S7).

Table 1. Summary of GLMMs examining the effect of environmental, growth, and disturbance factors on the age of the oldest individuals of four tree species. Results show explanatory variables used in the models, estimates of the regression coefficients (Est.), standard errors (SE), z-values (z), probabilities (p), variances of all four levels of random effects (τ_{00}), marginal determination coefficients, and conditional determination coefficients. The significant model parameters are displayed in bold.

	Fagus sylvatica				*Picea abies*				*Abies alba*				*Acer pseudoplatanus*			
Parameter	Est.	SE	z	p	Est.	SE	z	p	Est.	SE	z	p	Est.	SE	z	p
(Intercept)	**-3.74**	**0.20**	**-19.14**	**<0,001**	**-4.12**	**0.36**	**-11.40**	**<0,001**	**-3.70**	**0.56**	**-6.66**	**<0,001**	**-22.36**	**6.98**	**-3.20**	**0.001**
Disturbance severity	-0.11	0.09	-1.22	0.224	**-0.70**	**0.09**	**-7.60**	**<0,001**	-0.06	0.17	-0.33	0.738	**-9.19**	**3.81**	**-2.41**	**0.016**
Disturbance year	**-0.39**	**0.08**	**-4.72**	**<0,001**	**-0.29**	**0.06**	**-4.73**	**<0,001**	0.25	0.16	1.61	0.108	/	/	/	/
Early growth	**-0.63**	**0.11**	**-5.73**	**<0,001**	0.07	0.08	0.86	0.389	**-0.98**	**0.25**	**-3.90**	**<0,001**	/	/	/	/
Maximum growth	-0.05	0.07	-0.70	0.482	0.00	0.08	-0.04	0.967	0.06	0.17	0.36	0.719	2.87	1.90	1.51	0.131
Minimum growth	**-1.13**	**0.14**	**-7.99**	**<0,001**	**-1.99**	**0.10**	**-20.60**	**<0,001**	**-1.11**	**0.32**	**-3.48**	**0.001**	**-13.10**	**5.15**	**-2.55**	**0.011**
Number of releases	**1.11**	**0.06**	**19.70**	**<0,001**	**0.58**	**0.04**	**14.27**	**<0,001**	**1.08**	**0.15**	**7.42**	**<0,001**	/	/	/	/
Latitude	-0.34	0.20	-1.72	0.086	-0.06	0.13	-0.45	0.650	-0.01	0.45	-0.01	0.990	/	/	/	/
Northness	-0.09	0.10	-0.85	0.393	0.00	0.07	0.05	0.961	-0.28	0.17	-1.62	0.106	-2.54	2.47	-1.03	0.304
Slope	0.04	0.11	0.39	0.694	-0.03	0.08	-0.35	0.726	0.18	0.20	0.90	0.370	1.49	1.53	0.97	0.331
Mean T of vegetation season	-0.20	0.16	-1.25	0.211	0.13	0.10	1.27	0.204	**-0.50**	**0.25**	**-2.00**	**0.045**	**-6.45**	**3.17**	**-2.04**	**0.042**
Forest type	/	/	/	/	0.29	0.37	0.79	0.432	/	/	/	/	/	/	/	/
$\tau_{00\ \text{plot:(pairplot:(stand:landscape))}}$	0.57				0.47				0.00				464.87			
$\tau_{00\ \text{pairplot:(stand:landscape)}}$	0.37				0.57				0.41				0.00			
$\tau_{00\ \text{stand:landscape}}$	0.69				0.34				1.85				0.00			
$\tau_{00\ \text{landscape}}$	0.00				0.00				0.84				0.01			
R^2_m [%]	48.03				54.56				42.65				40.93			
R^2_c [%]	65.25				68.07				70.49				99.59			

5.1.3 Commonness of old trees

The densities of the oldest trees (≥ species-specific 90th percentile of age) were highly variable across the stands and landscapes, ranging from 0 to 48.8 trees/ha (Figure 7). 15 out of 68 stands had 10–20 old trees/ha, and 11 stands had densities greater than 20 old trees/ha. We identified 893 trees that were at least 300 years old, and 113 trees older than 400 years, of which 2 were maple (0.084 % of all maple trees), 4 were fir (0.29 % of all fir trees), 9 were spruce (0.08 % of all spruce trees), and 98 were beech (1.32 % of all beech trees). Three beech trees were older than 500 years (0.04 % of all beech trees).

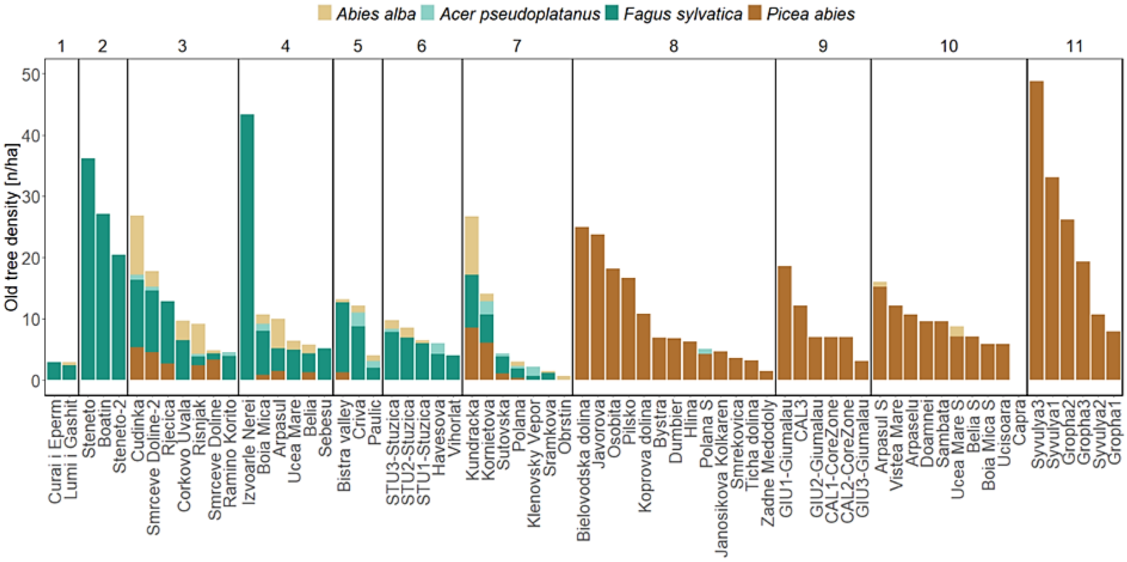

Figure 7. Densities of oldest trees (≥ species-specific 90th percentile of age) by species within each stand across the study region. The numbers indicate the forest landscape names: 1 – Albania, 2 – Bulgaria, 3 – Croatia, 4 – South Romania beech, 5 – North Romania beech, 6 – East Slovakia, 7 – Central Slovakia beech, 8 – Central Slovakia spruce, 9 – North Romania spruce, 10 – South Romania spruce, 11 – Ukraine

When calculated as a proportion of the canopy layer trees, the oldest trees made up from 0% to 23.9% of the canopy per stand (Figure 8).

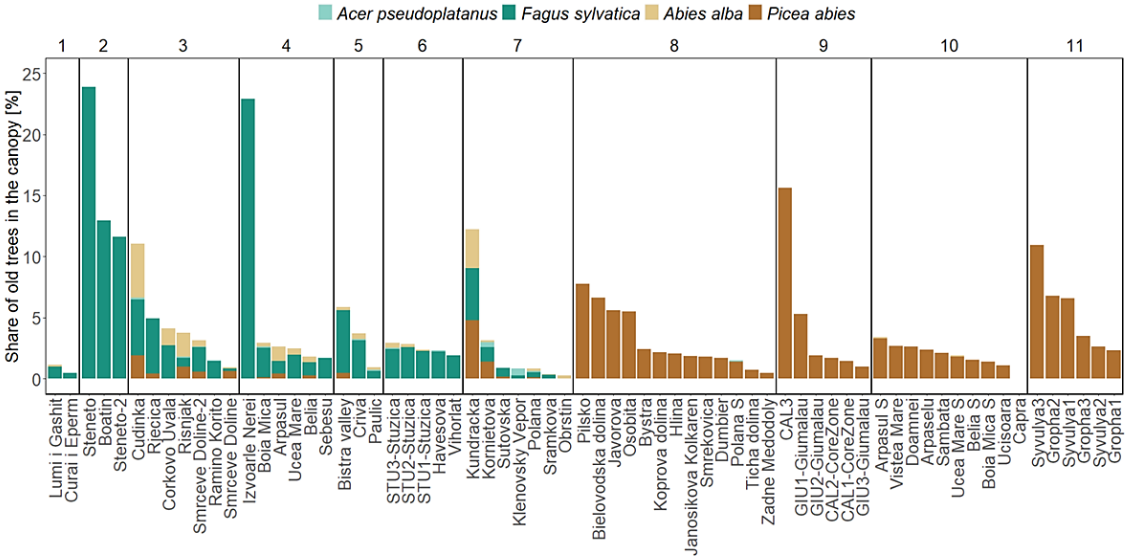

Figure 8. The percentages of oldest trees (≥ species-specific 90th percentile of age) among canopy individuals by species within each stand across the study region. The numbers indicate the forest landscape names: 1 – Albania, 2 – Bulgaria, 3 – Croatia, 4 – South Romania beech, 5 – North Romania beech, 6 – East Slovakia, 7 – Central Slovakia beech, 8 – Central Slovakia spruce, 9 – North Romania spruce, 10 – South Romania spruce, 11 – Ukraine

5.2 CANOPY ACCESSION ACROSS TEMPERATE PRIMARY FORESTS OF EUROPE

5.2.1 Interspecific differences in canopy accession patterns

There were notable differences in the dominant patterns of canopy accession among the species (Figure 9). The proportion of trees reaching the canopy by establishing in open canopy and exhibiting no subsequent releases increased significantly ($\chi^2 = 255.63$, $p < 0.001$) from beech (22.8%) to fir (40.1%), maple (54.9%), spruce from mixed beech forests (55.0%), and spruce from spruce forests (56.8%). Beech trees were least likely to attain the canopy with no release, while there were no significant differences among fir, maple, and spruce in mixed beech forests. The probability for spruce to reach the canopy with no release was significantly higher in spruce forests in comparison to mixed beech forests. Attaining the canopy after recruitment in open canopy and a subsequent release was not common for any of the species, and occurred most often for beech (11.3%), followed by fir (10.5%), maple (8.2%), spruce from spruce forests (6.9%), and spruce from mixed beech forests (6.0%). Attaining the canopy after initial suppression was the most common mode for beech (65.9%) and fir (49.4%). It was a less common mode for maple and spruce, albeit more than a third of all the individuals of maple and spruce in both forest types attained the canopy after being initially suppressed. (Figure 9, a; Table S7).

Although individuals of all four species with initial suppression exceeding at least a century in length were documented, the differences among the species were statistically significant ($\chi^2 = 152.42$, $p < 0.001$). The initial suppression was the longest for fir (median of 65 years) and beech (median of 64 years), followed by spruce from mixed beech forests (median of 54 years), which did not significantly differ from beech, but was significantly longer than for spruce from spruce forests (median of 35 years), and maple (median of 26 years) (Figure 9, b; Table S7).

Beech attained DBHc (canopy) later than the other four species (median value of 122 years), followed by fir (median of 97 years), while there was no significant differences among spruce from mixed beech forests, spruce from spruce forests, and maple which attained DBHc at a median of 81, 73, and 62 years, respectively ($\chi^2 = 646.62$, $p < 0.001$) (Table S4). Individuals of all species reaching the canopy accession DBH threshold after at least two centuries were identified, and the oldest tree at the time of attaining the threshold was a 421 years old beech (Figure 9, c).

The number of releases also significantly differed among the species ($\chi^2 = 288.79$, $p < 0.001$). Beech displayed significantly more releases than the other species (mean value of 1.07 releases per tree). Fir (mean value of 0.69 releases per tree) did not differ significantly from spruce in mixed beech forests (mean value of 0.52 releases per tree) or maple (mean value of 0.50 releases per tree). However, spruce in mixed beech forests exhibited significantly more releases than spruce in spruce forests (mean value of 0.49 releases per tree) (Figure 9, d; Table S7).

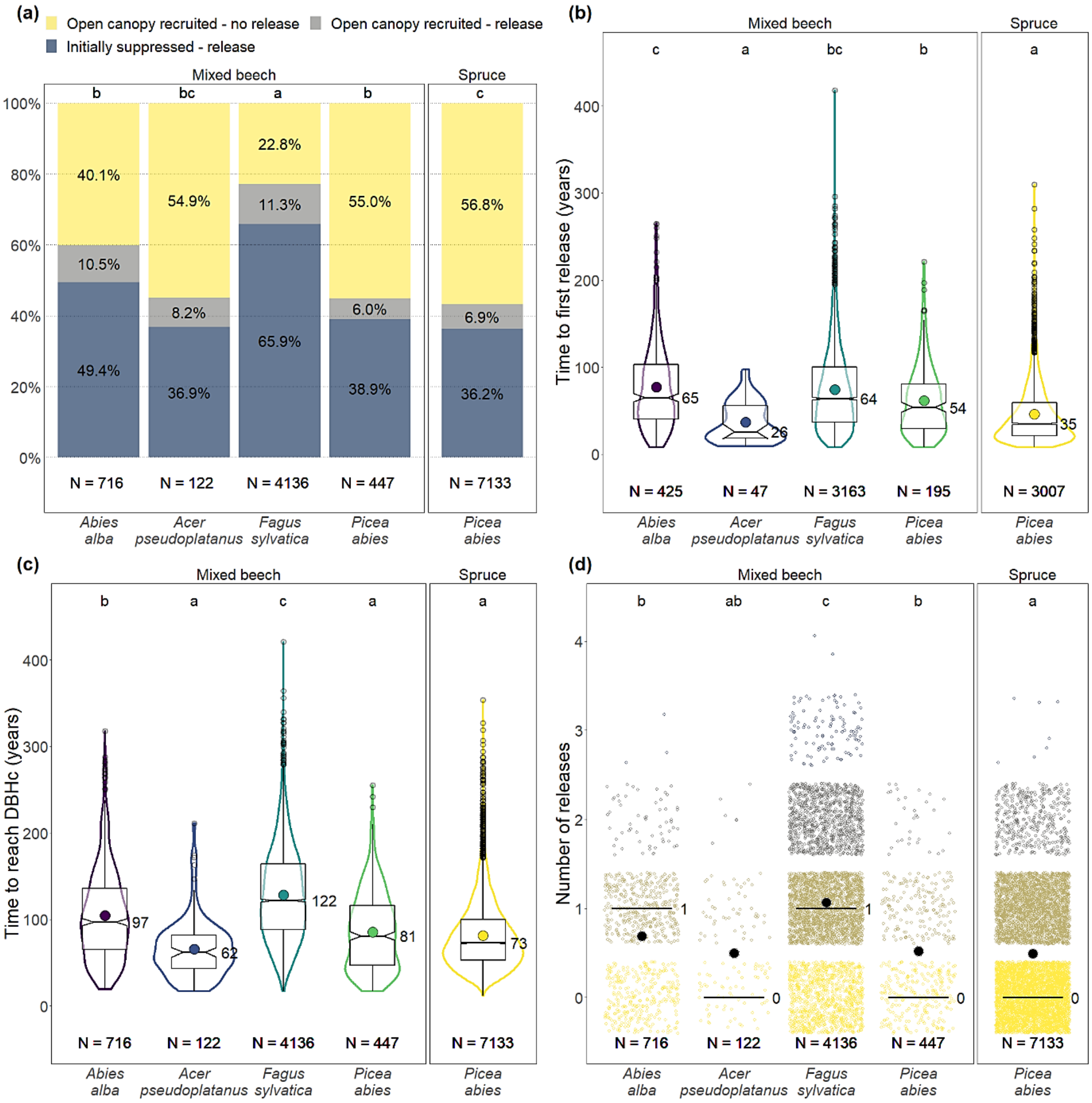

Figure 9. Distributions of canopy accession modes (a); time to first release (b); time to reach DBHc (c); and number of releases (d) of dominant species across mixed beech and spruce stands. The proportion of trees in each canopy accession mode per each species is marked on each bar (a). Boxes represent the interquartile ranges, median values are given by a horizontal line within each box, while notches show 95% confidence intervals of the median values. The lower and upper whiskers of each box extend 1.5 times the interquartile range, and black circles show outliers (b, c). Violin plots depict densities along the variables per each species (b, c). Median values per species are marked with a value on the right of the horizontal lines, the mean values per species are marked with a dot within each plot (b-d). Jittered circles represent single trees (d). The numbers above species names indicate the number of trees per species included in the representative distribution along each metric. The letters above each plot indicate significant differences in considered metrics among species ($p < 0.05$) based on Tukey's pairwise comparisons.

The species also showed significantly different minimum growth ($\chi^2 = 799.93$, $p < 0.001$), maximum growth ($\chi^2 = 447.86$, $p < 0.001$), minimum BAI ($\chi^2 = 644.05$, $p < 0.001$), and maximum BAI ($\chi^2 = 372.39$, $p < 0.001$). Beech had the slowest minimum growth, minimum BAI, maximum growth, and maximum BAI of all the species. Maple and spruce in mixed forests had the fastest rates of minimum growth and minimum BAI, and spruce from mixed forests had the fastest rates of maximum growth and maximum BAI. For fir, minimum growth and minimum BAI were significantly faster than beech only, and maximum growth was significantly slower than spruce in mixed beech forests only. Maximum growth of maple was significantly slower than spruce only, while maximum BAI significantly slower than spruce and fir. Both maximum growth and maximum BAI were significantly faster for spruce in mixed beech forests compared to spruce in spruce forests, whereas minimum growth and minimum BAI did not significantly differ between the two spruce groups (Figure S10; Table S8).

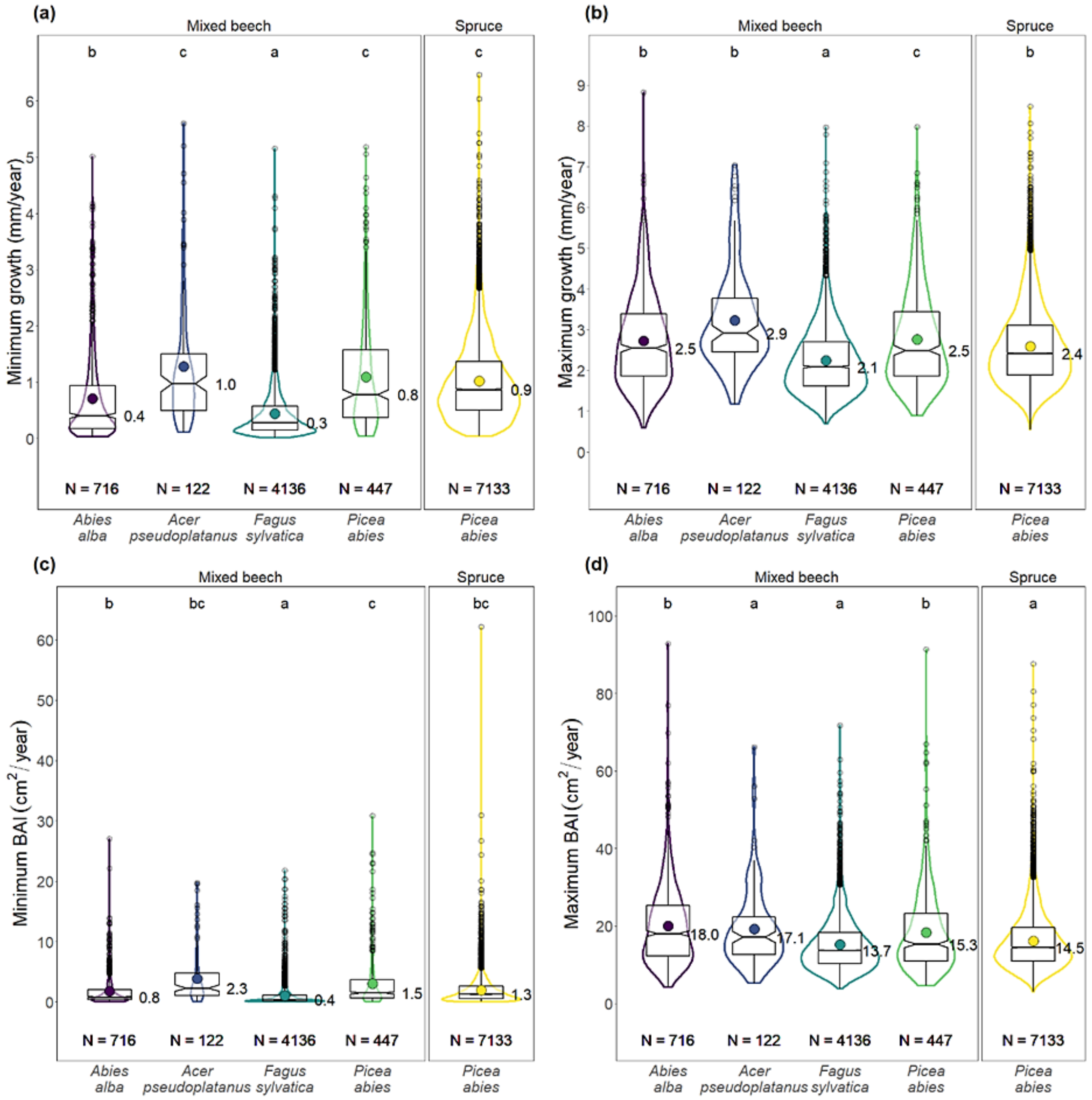

Figure 10. Distributions of minimum 10-year average tree ring widths (a); maximum 10-year average tree ring widths (b); minimum 10-year average basal area increments (c); and maximum 10-year average basal area increments (d) of dominant species before attaining the canopy across mixed beech and spruce stands. Boxes represent the interquartile ranges, median values are given by a horizontal line within each box, while notches are showing 95% confidence intervals of the median values. The lower and upper whiskers of each box extend 1.5 times the interquartile range, and black circles show outliers. Violin plots depict densities along the variables per each species. Median values per species are signified with a value on the right of the horizontal lines, the mean values per species are signified with a dot within each plot. Numbers above species names indicate the number of trees per species included in representative distribution along each of the metrics. The letters above each plot indicate significant differences in considered metrics among species ($p \leq 0.05$) based on Tukey's pairwise comparisons.

5.2.2 Driver models

Disturbance-related variables were found to markedly influence the metrics of canopy accession (Table 2, Figure S8). The later timing of the most severe disturbance event before attaining the canopy significantly decreased the probability of the tree to attain the canopy with no release and significantly prolonged the time to first release and time to attain DBHc. The magnitude of this maximum severity event had an opposite effect than its timing on time to first release, while it had no significant effect on the probability of attaining the canopy with no release and time to attain the canopy. The number of detected disturbance events before attaining the canopy was significantly positively related to the number of releases, while the cumulative disturbance severity had a significant negative effect. The effect sizes of disturbance parameters generally did not surpass the differences between the species. Beside a positive effect of higher PDIR on probability of attaining the canopy with no release, environmental variables did not prove to have a significant impact on any of the other three metrics (Table 2, Figure S8).

Table 2. Summary of generalized linear mixed models examining the effect of species, environmental (DMI and PDIR), and disturbance factors (maximum disturbance severity, maximum disturbance timing, cumulative disturbance severity, and the number of disturbance events) on canopy accession modes, time to first release, time to reach DBHc (canopy), and the number of releases of individuals of five tree species groups in the study area.

	Canopy accession				Time to first release				Time to reach DBHc				Number of releases			
Parameters	Est.	SE	t	p	Est.	SE	t	p	Est.	SE	t	p	Est.	SE	t	p
(Intercept) (*Abies alba*)	**-0.49**	**0.15**	**-3.21**	**0.001**	**4.16**	**0.05**	**87.39**	**<0.001**	**4.45**	**0.03**	**131.18**	**<0.001**	**-0.31**	**0.07**	**-4.25**	**<0.001**
Species (*Acer pseudoplatanus*)	-0.09	0.35	-0.27	0.787	-0.33	0.14	-2.31	0.021	-0.07	0.05	-1.25	0.213	-0.39	0.22	-1.79	0.073
Species (*Fagus sylvatica*)	**-0.71**	**0.15**	**-4.59**	**<0.001**	-0.12	0.05	-2.63	0.008	**0.20**	**0.02**	**9.76**	**<0.001**	0.26	0.07	3.58	<0.001
Species (*Picea abies* MB)	0.18	0.21	0.87	0.382	-0.20	0.07	-2.74	0.006	**-0.17**	**0.03**	**-6.11**	**<0.001**	-0.20	0.12	-1.75	0.081
Species (*Picea abies* S)	**0.64**	**0.17**	**3.81**	**<0.001**	**-0.36**	**0.05**	**-6.60**	**<0.001**	-0.07	0.04	-1.80	0.072	**-0.45**	**0.08**	**-5.55**	**<0.001**
DMI	0.00	0.06	0.04	0.967	0.01	0.02	0.45	0.650	0.01	0.02	0.57	0.566	0.00	0.03	0.14	0.888
PDIR	**0.09**	**0.05**	**2.09**	**0.036**	0.01	0.02	0.54	0.588	0.02	0.01	1.56	0.120	-0.04	0.02	-1.75	0.080
Maximum severity	0.08	0.04	1.93	0.054	**-0.06**	**0.01**	**-4.38**	**<0.001**	0.00	0.01	0.49	0.624	/	/	/	/
Disturbance timing	**-0.96**	**0.04**	**-22.36**	**<0.001**	**0.29**	**0.01**	**25.59**	**<0.001**	**0.19**	**0.00**	**39.44**	**<0.001**	/	/	/	/
Cumulative disturbance severity	/	/	/	/	/	/	/	/	/	/	/	/	**-0.06**	**0.02**	**-2.66**	**0.008**
N of disturbance events	/	/	/	/	/	/	/	/	/	/	/	/	**0.23**	**0.02**	**9.90**	**<0.001**
$\tau_{00\ plot}$	0.27				0.05				0.05				0.06			
$\tau_{00\ stand}$	0.12				0.01				0.02				0.02			
R^2_m [%]	30.0				28.3				30.3				13.1			
R^2_c [%]	37.4				40.5				64.0				20.1			
Observations	6681				3464				6681				6681			

Note: Results show explanatory variables used in the models, estimates of the regression coefficients (Est.), standard errors (SE), t- values (t), probabilities (p), variances of random effects levels (τ00), marginal determination coefficients (R^2_m), and conditional determination coefficients (R^2_c). All significant model parameters ($p < 0.05$) are in bold. Coefficients for the categorical variable ‘Species’ stand for contrasts with the base level of *Abies alba*. *Picea abies* MB stands for spruce trees from mixed beech forests and *Picea abies* S for spruce trees from spruce forests

5.3 GROWTH RATES AND DURATIONS OF GROWTH RELEASES OF BEECH AND SPRUCE AND THEIR DRIVERS

There were no apparent major differences in average growth rates and durations of growth releases between beech and spruce. Spruce trees, however, grew marginally faster on average (Figure 11). The spruce release average growth model accounting for average EQ during release and age at release onset outperformed the rest of the modeled combinations (Table 3). With beech release magnitude, beech release duration, and spruce release duration as responses, the models accounting for the combination of EQ during release and DBH at release onset outperformed the rest of the combinations (Table S2). In general, including EQ instead of average T in the model resulted in a lower AIC across all the comparative models, however the differences were rather marginal (Table 3). The differences between the comparative models accounting for either age or DBH during release were larger and surpassed the threshold warranting any support for the lower-ranked model (ΔAIC > 7) (Burnham et al., 2011). Models accounting for DBH outperformed the age models using beech release magnitude, beech release duration, and spruce release duration as a response, while the spruce release magnitude models accounting for age outperformed those accounting for DBH (Table 3).

Table 3. Model ranking based on AIC values of generalized linear mixed models examining the effect of disturbance severity, PDIR, and a combination of either DBH at release onset (DBH) or age at release onset (Age) and Ellenberg quotient during release event (EQ) or average temperature during release event (T) on average growth during release (a) and duration of the release event (b) for beech and spruce. In the average growth models calendar year at release onset was used as an additional explanatory variable.

a)	*Fagus sylvatica*			*Picea abies*		
	AIC	ΔAIC	Rank	AIC	ΔAIC	Rank
DBH + EQ	**1078.3**	**0**	**1**	1753.7	52.9	3
DBH + T	1079.4	1.1	2	1755.4	54.6	4
Age + EQ	1110.3	32	3	**1700.8**	**0**	**1**
Age + T	1112.1	33.8	4	1701.7	0.9	2

b)	*Fagus sylvatica*			*Picea abies*		
	AIC	ΔAIC	Rank	AIC	ΔAIC	Rank
DBH + EQ	**4776**	**0**	**1**	**6765**	**0**	**1**
DBH + T	4776.6	0.6	2	6767.2	2.2	2
Age + EQ	5085.5	309.5	3	7251	486	3
Age + T	5088.4	312.4	4	7255.8	490.8	4

Disturbance severity explained the most variability in average growth out of all extrinsic factors for both beech and spruce. It showed a significant positive effect on radial increment during the release of both species, whereby the effect size was markedly larger for beech compared to spruce. (Figure 12a, e; Table S10a). There was no significant relationship between EQ and release magnitude for either of the species. The response of average growth to variability in topography and potential radiation was slightly different between species, whereby there was a weak negative relationship between PDIR and average beech growth, while there was no significant relationship for spruce (Figure 12b; Table S10a). Average increment variability further proved to be significantly dependent on intrinsic factors and the size/age dynamics of both species. Beech release magnitudes were positively related to the tree DBH at release onset, while spruce average growth responded negatively to older age at release onset. The effect size of age at release onset also surpassed the effect sizes of all other predictors in the spruce model (Figure 12c, f; Table S10a). Additionally, average growth of both species showed a weak increasing trend throughout the study period (Figure 12d, g; Table S10a).

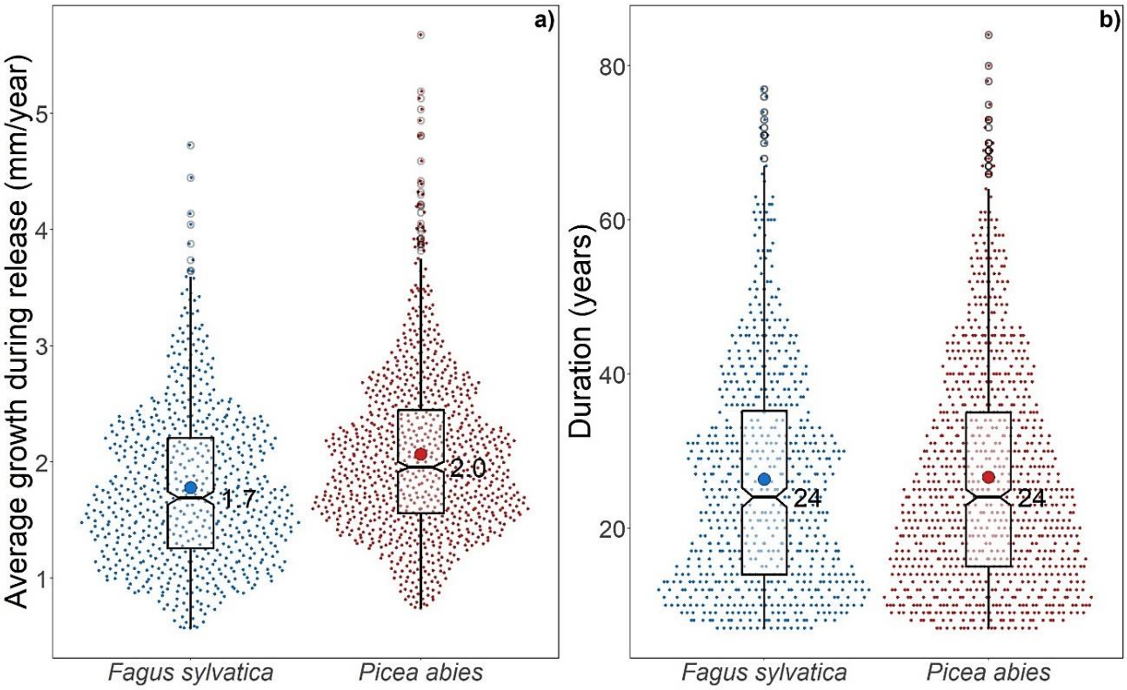

Figure 11. Distribution of average growth during release (a) and release durations (b) of beech (blue) and spruce (red). Boxes envelope the interquartile ranges, while the median values are given by a horizontal line within each box, and numeric value on the right of each representative boxplot. Notches represent 95% confidence intervals of the median values. Each of the upper and lower whiskers depicts 1.5 times the interquartile range and the black circles show outliers. The mean value of each distribution is represented by a large colored dot within each boxplot. The small colored dots represent single release events.

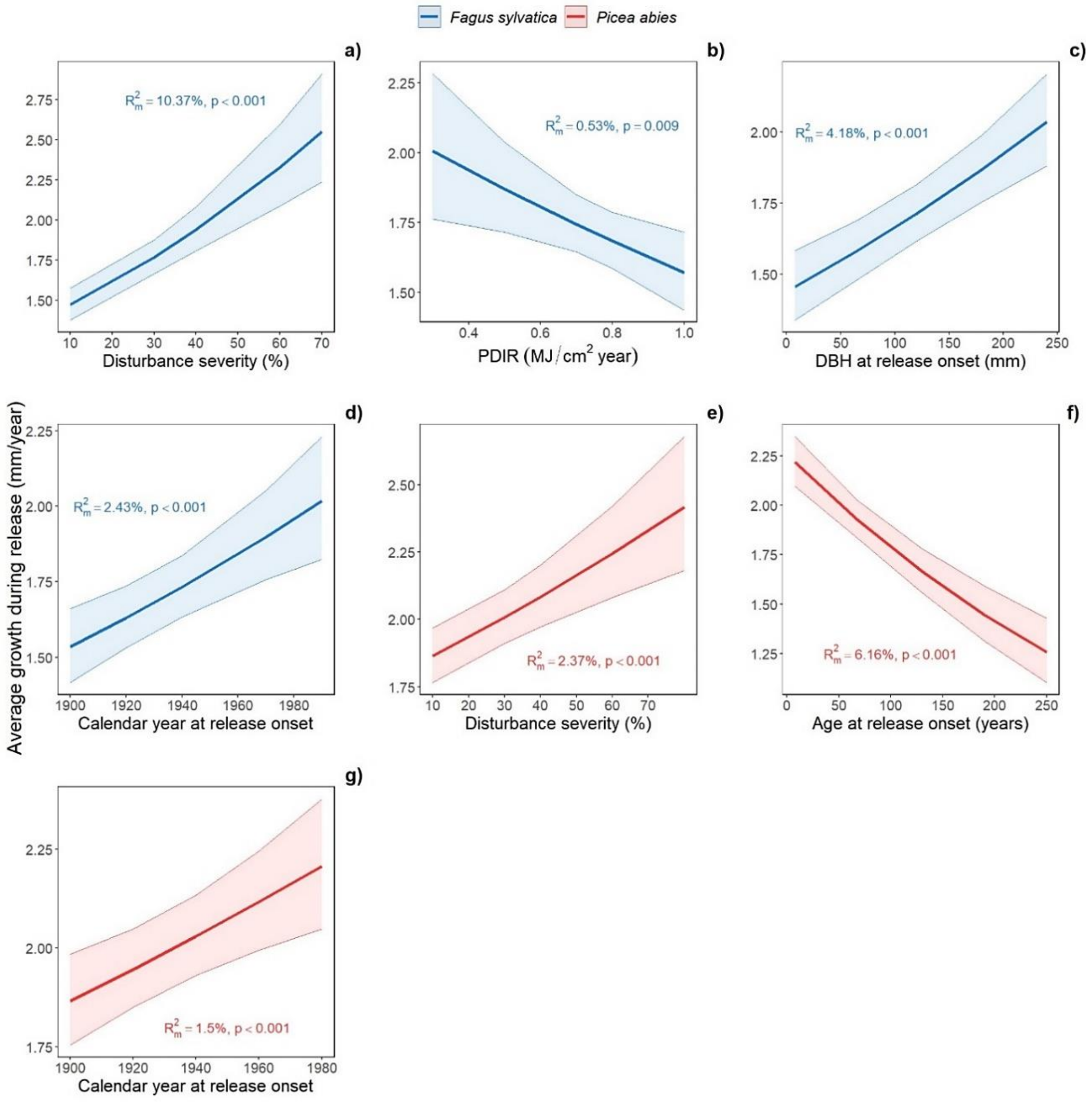

Figure 12. Predictions of effects on average growth during release events of beech (blue) and spruce (red) based on the representative generalized linear mixed models. Significant effects are represented by solid lines alongside the semipartial marginal determination coefficients (R^2_{m}) and probabilities (p) for all the effects. The colored bands represent the respective 95% confidence intervals. For further details of the respective models refer to the Table S3a.

There were no significant effects of the included extrinsic factors (disturbance severity, EQ, or PDIR) on release duration for either of the species (Table S10b). Alternatively, release duration of both species showed a strong negative response to increasing DBH at release onset, whereby the effect sizes were relatively similar in the models of both species (Figure 12a, b; Table S10b).

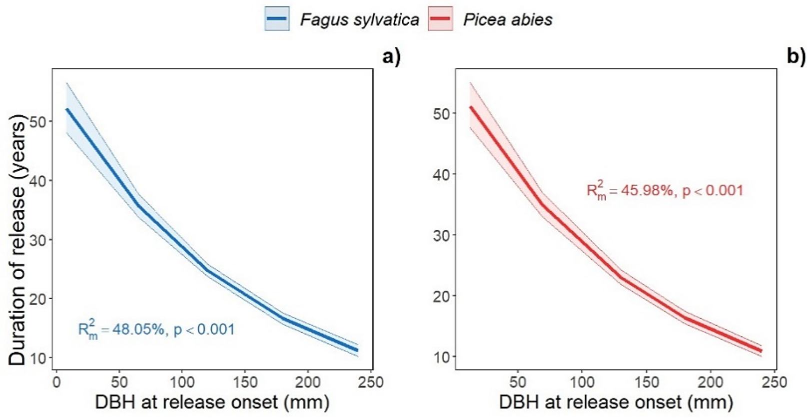

Figure 13. Predictions of effects on duration of beech (blue) and spruce (red) releases based on the representative generalized linear mixed models. Significant effects are represented by solid lines alongside the semipartial marginal determination coefficients (R^2_m) values and probabilities (p). The colored bands represent the respective 95% confidence intervals. For further details of the respective models refer to the Table S3b.

6. DISCUSSION

This chapter follows a similar order as the methods and results chapters presented earlier. The results presented in *5.1* are thus discussed in section *6.1 Tree life span in temperate primary forests*, results from *5.2.* are then discussed in *6.2 Patterns and drivers of canopy accession across temperate primary forests of Europe*, followed by a discussion of results from *5.3* in section *6.3 Growth rates and durations of growth releases of beech and spruce and their drivers*. These sections are then followed by more general discussion on significance of presented results and implications for nature conservation and forest management in *6.4*.

6.1 TREE LIFE SPAN IN TEMPERATE PRIMARY FORESTS OF EUROPE

6.1.1 Overview and study caveats

We found compelling evidence of biological differences in life span among the four coexisting trees species across mountain regions of Europe, yet these differences are not entirely consistent with published literature on the ecology of European tree species. We also found that local disturbance history, rather than plot-scale and broad-scale environmental factors, was a key driver of life span. The particular history of local disturbance likely contributes to the highly variable density of the oldest trees that was documented across the study region. Before we elaborate on these main findings, we highlight several caveats that are important for the discussion that follows.

The estimates of tree life span used in our study, in particular the ages of the oldest living stems above the species-specific 90th percentiles, provide an indication of the longevity of a given individual, but not actual longevity, or the number of years from seed germination to death of an adult tree. Because we cored trees at 1m in height, we underestimate the number of years required to reach 1 m, which could range from years to decades depending on light conditions, particularly for shade tolerant species (Nagel et al., 2006; Wong and Lertzman, 2001). We also only worked with live trees, mainly due to the challenges of obtaining a large sample of recently dead trees with intact wood for tree coring. The species sampled in our study, especially the broadleaf species, have relatively fast decay rates, such that tree ring counts of dead and declining trees are often extremely difficult (Di Filippo et al., 2012). Finally, given that larger trees often had bole decay, more larger stems were excluded from the sample compared to smaller stems, which is an additional reason why our dataset may underestimate life span. Despite these limitations, the large population-based dataset of randomly sampled trees in remaining primary forests across a sub-continental scale should provide a robust estimate of interspecific differences in tree life span.

6.1.2 Interspecific differences in tree life span across temperate primary forests of Europe

Beech, the dominant broadleaf species, was markedly older than the other species, and fir was older than spruce, but there were no significant differences in life span between maple and the two conifer species. As previous studies have pointed out, interspecific differences in life history traits at both juvenile and adult life stages may contribute to tree coexistence, whereby adult longevity may compensate for lower competitiveness of juveniles compared to co-occurring species (Lusk and Smith, 1998; Veblen, 1986). In temperate mixed-mountain forests of Europe, beech is both one of the most shade-tolerant species as a juvenile and long-lived as an adult, likely contributing to its dominance across the region. Compared to juveniles of beech and fir, maple and spruce are less tolerant of shade, but grow more rapidly in larger gaps with higher light levels (Leuschner and Meier, 2018; Petritan et al., 2007; Stancioiu and O'hara, 2006). For example, in a mixed-mountain forest in the Dinaric region, (Nagel et al., 2010) found that maple required relatively large gaps (> 400m^2) to access the canopy, while smaller gaps were captured by beech and fir, which were often present prior to gap formation. Although the lower shade tolerance of maple may be a disadvantage in forests that lack moderate severity disturbance for long time periods, its relatively high longevity likely contributes to its persistence in the landscape. Indeed, there are likely other interspecific trait differences associated with various life stages that may contribute to the coexistence of these species (Nakashizuka, 2001), such as long-distance dispersal of maple seeds or the tall canopy stature of fir and spruce. However, further research is required to better understand the life history traits and life stages that contribute to tree species coexistence in these forests.

It is important to point out that our findings are not consistent with the classic literature on life span of European tree species. For example, Korpel' (1995) reported life spans of 230 and 350 years for beech and fir, respectively, which is in complete contrast to our findings. Leuschner and Ellenberg (2017) report maximum ages of 450 years for both beech and fir, and 300 years for spruce and maple. However, the maximum ages found in our dataset are considerably older than the median ages of trees above the 90th percentile ages; these median ages are a better predictor of expected tree life spans in forests regulated by natural disturbance processes. We believe that the range of life span estimates provided here may serve as an important reference for future studies that must prescribe values for them, such as simulation models of forest dynamics. Relying on estimates from earlier work may lead to spurious conclusions regarding long-term forest dynamics. In support of our findings, other recent dendroecological studies that focused on local sites or other regions in Europe have reported similar values of maximum life span for the four species studied here (Bigler and Veblen, 2009; Di Filippo et al., 2015; Motta et al., 2011; Nagel et al., 2014; Piovesan et al., 2019b).

6.1.3 Drivers of tree life span across temperate primary forests of Europe

In addition to life history differences, we also sought to identify drivers of longevity across the large gradient of environmental conditions and disturbance histories present in the dataset. The analyses indicated significant links between disturbance metrics and longevity in three of the four species level models. There was a higher probability of finding old trees on plots with a lower maximum severity of plot-level disturbance, or where the maximum severity event occurred further back in time. These findings are not at all surprising given that both the beech and spruce dominated primary forests studied here experience a disturbance regime characterized by relatively frequent moderate severity, partial canopy disturbances that are likely to remove susceptible individuals (i.e. large, old trees) in the canopy layer (Čada et al., 2020; Frankovič et al., 2020; Nagel et al., 2014).

Disturbance history is also intrinsically linked to lifetime growth of trees in that it regulates canopy structure, and thereby the growth of understory trees via changes in light. Depending on the size, location, and timing of disturbance relative to a given understory tree, some individuals will gain access to the forest canopy quickly, others will reach the canopy after multiple periods of suppression and release, and yet others will die due to prolonged periods of suppression. Across all four of the species studied here, trees that survived periods of very suppressed growth were more likely to reach old age. For example, average annual growth rates during the minimum 10-year growth periods for all the trees older than 300 years was < 0.62 mm/year, < 0.36 mm/year for all the trees older than 400 years, and < 0.17 mm/year for all the trees older than 500 years (Figure S5). Likewise, trees that had slow early growth rates were also more likely to reach old age (Figure S4). These findings are consistent with previous literature for a number of different species (Bigler, 2016; Di Filippo et al., 2015; Larson, 2001; Piovesan et al., 2019b), including beech (Di Filippo et al., 2012; Piovesan et al., 2019a, 2005) and spruce (Bigler and Veblen, 2009; Castagneri et al., 2013; Rötheli et al., 2012). Finally, the results show a positive relationship between the number of suppression-release periods experienced by a tree and longevity (Figure S6). Trees with multiple suppression-release periods persist in the understory for a large proportion of their life span, while trees that access the canopy quickly, such as those that establish in large gaps, spend a longer proportion of their life in the canopy. These results lend support to the idea that time spent in the canopy, where there is higher risk of disturbance, may have a stronger influence on longevity than other factors, such as environmental constraints or genetics.

Indeed, one of the more surprising findings was that we did not identify a consistent relationship between life span and environmental factors, such as temperature and elevation, which has been documented in previous studies of the same species (Bigler, 2016; Di Filippo et al., 2015; Rötheli et al., 2012). Aside from the negative correlation between the mean temperature of the vegetation season and longevity for fir and maple, none of the other environmental factors (i.e. slope, northness, latitude) were related to longevity across the four species. The strong influence of disturbance and slow growth rates on longevity documented here may simply override the influence of other environmental factors. In a study on mountain pine in Switzerland, Bigler (2016) also suggested that a lack of an expected temperature effect on the early growth of mountain pines was likely due to superimposing effects of stand structure. Furthermore, past studies that have documented extremely old trees for a given species were often located within extreme site conditions (Larson et al., 2000), whereas our dataset is likely to be more representative of site conditions found across mountain forests in the region.

A notable drawback of our study is that we cannot tease apart how various drivers influence longevity. Previous work has often hypothesized that slow growing trees invest more in defense, such as chemicals or other wood properties that promote resistance to decay (Loehle, 1988), or that slow radial growth may incur greater mechanical resistance to canopy disturbance (Larson, 2001). For the species studied here, the literature does not provide clear evidence on how slow growth or other wood properties may increase longevity. Previous research does not indicate a clear or consistent relationship between radial growth and wood density for beech (Bouriaud et al., 2004; Diaconu et al., 2016), while faster radial growth has been found to decrease wood density in spruce (Piispanen et al., 2014). Moreover, in a study of deadwood decay across temperate tree species in Europe, wood density was positively correlated with decay rates for beech, maple, and spruce, whereas chemicals such as phenols organic extractives were negatively correlated with decay rate (Kahl et al., 2017). However, if understory trees are growing slowly due to light limitation, then presumably they have limited resources to invest in chemical defense (Herms and Mattson, 1992). Finally, it is important to note that we cannot rule out genetic control on intraspecific variation in life span, or other tradeoffs between growth and longevity related to physiology (Roskilly et al., 2019).

6.1.4 Commonness of old trees across temperate primary forests of Europe and concluding remarks

A final objective of our study was to quantify the commonness of old-trees across the primary forest landscapes sampled in the study region. In general, very old trees are exceptionally rare; out of 20,600 cores dated to ≥50 years of age, only 115 were dated to more than 400 years. Although these exceptionally old trees are rare, 26 out of the 68 stands had more than 10 trees ha^{-1} that reached the species-specific 90th percentile age. Moreover, the remarkable variation in the density of these trees across the stands likely highlights how tree longevity is strongly influenced by local disturbance histories, which cover a gradient from low intensity gap dynamics, to partial canopy disturbance, to severe stand replacement in the study region (Čada et al., 2020; Frankovič et al., 2020; Janda et al., 2017; Schurman et al., 2018; Svoboda et al., 2014; Trotsiuk et al., 2014). Our results imply that disturbance and phenotypic plasticity play a strong role in controlling tree life span. By consequence, if disturbance regimes shift toward larger and more intense events under global change (Seidl et al., 2017), speeding up canopy accession, then future forests may support fewer long lived trees.

6.2 CANOPY ACCESSION ACROSS TEMPERATE PRIMARY FORESTS OF EUROPE

6.2.1 General trends along inter- and intra-specific variability in canopy accession patterns

Our study documents significant differences in canopy accession patterns of dominant tree species across primary temperate forests of Europe (Figure 9, 10; Table S7, S8). The species-specific patterns found here are largely consistent with their previously recognized shade tolerance capacities (Ellenberg et al., 1991; Leuschner and Meier, 2018; Niinemets and Valladares, 2006), yet the large intraspecific variability found across all species indicates significant heterogeneity in canopy attainment. Furthermore, we found significant differences in canopy accession between spruce populations of two distinct forest types, whereby spruce in mixed forests growing in milder conditions at lower elevations had a higher capacity to sustain shading than spruce in higher-elevation spruce-dominated forests. Finally, local disturbance history was the primary driver of canopy accession, largely overriding any environmental effects.

All the species exhibited a wide range of canopy accession modes, from initial suppression and subsequent release to continuously growing in the open canopy. Among the four species, beech and fir exhibited patterns characteristic of shade tolerant species, while the patterns for spruce and maple were consistent with more light demanding species. More than half of firs and more than three quarters of the beech trees exhibited a release before attaining the canopy. Additionally, even though attaining the canopy with no release was the prevailing canopy accession mode for maple and spruce in both forest types, more than 40% exhibited a release. The interspecific differences in distributions of canopy accession modes were consistent with the periods of extended suppressed growth before release, with beech and fir growing for longer periods of time in the understory than the other two species. The number of detected releases was another metric that pointed to interspecific differences in abilities to adjust growth rates following multiple suppression-release cycles (Baker and Bunyavejchewin, 2006; Brienen and Zuidema, 2006; Nagel et al., 2014), where beech growth patterns in particular exhibit high plasticity. By minimising the risk of photoinhibitory damage, the annually changing foliage of beech in contrast to conifers likely helps it to adapt to shifting irradiation with minimal delay(Čater, 2021; Wyka et al., 2007; Zhang et al., 2020), potentially benefiting its capacity to survive multiple suppression-release cycles.

Persisting in the shade is linked to maximizing light capture while minimizing maintenance respiration costs (Givnish, 1988; Valladares and Niinemets, 2008), whereby more shade-tolerant trees are able to exhibit slower growth rates in low light conditions in comparison to less shade-tolerant species (Petrovska et al., 2021; Poorter, 1999; Wright et al., 2000). This is largely consistent with results presented here, where fir and beech, in particular, are able to survive with remarkably slow growth rates, while the slow growth of maple and spruce is multiple times faster on average (Figure 10, a, c; Table S8, a, c). Consistently, beech, in particular, lagged behind other species in its potential to grow fast, which is a disadvantage in high-light conditions (Figure 10, b, d;

Table S8, b, d; Poorter 1999; Lin et al. 2002). Nonetheless, the ability to sustain long periods of shading and high growth plasticity likely contributed to the proliferation of European beech as one of the most dominant species in European temperate forests (Giesecke et al., 2007; Muffler et al., 2021). Slow growth and multiple periods of sustained suppression have also been recognized as a typical lifetime growth history to attain old age (Begović et al., 2023; Brienen et al., 2020; Brienen and Zuidema, 2006; Di Filippo et al., 2015; Pavlin et al., 2021; Piovesan et al., 2019a).

Beech trees generally spend longer periods in the subcanopy than their faster-growing competitors, attaining the canopy (DBHc) at over 120 years on average. In contrast, the less shade-tolerant and faster-growing maples generally attain the canopy at half that age. Differences were also apparent between beech and fir. Even if beech and fir are recognized as having similar shade tolerance (Leuschner and Meier, 2018; Nagel et al., 2014; Niinemets and Valladares, 2006), we observed that fir trees attained the canopy faster than beech trees. The younger age at canopy accession was, however, not linked to the lower capacity of fir to sustain suppression (Figure 9, a, c; Table S7, a, c), but with fir's capacity to grow faster than beech (Figure 10, b, d; Table 8, b, d). Reaching the canopy for less shade-tolerant species such as maple or spruce more notably relies on unsuppressed growth and attaining the canopy earlier than more shade-tolerant fir or beech (Figure 9, a, c; Table S7, a, c). The observed trends presented here conform with the widely recognized trade-off between survival in low light conditions and growth in high-light conditions, one of the mechanisms often suggested to contribute to species coexistence in closed-canopy forests (Gravel et al., 2010; Gutiérrez et al., 2008; Kobe et al., 1995; Lin et al., 2002; Nagel et al., 2014; Petrovska et al., 2022; Poorter, 1999). It is also important to note that individuals of all the analysed species may access the canopy long beyond a century in age (Figure 2, c). The time many of these trees spend in the subcanopy exceeds the rotation periods applied in most managed forest stands across Europe (e.g., Bouriaud et al. 2016). As a result, many trees are harvested before they develop key microhabitats, such as canopy deadwood, which are important for maintaining biodiversity in old-growth forests (Kozák et al., 2023).

The results also highlight intra-specific differences in canopy accession patterns between the two analysed groups of spruce trees growing in two distinct forest types. Namely, spruce in mixed beech forests is somewhat more productive and exhibits a higher potential to persist in the shade than spruce from spruce forests. These differences may be partly related to the temperature limited growth of spruce at higher elevations

(Schurman et al., 2019), in contrast with warmer lower elevation mixed beech forests. If so, these growth patterns would be consistent with the inverse relationship between the magnitude of competition and cold temperature stress documented in the literature (Anderegg and HilleRisLambers, 2019; Laanisto and Niinemets, 2015).

6.2.2 Drivers of canopy accession

Finally, the results suggest that all the canopy accession metrics were influenced by disturbance, with effect sizes similar in magnitude to only those of differences between the species, which were broadly consistent with full dataset models. Earlier occurrence of maximum severity disturbance was linked with higher probability of accessing the canopy without a release, faster canopy accession, and a shorter period of initial suppression, which was additionally inversely related to the maximum disturbance severity. Additionally, trees that experienced higher cumulative disturbance severity exhibited fewer growth releases, whereas trees that experienced more disturbance events prior to canopy accession had more releases. A higher disturbance severity might be linked to larger canopy openings which lead to faster growth rates and earlier canopy accession. In contrast, more low severity canopy disturbances likely create smaller canopy openings, less often leading to direct canopy accession (Baker and Bunyavejchewin, 2006; Lertzman et al., 1996; Martin-Benito et al., 2020).

In contrast to the notable influence of disturbance, environmental variables had little influence on canopy accession, except for a weak significant relationship between canopy accession modes and PDIR. One of the possible explanations might be that stand structural changes driven by local disturbances may override the potential canopy accession trends along environmental gradients, as has previously been indicated in tree longevity studies in temperate Europe (Bigler, 2016; Pavlin et al., 2021). Nonetheless, our results indicate that topography affects canopy accession to some degree, whereby trees on more sunny positions access the canopy without exhibiting a release more often than trees on more shaded positions. As light availability is contingent on topography and gap size (Canham et al., 1990; Prévost and Raymond, 2012), trees may need larger canopy openings to exhibit open canopy recruitment and growth releases on more shaded north slopes.

6.2.3 Caveats and concluding remarks

Although the analyses applied in this study are based on established approaches, it is important to point out several caveats. Since we cored the trees at 1 m in height, we lack information on their growth patterns before reaching this height. Depending on light conditions, the number of missing rings could range from years to decades (Wong and Lertzman, 2001). The reconstructed metrics of canopy accession (such as time to first release and time to reach the canopy) are therefore underestimated. However, it is unlikely that the results were significantly influenced due to the omission of the earliest growth patterns (Petrovska et al. 2022). Additionally, diverse canopy structures over small spatial scales in primary forests cause trees to establish in the dominant canopies at different dimensions, whereby even relatively small trees can form the dominant canopy. Therefore, using a DBH canopy accession threshold as an indicator of the point when trees attained the canopy cannot be interpreted as an absolute measure of canopy accession time, but merely as an indicator of the size when trees likely ascend to the canopy (Brienen et al., 2010; Clark and Clark, 1999). Lastly, the amount of light trees received during their growth to the canopy was not known. The presented suppression and release period metrics are derived exclusively from the radial growth patterns, whereby the growth response of different species to a gradient of light conditions may vary (Annighöfer et al., 2017; Wright et al., 2000). The interspecific differences presented here are, however, generally consistent with the trends presented in some of the previous studies focusing on sapling growth in known light conditions (Annighöfer et al., 2017; Petritan et al., 2009; Petrovska et al., 2022).

Based on an extensive tree ring dataset, this study presents the intra- and inter-specific variability in canopy accession patterns across dominant species of temperate primary forests in Europe. Canopy accession strategies in the studied closed-canopy forests are closely linked with species shade tolerances. Metrics such as survival times under suppression, canopy accession age or radial growth rates presented here complement existing shade tolerance rankings (e.g., Niinemets and Valladares 2006; Ellenberg et al. 1991; Leuschner and Meier 2018). Additionally, contingency of canopy accession patterns on disturbance history implies that a potential future intensification of disturbance regimes (Senf and Seidl, 2021a, 2021c) might alter the competitive interactions, particularly in favour of more light-demanding, faster-growing tree species.

6.3 GROWTH RATES AND DURATIONS OF GROWTH RELEASES OF BEECH AND SPRUCE AND THEIR DRIVERS

6.3.1 Overview of release patterns and drivers of growth rates during releases

Advanced regeneration is one of the crucial structural and functional elements of closed-canopy forests (Piovesan and Lüttge, 2018). It is instrumental for the resilience of forest cover (Senf et al., 2019), whereby abrupt growth increases after competitive releases are an important pathway of canopy accession and replacement, particularly for late successional species such as beech and spruce (Pavlin et al., 2024). Here, we quantified the average growth rates and durations of release events in beech and spruce across the Carpathian primary mountain forests. Spruce exhibited faster growth rates during releases on average compared to beech, consistent with prior studies that reported generally faster juvenile growth rates of spruce (Marchand et al., 2023) and faster maximum growth rates relative to beech (Pavlin et al., 2024; Pretzsch et al., 2020). In contrast to growth rates, release durations were largely similar between the species. Additionally, while the dominant identified drivers of growth during releases were similar between the species, the ranks of the relationships with different drivers differed, pointing at differences in gradients of growth drivers in the sampled regions for both species but potentially also at differences in life history traits between beech and spruce. Disturbance severity was the dominant driver of beech growth response, while spruce responded more strongly to age at release onset. Lastly, release durations of both species responded primarily and negatively to tree size at release onset.

The percentage of plot canopy area removed as the primary extrinsic driver of radial growth during release events revealed here for both species is consistent with previous reports of positive tree growth response to increased light levels (Annighöfer, 2018; Noyer et al., 2017; Vašíčková et al., 2019; Wright et al., 2000, 1998). Namely, the size of the canopy opening is an important determinant of light availability (e.g. Canham et al. 1990; Gálhidy et al. 2006; Prévost & Raymond 2012; Diaci et al. 2020), one of the crucial factors for growth and survival of forest understorey individuals (Canham et al., 1994; Valladares and Niinemets, 2008). Nevertheless, the photosynthetic efficiency and growth response generally culminate at sub-light saturation levels (Kašpar et al., 2024; Körner, 2015). However, under a mixed-severity disturbance regime dominant in the analyzed region (e.g. Čada et al. 2020; Frankovič et al. 2020; Kameniar et al. 2023), released trees are mostly still experiencing light levels lower than most of the canopy trees. Very high severity events that would remove, e.g. > 80% of canopy cover on the plot, are very rare (Figure 12a, e), while the taller residual trees in the vicinity also likely decrease the radiation received by a released tree (Canham et al., 1990; Mališ et al., 2023). Released trees are thus less likely to respond negatively to progressively larger canopy openings and higher irradiance. The magnitude of the effect, however, differed substantially between the two analyzed species, with a more pronounced response of beech compared to spruce. This might reflect the life history and shade tolerance differences between the species, whereby beech tends to be more flexible than spruce in adjusting its assimilation efficiency and growth in response to shifting environmental conditions, primarily to shifting irradiance (Čater, 2021; Pavlin et al., 2024). Additionally, the differences in response magnitudes may also be attributed to trade-offs between competitiveness and stress (Anderegg and HilleRisLambers, 2019; Laanisto and Niinemets, 2015; Schurman et al., 2024). Lower elevation mixed beech stands exhibit a generally lower among tree growth synchrony, reflecting higher levels of competition compared to higher elevation spruce-dominated forests, which, in contrast, exhibit higher sensitivity to climatic variability (Schurman et al., 2024). A canopy area removal could, therefore, also be associated with more pronounced light increases in lower-elevation mixed-beech forests compared to higher-elevation spruce-dominated forests. Competitive releases could thus be relatively less influential on spruce growth compared to beech growth. Finally, prior research has shown that factors such as canopy opening shape, orientation, and location alongside the position of a tree within the gap may be additional determinants of light received by the specific individual (Canham et al., 1990; Gálhidy et al., 2006; Stan and Daniels, 2014). The reconstructed percentage of plot canopy area removed may thus not be used as an absolute measure of light conditions for specific trees. Nevertheless, the size of the canopy opening is consistently related to elevated light availability in the published literature (Barton et al., 1989; Canham et al., 1990; Diaci et al., 2020; Gálhidy et al., 2006; Prévost and Raymond, 2012).

Interestingly, we did not document average growth during releases of either of the species to be sensitive to the analyzed climate variables. Namely, annual growth sensitivities of different demographic groups to temperature and water availability-related metrics were previously reported for both species in the Carpathian region (Begović et al., 2023; Bosela et al., 2021, 2018; Marchand et al., 2023; Saulnier et al., 2020; Schurman et al., 2024; Sedmáková et al., 2022, 2019). Generally, spruce exhibits stronger climatic signals compared to beech in the region. Spruce growth is more positively related to temperature, however, the temperature optimum appears to be similar for both species (Marchand et al., 2023; Schurman et al., 2024). Growth in spruce is also more sensitive to moisture availability relative to beech (Marchand et al., 2023) and is particularly strongly related to late winter and early spring water supply. Nevertheless, both species exhibit a wider range of growth responses to intra-annual climate variability (Saulnier et al., 2020; Schurman et al., 2024; Sedmáková et al., 2019). This typically diverse response of the species to climate likely contributed to the absence of detected climatic signals using relatively coarse multi-annual averages as predictors in our analyses. The climate dataset used in our analyses is characterized by a relatively long temporal coverage (covering the period after 1901), however, the spatial coverage is relatively coarse (0.5°), likely contributing to the absence of significant climate signals. Additionally, this study was not tailored to maximize the detection of growth climate sensitivity specifically, wherein the residual "noise" signal would be minimized. The climate signal was thus likely overridden by disturbance-, age-, and size-related growth trends (Carrer, 2011; Jiang et al., 2022; Rydval et al., 2018).

Apart from the absence of a strong climate signal in average growth rates during releases, a weak but significant negative growth trend response to potential direct incident radiation was detected for beech but not for spruce. The incident irradiance may importantly alter the microclimate, whereby south-facing slopes typically experience significantly higher temperatures compared to north-facing slopes (Rita et al., 2021; Suggitt et al., 2011). As the vapour pressure deficit (VPD) in the warmest part of the growing season is typically higher in canopy gaps compared to the forest understorey (Máliš et al., 2023), higher temperatures on more illuminated localities might increase the VPD further. This may impose higher drought stress on individuals on more sunny slopes through higher transpiration rates (Will et al., 2013), potentially leading to slower growth (Kašpar et al., 2024). Nonetheless, the effect size of the PDIR was significantly lower compared to the effect size of the disturbance severity. The positive effect of increased light availability on growth of released trees thus appears to largely surpass the potential risk of drought stress resulting from higher irradiance and related higher evapotranspiration. Due to the reported trend of rising VPD in recent decades in our study region (Marchand et al., 2023), growth particularly on more sunny and lower elevation slopes may be increasingly limited by moisture availability.

In accordance with prior studies, ontogeny-related effects on growth largely surpassed the effects of local climate (Anderson-Teixeira et al., 2021; Foster et al., 2016; Marchand et al., 2023; Martínez-Vilalta et al., 2012; Mašek et al., 2021; Michaletz et al., 2014), whereas beech responded primarily to DBH and spruce to age. Both the generally positive response of juvenile beech growth to increasing DBH and the negative response of juvenile spruce growth to increasing age are consistent with past studies on tree growth (Anderson-Teixeira et al., 2021; Begović et al., 2023; Foster et al., 2016; Marchand et al., 2023). However, the contrasting magnitudes of responses to DBH and age could stem from differences in life history traits between the two species. Age and size are generally correlated, and their effects on tree growth are intertwined (Foster et al., 2016). Nonetheless, the variability of prior growth rates may regulate how closely correlated age and size are in a population at a certain point in time. With shade-tolerant species, it is thus common that trees attain certain sizes at very different ages, whereby progression through juvenile classes, in particular, is largely regulated by the rate of competitive suppression (Begović et al., 2023; Bigler, 2016). Age at release onset may thus be correlated with and indicative of the duration of prior suppression (Orwig and Abrams, 1994). Growth sensitivity to age at release onset may thus depend also on species‘ shade tolerance. A somewhat lower shade tolerance capacity of high-elevation spruce compared to beech (Pavlin et al., 2024) could thus predispose spruce to a more pronounced decline of growth rates during releases with age progression. Interestingly, spruce releases were also markedly younger than beech releases (Figure 5e), additionally pointing at a faster decline in spruce’s capacity to sustain shade and react to canopy opening with advancing age relative to beech.

Average growth during releases exhibited a mild increase for both species during the analysed period. This trend is generally consistent with the trends reported for spruce and beech saplings across primary mountain forests of Central, Eastern, and Southeastern Europe, where tree growth increases are likely concomitant with ongoing temperature rises (Marchand et al., 2023). Positive growth trends were also documented for mature trees of both species (Begović et al., 2023; Bosela et al., 2016; Cienciala et al., 2018; Schurman et al., 2019; Sedmáková et al., 2019). However, a slowdown in growth increases as well as growth decreases were reported for both beech (Bosela et al., 2018) and spruce (Anderson-Teixeira et al., 2021) growing in European mountain forests. The latter phenomenon is likely an indicator of a potential transition from predominantly temperature- to predominantly moisture-limited growth, with warmer and drier conditions, progressively affecting European forests, particularly those at lower latitudes and elevations (Bosela et al., 2018; Schurman et al., 2019; Sedmáková et al., 2019; Tumajer et al., 2017). A generally positive growth trend of advanced regeneration of both dominant species of temperate European mountain forests documented here may thus slow down, level off, and eventually reverse in response to ongoing and future climatic perturbations. However, the responses may differ along the latitudinal and altitudinal gradients and will also likely be modified by local topography.

6.3.2 Drivers of release duration and concluding remarks

Ontogeny with particularly DBH at release onset was also the dominant and only significant determinant of release duration, whereby there were no apparent differences between the species. The decreasing radial growth release duration with increasing DBH was previously also reported for a few coniferous species in British Colombia (Stan and Daniels, 2010). Prior studies have indicated that release duration depends also on the position within the gap and have suggested that the lateral branch extension of boundary trees may influence release duration by affecting the light environment of the focal tree (Stan and Daniels, 2014, 2010; Vašíčková et al., 2019). As noted earlier, we were unable to account for tree positions inside the canopy gaps as we were also not able to account for the gradual nature of gap formation and closure (Krüger et al., 2024). Nonetheless, neither of the species exhibited a significant response of release duration to disturbance severity and associated irradiance, as previously demonstrated for spruce (Saulnier et al., 2020). This might be a consequence of a strong contingency of release duration on tree size, which potentially overrides the magnitudes of other less pronounced influences.

The growth response of released beech and spruce trees is controlled by several intrinsic and extrinsic factors, with important differences between the two species dominating neighbouring elevational belts of European temperate mountain forests. Disturbance severity and ontogeny-related factors are dominant drivers of released growth for both species, whereby the interspecific differences in response magnitudes to different drivers likely depend on contrasting life-history traits as well as differences in the dominant environmental drivers between the species. Although direct climatic controls of released growth were not clearly discernible from our analyses, indirect relationships suggest environmental factors play a significant role in controlling tree growth in the region. These include positive trends in growth rates during releases throughout the 20th century and a negative growth rate response of beech to potential irradiance. The growth of both species is generally positively related to the proportion of disturbed canopy. It is, however, unclear how the response of advanced regeneration in the analysed forests may change with potential future disturbance regime intensifications and shifts in climatic drivers of tree growth. These may be contingent on topography, as also partly shown by our results, where particularly populations on south-facing slopes may be the ones experiencing growth declines with further warming.

6.4 MANAGEMENT IMPLICATIONS

Structure, dynamics, and function of majority of European temperate forests have been significantly altered by past land use change and forestry practices. Namely, forest management practices typically significantly shorten return intervals between stand-replacing disturbances, resulting in younger forests and shorter carbon turnover rates in managed forest landscapes compared to primary forests (Pugh et al., 2024). The maintenance of several ecosystem services, such as carbon storage or habitat provision for a plethora of species, is thus often largely modified and diminished across large landscapes and regions. Some of the most prominent elements that are commonly curtailed to rare occurrence or complete absence from most of these land-use-driven ecosystems are the presence and development of old and large trees and deadwood (Nagel et al., 2014). The lengths of tree life cycles are crucial determinants of carbon residence times, a crucial factor dictating the long-term carbon storage capacities of forests (Körner, 2017; Martin-Benito et al., 2021). This work analyses the variability and drivers of developmental pathways and longevities of dominant tree species of European temperate mountain forests. The documented ages at canopy accession and life spans of trees significantly exceed the typical ages and life spans observed in managed stands, highlighting the important role of these unmanaged forests as long-term carbon stores. Additionally, considering their relatively low densities the old and large trees contribute disproportionately to both biomass carbon pools (Keith et al., 2024) as well as to supporting biodiversity (Kozák et al., 2023; Lindenmayer et al., 2014). Besides rare individuals, trees are rarely allowed to attain old ages and great sizes outside of strictly protected forest landscapes. Maintaining the strictly protected status of areas harboring large numbers of old and large trees, along with elevating the protection status in areas where these trees are still harvested, are thus necessary steps to halt the decline of forest ecosystem carbon pools and their biodiversity-supporting role. Given the relative scarcity of such remnants in the European temperate zone, setting aside additional areas from active management should be encouraged, especially where existing areas with old-growth attributes are below the functional size threshold needed to support native biodiversity. Moreover, in order to diminish the diverging dynamics of managed and protected forest areas, the retention of biological legacies across the managed forest landscapes, including deadwood and old and large trees, could be further promoted.

The results presented here show significant differences in canopy accession patterns and life spans between the dominant species of the analyzed temperate mountain forests, both bearing important implications for competitive success and species coexistence. A comparatively larger share of spruce and maple trees accessing the canopy without patterns of suppressed growth and exhibiting faster growth rates than particularly beech indicated that their successful progression through juvenile life stages is relatively more reliant on high light availability. A regime of predominantly small-scale, low-severity disturbance events presumably benefits the shade-tolerant regeneration of beech and fir. In contrast, the establishment and canopy recruitment of spruce, maple, and potentially other less shade-tolerant species, such as European ash or Scots elm, are more dependent on more intense, larger disturbances within such mixed forests. Compared to the typical harvesting patterns in forests governed by dominant management approaches (both even- and uneven-aged) in Europe, natural disturbance regimes generally cover a significantly wider range of disturbance sizes, frequencies, as well as severities (Aszalós et al., 2022). The structure of managed forests is thus mostly comparatively more homogenized relative to primary or long unmanaged forests. This often results in a narrower range of light and other stand conditions, failing to replicate the range of conditions necessary to promote the recruitment of species across different ecological niches (Ujházy et al., 2017). To more closely emulate natural mortality and structural patterns, it is thus necessary to combine approaches from various conventional silvicultural systems (Boncina, 2011; Nagel et al., 2014). For example, employing the single selection system takes great care to maintain a diverse vertical structure at the stand level. However, the sole application of this system across larger landscapes emulates an almost exclusively small-scale disturbance regime, which is particularly in favor of the late-seral, highly shade-tolerant species but may result in loss of the less shade-tolerant species (Boncina, 2011; Nagel et al., 2014). Supplementing this system with elements of other systems, such as irregular shelterwood or group selection with sporadic larger-scale harvests, may thus support a wider range of conditions needed to support a wider set of species.

Furthermore, the results revealed notable intraspecific differences in certain canopy accession metrics, but no differences in the life span of spruce growing in lower-elevation mixed forests compared to higher-elevation spruce-dominated forests. Shade tolerance capacity appears to diminish with elevation, as spruce at higher elevations tends to attain the canopy later than spruce at lower elevations, whereas it also sustains a shorter period of initial suppression. Nevertheless, a relatively high share of spruce trees growing in monodominant stands sustained a competitive suppression and was subsequently released (ca. 40%), indicating the notable role of advanced regeneration and diverse vertical structure in these forests. A large share of such spruce mountain forests in temperate Europe that are actively managed primarily for wood production are managed by even-aged silvicultural systems such as clearcutting or shelterwood promoting structures significantly more homogenized compared to similar natural stands. Compared to the natural disturbance regime variability in spruce mountain forests, the prevalent treatments of these management systems are generally relatively small, very severe, with relatively short rotation periods and often omitting or minimizing the retention of biological legacies (Čada et al., 2020). The near absence of deadwood, especially large logs, may not only negatively impact habitat availability but also hinder the development of spruce regeneration (Bače et al., 2012). To facilitate the habitat provision for the whole array of native species and to support the continuity of diverse structural elements, retention of a portion of trees and deadwood should be maintained at all times. The severities and spatial extent of treatments should be further diversified to better mimic the natural mixed-severity disturbance regime, focusing on small-scale but also moderate-scale and moderate-severity interventions (with patches of up to several hectares) (Čada et al., 2020). Maintaining the diverse vertical multi-age stand structure at different spatial scales may create conditions for the multiple tree and stand developmental pathways ultimately contributing to both resistance and resilience of forest stands to prevailing disturbance agents (O’Hara and Ramage, 2013).

Nevertheless, species composition and recruitment rates of trees in these forests are not dependent solely on the distribution of canopy openings in space and time and associated light levels but also depend on and interact with several other factors. For instance, herbivory (particularly deer browsing), soil conditions, microclimate, or topography may all drive species composition dynamics and need to be considered with silvicultural measures (Klopcic et al., 2014). The influence of physiographic features was documented in this work also. Namely, trees on more shaded north-facing slopes exhibit more releases compared to south-facing slopes. Trees on the north-facing slopes thus likely need larger canopy openings to successfully recruit in the canopy as trees on south-facing slopes.

The negative response of beech growth during releases to PDIR, however, indicates that the more intense insolation on south-facing slopes may also be related to decreased water supply. As global temperatures rise and the occurrence of climatic extremes increases, forests are increasingly impacted by droughts even in the mountainous areas of temperate Europe (Begović et al., 2020).

Along with a rising trend in disturbance activity in European forests (Seidl et al., 2014), the future resilience capacities of forest ecosystems in the region are increasingly uncertain. Assessing post-disturbance recovery of trees in contemporary forests provides a crucial baseline for assessing forest resilience in the future, whereby the growth of released beech and spruce trees showed a largely stable and slowly increasing trend in the recent past across the natural unmanaged mountain forests of Carpathians. Management interventions may accelerate the forest post-disturbance recovery rates. However, European temperate forests generally recover well in the absence of management interventions also (Senf et al., 2019). Particularly advanced regeneration is often damaged in the scope of post-disturbance salvage logging activities, by which the course of stand recovery may be altered (Cerioni et al., 2024; Taeroe et al., 2019). Additionally, salvage logging tends to homogenize the stand structure, often bearing negative consequences for biodiversity through lower habitat heterogeneity (Bace et al., 2023). Salvage logging may also negatively affect the protective function of removed legacy structures, thereby magnifying erosion and potential flood impacts. Additionally, it may increase stand susceptibility to further disturbances, such as windthrow, especially at pronounced stand edges (Leverkus et al., 2021; Stritih et al., 2021). Potential salvage logging implementation must, therefore, carefully evaluate its capacity to mitigate future disturbance risk alongside its short-, mid-, and long-term effects on the provision of various forest functions and should not be regarded as a default and uniform post-disturbance management activity.

7. CONCLUSIONS

In this dissertation thesis, patterns and drivers of selected tree life history traits of four dominant tree species of European temperate mountain forests were examined. Capitalizing on an extensive data set of tree cores collected across remnants of primary mountain forests in the Balkan Mountains, Carpathians, and Dinarides, the analyses were focused specifically on: i) life span variability among dominant tree species and its dominant drivers, as well as landscape variability of old tree densities, ii) the variability of canopy accession patterns across dominant tree species and quantification of how these patterns are influenced by disturbance history, climate, and topography, iii) growth releases in dominant tree species and the species-specific relationships between the growth and duration of growth releases and disturbance, climate conditions during release, topography, tree age and size, as well as associated temporal trends. The results demonstrate significant biological differences among analyzed species in their life span as well as canopy accession patterns, which may have an important role in the structural and compositional dynamics of European temperate forests. Additionally, disturbance history emerged as the prevailing driver of individual trees' progression through life stages and their life span.

The assessment of tree life spans in the region revealed that all four dominant species are capable of reaching relatively old ages, with individuals of each species exceeding 400 years. Nonetheless, significant differences in life span between these species also emerged, with beech exhibiting the oldest ages (the oldest individual dated to 578 years), followed by silver fir, Norway spruce, and maple as the least long-living species of the four. These differences may importantly contribute to multispecies coexistence, whereby the lesser competitive and colonizing power of tree species may be offset by the longer persistence of individuals in the landscape. The results further demonstrated that tree life spans were driven primarily by disturbance histories in the landscape. Namely, dominant disturbance agents in the region cause disproportionately higher mortality of older and larger individuals compared to younger and smaller ones, which results in lower densities of old trees and younger forests in areas with relatively more severe and more frequent disturbances. Additionally, disturbances modulate forest structure and release the lower stature understorey trees of light suppression and thus enable them to increase their growth. The probability of reaching a longer life span proved to be tied to lifetime growth rates, whereby trees that survived periods of very suppressed growth and/or exhibited multiple suppression release cycles were more likely to reach old age. Tree longevity in these forests is thus closely related to canopy accession. Effects of other factors on probability of attaining old age were less apparent, nevertheless a week negative relationship with mean vegetation season was significant for fir and maple. Densities of the old trees showed marked variation across the study region which is likely linked to variability in local disturbance histories. With shifting climatic growth drivers and disturbance regimes it is uncertain how tree longevity patterns may change in the future. However, reported trends of increasing disturbance activity across temperate forest ecosystems (Seidl et al., 2017) are likely to drive a decrease in old tree densities, promoting comparatively younger forests associated with shorter carbon residence times.

In addition to significant differences in tree life span among the four most prevalent species in the analyzed landscapes, the presented analyses also reveal distinct differences in their canopy accession patterns, as well as considerable intraspecific variability in the growth patterns leading to canopy accession. Individuals of all four species survived after at least 100 years of initially suppressed growth, yet fir and especially beech, on average, attained canopy later and survived longer periods of initial suppression, with a larger share of individuals attaining the canopy after initial suppression compared to spruce and maple. Alternatively, canopy accession of spruce and maple depended more on faster growth, indicating their competitive success is tied more to non-suppressed conditions. Furthermore, spruce from lower-elevation mixed forests exhibited a more shade-tolerant character compared to spruce from higher-elevation spruce-dominated forests. A larger proportion of spruce trees from mixed forests, relative to those from high elevations, reached the canopy after initially suppressed growth and sustained longer periods of initial suppression. Lastly, the modeling results showed that canopy accession patterns in these forests are contingent primarily on disturbance histories, which regulate light availability, a key limiting growth factor for juvenile trees in closed-canopy forests. No significant relationship between climatic variability during canopy accession and canopy accession patterns was documented here, which might be a consequence of strong disturbance effects overriding the canopy accession relationships with climatic gradients. Light availability is further regulated by topography, which apparent from presented results, also indirectly affects the canopy accession patterns. Namely, a larger share of trees on lighter, south-facing slopes reached the canopy without exhibiting a release, indicating that on more illuminated slopes trees need smaller canopy openings to avoid suppression. No significant relationship between climatic variability during canopy accession and canopy accession patterns was documented here, which might be a consequence of strong disturbance effects overriding the canopy accession relationships with environmental gradients. Amplified disturbance regimes may shift the competitive relationships between the species in these forests, whereby particularly the faster-growing, more light-demanding species could benefit. Yet it is less clear how species' growth rates will respond to future environmental change across geographical gradients, whereby relationships in productivity gradients between different species may also shift.

Both beech and spruce growth releases across primary mountain forests of the Carpathians showed a marginal increase throughout the past century, indicating stable rates of canopy recovery by advanced regeneration in natural mountain forests of the region. Growth rates during releases of both species responded positively to disturbance severity. However, the magnitude of the relationship was much stronger for beech compared to spruce. The effect of age and size dynamics on growth release response also differed between the species. Growth of released beeches responded primarily positively to increasing DBH, whereas spruce growth responded primarily negatively to age at release onset. This decreasing response of spruce with advancing age may suggest that the negative impact of prolonged prior suppression on its reactive capacity after release is more pronounced compared to beech. These differences further attest to the relatively lower shade tolerance of spruce compared to beech. Growth releases of neither of the species showed a consistent response to long-term climatic averages, nevertheless, beech growth response decreased mildly on the gradient from less illuminated north-facing slopes towards more illuminated south-facing slopes. This could imply that decreasing water availability towards south-facing positions might be a limiting growth factor for beech. In contrast to growth rates during releases, the durations of these releases were largely unaffected by extrinsic factors and showed a strong negative correlation with DBH for both species and are thus less likely to change with alterations in extrinsic growth drivers. In light of ongoing environmental shifts, these documented growth release responses of the two major European tree species collected across ranges of their high natural prevalence provide a baseline that may serve to monitor the future canopy recovery and resilience capacities of these important natural forests.

8. LITERATURE

Abrams, M.D., Ruffner, C.M., DeMeo, T.E., 1998. Dendroecology and species co-existence in an old-growth Quercus-Acer-Tilia talus slope forest in the central Appalachians, USA. For. Ecol. Manage. 106, 9–18. https://doi.org/10.1016/S0378-1127(97)00234-X

Acasuso-Rivero, C., Murren, C.J., Schlichting, C.D., Steiner, U.K., 2019. Adaptive phenotypic plasticity for life-history and less fitness-related traits. Proc. R. Soc. B Biol. Sci. 286, 1–9. https://doi.org/10.1098/rspb.2019.0653

Adler, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C., Franco, M., 2014. Functional traits explain variation in plant life history strategies. Proc. Natl. Acad. Sci. 111, 740–745. https://doi.org/10.1073/PNAS.1315179111

Ally, D., Ritland, K., Otto, S.P., 2010. Aging in a long-lived clonal tree. PLoS Biol. 8, 19–20. https://doi.org/10.1371/journal.pbio.1000454

Altman, J., Fibich, P., Trotsiuk, V., Altmanova, N., 2024. Global pattern of forest disturbances and its shift under climate change. Sci. Total Environ. 915. https://doi.org/10.1016/j.scitotenv.2024.170117

Anderegg, L.D.L., HilleRisLambers, J., 2019. Local range boundaries vs. large-scale trade-offs: climatic and competitive constraints on tree growth. Ecol. Lett. 22, 787–796. https://doi.org/10.1111/ele.13236

Anderson-Teixeira, K.J., Herrmann, V., Rollinson, C.R., Gonzalez, B., Gonzalez-Akre, E.B., Pederson, N., Alexander, M.R., Allen, C.D., Alfaro-Sánchez, R., Awada, T., Baltzer, J.L., Baker, P.J., Birch, J.D., Bunyavejchewin, S., Cherubini, P., Davies, S.J., Dow, C., Helcoski, R., Kašpar, J., Lutz, J.A., Margolis, E.Q., Maxwell, J.T., McMahon, S.M., Piponiot, C., Russo, S.E., Šamonil, P., Sniderhan, A.E., Tepley, A.J., Vašíčková, I., Vlam, M., Zuidema, P.A., 2021. Joint effects of climate, tree size, and year on annual tree growth derived from tree-ring records of ten globally distributed forests. Glob. Chang. Biol. 1–22. https://doi.org/10.1111/gcb.15934

Annighöfer, P., 2018. Stress relief through gap creation? Growth response of a shade tolerant species (Fagus sylvatica L.) to a changed light environment. For. Ecol. Manage. 415–416, 139–147. https://doi.org/10.1016/j.foreco.2018.02.027

Annighöfer, P., Petritan, A.M., Petritan, I.C., Ammer, C., 2017. Disentangling juvenile growth strategies of three shade-tolerant temperate forest tree species responding to a light gradient. For. Ecol. Manage. 391, 115–126. https://doi.org/10.1016/j.foreco.2017.01.010

Asbeck, T., Kozák, D., Spînu, A.P., Mikoláš, M., Zemlerová, V., Svoboda, M., 2022. Tree-Related Microhabitats Follow Similar Patterns but are More Diverse in Primary Compared to Managed Temperate Mountain Forests. Ecosystems 25, 712–726. https://doi.org/10.1007/s10021-021-00681-1

Asbeck, T., Pyttel, P., Frey, J., Bauhus, J., 2019. Predicting abundance and diversity of tree-related microhabitats in Central European montane forests from common forest attributes. For. Ecol. Manage. 432, 400–408. https://doi.org/10.1016/j.foreco.2018.09.043

Aszalós, R., Thom, D., Aakala, T., Angelstam, P., Brūmelis, G., Gálhidy, L., Gratzer, G., Hlásny, T., Katzensteiner, K., Kovács, B., Knoke, T., Larrieu, L., Motta, R., Müller, J., Ódor, P., Roženbergar, D., Paillet, Y., Pitar, D., Standovár, T., Svoboda, M., Szwagrzyk, J., Toscani, P., Keeton, W.S., 2022. Natural disturbance regimes as a guide for sustainable forest management in Europe, Ecological Applications. https://doi.org/10.1002/eap.2596

Babst, F., Bouriaud, O., Poulter, B., Trouet, V., Girardin, M.P., Frank, D.C., 2019. Twentieth century redistribution in climatic drivers of global tree growth. Sci. Adv. 5, 1–10. https://doi.org/10.1126/sciadv.aat4313

Bace, R., Hofmeister, J., Vitkova, L., Brabec, M., Begovic, K., Cada, V., Janda, P., Kozak, D., Mikolas, M., Nagel, T.A., Pavlin, J., Rodrigo, R., Vostarek, O., Svoboda, M., 2023. Response of habitat quality to mixed severity disturbance regime in Norway spruce forests. J. Appl. Ecol. 60, 1–12. https://doi.org/10.1111/1365-2664.14409

Bače, R., Svoboda, M., Pouska, V., Janda, P., Červenka, J., 2012. Natural regeneration in Central-European subalpine spruce forests: Which logs are suitable for seedling recruitment? For. Ecol. Manage. 266, 254–262. https://doi.org/10.1016/j.foreco.2011.11.025

Baillie, M.G.L., 1992. Dendrochronology and past environmental change. Proc. Br. Acad. 77, 5–23.

Baker, P.J., Bunyavejchewin, S., 2006. Suppression, release and canopy recruitment in five tree species from a seasonal tropical forest in western Thailand. J. Trop. Ecol. 22, 521–529. https://doi.org/10.1017/s0266467406003312

Bakker, J.P., Olff, H., Willems, J.H., Zobel, M., 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? J. Veg. Sci. 7, 147–156. https://doi.org/10.2307/3236314

Barredo, J.I., Brailescu, C., Teller, A., Sabatini, F.M., Mauri, A., Janouskova, K., 2021. Mapping and assessment of primary and old-growth forests in Europe. Publications Office of the European Union, Luxembourg. https://doi.org/doi:10.2760/797591

Barton, A.M., Fetcher, N., Redhead, S., 1989. The Relationship Between Treefall Gap Size And Light Flux In A Neotropical Rain Forest In Costa Rica. J. Trop. Ecol. 5, 437–439. https://doi.org/10.1017/S0266467400003898

Barton, K., 2019. MuMIn: Multi-Model Inference.

Baudisch, A., Salguero-Gómez, R., Jones, O.R., Wrycza, T., Mbeau-Ache, C., Franco, M., Colchero, F., 2013. The pace and shape of senescence in angiosperms. J. Ecol. 101, 596–606. https://doi.org/10.1111/1365-2745.12084

Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. For. Ecol. Manage. 258, 525–537. https://doi.org/10.1016/j.foreco.2009.01.053

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. Agric. For. Meteorol. 288–289, 108000. https://doi.org/10.1016/j.agrformet.2020.108000

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. Glob. Chang. Biol. 29, 143–164. https://doi.org/10.1111/gcb.16461

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of european forests. For. Ecol. Manage. 132, 39–50. https://doi.org/10.1016/S0378-1127(00)00378-9

Biedermann, P.H.W., Müller, J., Grégoire, J.C., Gruppe, A., Hagge, J., Hammerbacher, A., Hofstetter, R.W., Kandasamy, D., Kolarik, M., Kostovcik, M., Krokene, P., Sallé, A., Six, D.L., Turrini, T., Vanderpool, D., Wingfield, M.J., Bässler, C., 2019. Bark Beetle Population Dynamics in the Anthropocene: Challenges and Solutions. Trends Ecol. Evol. 34, 914–924. https://doi.org/10.1016/j.tree.2019.06.002

Bigler, C., 2016. Trade-Offs between Growth Rate, Tree Size and Lifespan of Mountain Pine (Pinus montana) in the Swiss National Park. PLoS One 11, 1–19. https://doi.org/10.1371/journal.pone.0150402

Bigler, C., Veblen, T.T., 2009. Increased early growth rates decrease longevities of conifers in subalpine forests. Oikos 118, 1130–1138. https://doi.org/10.1111/j.1600-0706.2009.17592.x

Biondi, F., Qeadan, F., 2009. A Theory-Driven Approach to Tree-Ring Standardization: Defining the Biological Trend from Expected Basal Area Increment. Tree-Ring Res. 64, 81–96. https://doi.org/10.3959/2008-6.1

Black, B.A., Colbert, J.J., Pederson, N., 2008. Relationships between radial growth rates and lifespan within North American tree species. Écoscience 15, 349–357. https://doi.org/10.2980/15-3-3149

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24, 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Bonan, G.B., 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. Science (80-.). 320, 1444–1449. https://doi.org/10.1126/science.1155121

Boncina, A., 2011. History, current status and future prospects of uneven-aged forest management in the Dinaric region: An overview. Forestry 84, 467–478. https://doi.org/10.1093/forestry/cpr023

Bonsall, M.B., 2006. Longevity and ageing: Appraising the evolutionary consequences of growing old. Philos. Trans. R. Soc. B Biol. Sci. 361, 119–135. https://doi.org/10.1098/rstb.2005.1738

Bormann, F.H., 2016. Changes in the Growth Pattern of White Pine Trees Undergoing Suppression. Ecology 46, 269–277.

Bosela, M., Lukac, M., Castagneri, D., Sedmák, R., Biber, P., Carrer, M., Konôpka, B., Nola, P., Nagel, T.A., Popa, I., Roibu, C.C., Svoboda, M., Trotsiuk, V., Büntgen, U., 2018. Contrasting effects of environmental change on the radial growth of co-occurring beech and fir trees across Europe. Sci. Total Environ. 615, 1460–1469. https://doi.org/10.1016/j.scitotenv.2017.09.092

Bosela, M., Štefančík, I., Petráš, R., Vacek, S., 2016. The effects of climate warming on the growth of European beech forests depend critically on thinning strategy and site productivity. Agric. For. Meteorol. 222, 21–31. https://doi.org/10.1016/j.agrformet.2016.03.005

Bosela, M., Tumajer, J., Cienciala, E., Dobor, L., Kulla, L., Marčiš, P., Popa, I., Sedmák, R., Sedmáková, D., Sitko, R., Šebeň, V., Štěpánek, P., Büntgen, U., 2021. Climate warming induced synchronous growth decline in Norway spruce populations across biogeographical gradients since 2000. Sci. Total Environ. 752. https://doi.org/10.1016/j.scitotenv.2020.141794

Bouriaud, O., Bréda, N., Le Moguédec, G., Nepveu, G., 2004. Modelling variability of wood density in beech as affected by ring age, radial growth and climate. Trees - Struct. Funct. 18, 264–276. https://doi.org/10.1007/s00468-003-0303-x

Bouriaud, O., Marin, G., Bouriaud, L., Hessenmöller, D., Schulze, E., 2016. Romanian legal management rules limit wood production in Norway spruce and beech forests. For. Ecosyst. 3, 1–11. https://doi.org/10.1186/s40663-016-0079-2

Bräker, O.U., 2002. Measuring and data processing in tree-ring research - A methodological introduction. Dendrochronologia 20, 203–216. https://doi.org/10.1078/1125-7865-00017

Breheny, P., Burchett, W., 2017. Visualization of Regression Models Using visreg. R J. 9, 56–71.

Brienen, R.J.W., Caldwell, L., Duchesne, L., Voelker, S., Barichivich, J., Baliva, M., Ceccantini, G., Di Filippo, A., Helama, S., Locosselli, G.M., Lopez, L., Piovesan, G., Schöngart, J., Villalba, R., Gloor, E., 2020. Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. Nat. Commun. 11, 1–10.

https://doi.org/10.1038/s41467-020-17966-z

Brienen, R.J.W., Zuidema, P.A., 2006. Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. J. Ecol. 94, 481–493. https://doi.org/10.1111/j.1365-2745.2005.01080.x

Brienen, R.J.W., Zuidema, P.A., Martínez-Ramos, M., 2010. Attaining the canopy in dry and moist tropical forests: Strong differences in tree growth trajectories reflect variation in growing conditions. Oecologia 163, 485–496. https://doi.org/10.1007/s00442-009-1540-5

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 378–400. https://doi.org/10.32614/rj-2017-066

Brutovská, E., Sámelová, A., Dušička, J., Mičieta, K., 2013. Ageing of trees: Application of general ageing theories. Ageing Res. Rev. 12, 855–866. https://doi.org/10.1016/j.arr.2013.07.001

Buechling, A., Martin, P.H., Canham, C.D., 2017. Climate and competition effects on tree growth in Rocky Mountain forests. J. Ecol. 105, 1636–1647. https://doi.org/10.1111/1365-2745.12782

Büntgen, U., Krusic, P.J., Piermattei, A., Coomes, D.A., Esper, J., Myglan, V.S., Kirdyanov, A. V., Camarero, J.J., Crivellaro, A., Körner, C., 2019. Limited capacity of tree growth to mitigate the global greenhouse effect under predicted warming. Nat. Commun. 10, 2171. https://doi.org/10.1038/s41467-019-10174-4

Burian, A., Barbier de Reuille, P., Kuhlemeier, C., 2016. Patterns of Stem Cell Divisions Contribute to Plant Longevity. Curr. Biol. 26, 1385–1394. https://doi.org/10.1016/j.cub.2016.03.067

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65, 23–35. https://doi.org/10.1007/s00265-010-1029-6

Čada, V., Morrissey, R.C., Michalová, Z., Bače, R., Janda, P., Svoboda, M., 2016. Frequent severe natural disturbances and non-equilibrium landscape dynamics shaped the mountain spruce forest in central Europe. For. Ecol. Manage. 363, 169–178. https://doi.org/10.1016/j.foreco.2015.12.023

Čada, V., Trotsiuk, V., Janda, P., Mikoláš, M., Bače, R., Nagel, T.A., Morrissey, R.C., Tepley, A.J., Vostarek, O., Begović, K., Chaskovskyy, O., Dušátko, M., Kameniar, O., Kozák, D., Lábusová, J., Málek, J., Meyer, P., Pettit, J.L., Schurman, J.S., Svobodová, K., Synek, M., Teodosiu, M., Ujházy, K., Svoboda, M., 2020. Quantifying natural disturbances using a large-scale dendrochronological reconstruction to guide forest management. Ecol. Appl. 30, 1–13. https://doi.org/10.1002/eap.2189

Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Čada, V., Camarero, J.J., Cherubini, P., Cochard, H., Coyea, M.R., Čufar, K., Das, A.J., Davi, H., Delzon, S., Dorman, M., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hartmann, H., Hereş, A.M., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Kramer, K., Lens, F., Levanic, T., Linares Calderon, J.C., Lloret, F., Lobo-Do-Vale, R., Lombardi, F., López Rodríguez, R., Mäkinen, H., Mayr, S., Mészáros, I., Metsaranta, J.M., Minunno, F., Oberhuber, W., Papadopoulos, A., Peltoniemi, M., Petritan, A.M., Rohner, B., Sangüesa-Barreda, G., Sarris, D., Smith, J.M., Stan, A.B., Sterck, F., Stojanović, D.B., Suarez, M.L., Svoboda, M., Tognetti, R., Torres-Ruiz, J.M., Trotsiuk, V., Villalba, R., Vodde, F., Westwood, A.R., Wyckoff, P.H., Zafirov, N., Martínez-Vilalta, J., 2017. A synthesis of radial growth patterns preceding tree mortality. Glob. Chang. Biol. 23, 1675–1690. https://doi.org/10.1111/gcb.13535

Camarero, J.J., Ortega-Martínez, M., 2021. Tree growth in the aftermath of A flood: A tree-ring based reconstruction of the impacts of the 1996-Biescas catastrophe. Dendrochronologia 65. https://doi.org/10.1016/j.dendro.2020.125783

Camarero, J.J., Ortega-Martínez, M., 2019. Sancho, the oldest known Iberian shrub. Dendrochronologia 53, 32–36. https://doi.org/10.1016/j.dendro.2018.11.003

Canadell, J.G., Schulze, E.D., 2014. Global potential of biospheric carbon management for climate mitigation. Nat. Commun. 5. https://doi.org/10.1038/ncomms6282

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. 20, 620–631. https://doi.org/10.1139/x90-084

Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H., 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can. J. For. Res. 24, 227–349. https://doi.org/10.1139/x94-046

Cannon, C.H., Piovesan, G., Munné-Bosch, S., 2022. Old and ancient trees are life history lottery winners and vital evolutionary resources for long-term adaptive capacity. Nat. Plants 8, 136–145. https://doi.org/10.1038/s41477-021-01088-5

Carrer, M., 2011. Individualistic and Time-Varying Tree-Ring growth to climate sensitivity. PLoS One 6. https://doi.org/10.1371/journal.pone.0022813

Castagneri, D., Storaunet, K.O., Rolstad, J., 2013. Age and growth patterns of old Norway spruce trees in Trillemarka forest, Norway. Scand. J. For. Res. 28, 232–240. https://doi.org/10.1080/02827581.2012.724082

Čater, M., 2021. Response and mortality of beech, fir, spruce and sycamore to rapid light exposure after large-scale disturbance. For. Ecol. Manage. 498, 119554. https://doi.org/10.1016/j.foreco.2021.119554

Cerioni, M., Brabec, M., Bače, R., Bāders, E., Bončina, A., Brůna, J., Chećko, E., Cordonnier, T., de Koning, J.H.C., Diaci, J., Dobrowolska, D., Dountchev, A., Engelhart, J., Fidej, G., Fuhr, M., Garbarino, M., Jansons, Ā., Keren, S., Kitenberga, M., Klopčič, M., Konôpka, B., Kopecký, M., Köster, K., Kucbel, S., Lacombe, E., Laurent, L., Leyman, A., Lingua, E., Macek, M., Maciejewski, Z., Malandra, F., Marzano, R., Metslaid, M., Morresi, D., Panayotov, M., Pawlak, B., Pittner, J., Šebeň, V., Socha, J., Svoboda, M., Szwagrzyk, J., Tsvetanov, N., Urbinati, C., Vallet, P., Van de Kerckhove, P., Vandekerkhove, K., Vencurik, J., Vitali, A., Vodde, F., Wild, J., Nagel, T.A., 2024. Recovery and resilience of European temperate forests after large and severe disturbances. Glob. Chang. Biol. 30, 1–18. https://doi.org/10.1111/gcb.17159

Charnov, E.L., Berrigan, D., 1991. Dimensionless numbers and the assembly rules for life histories. Philos. Trans. R. Soc. London. Ser. B Biol. Sci. 332, 41–48. https://doi.org/10.1098/rstb.1991.0031

Cienciala, E., Altman, J., Doležal, J., Kopáček, J., Štěpánek, P., Ståhl, G., Tumajer, J.,

2018. Increased spruce tree growth in Central Europe since 1960s. Sci. Total Environ. 619–620, 1637–1647. https://doi.org/10.1016/j.scitotenv.2017.10.138

Clark, D.A., Clark, D.B., 1999. Assessing the Growth of Tropical Rain Forest Trees : Issues for Forest Modeling and Management. Ecol. Appl. 9, 981–997.

Coley, P.D., Bryant, J.P., Chapin, F.S., 1985. Resource Availability and Plant Antiherbivore Defense. Science (80-.). 230, 895–899. https://doi.org/10.1126/science.230.4728.895

Coomes, D.A., Allen, R.B., 2007a. Effects of size, competition and altitude on tree growth. J. Ecol. 95, 1084–1097. https://doi.org/10.1111/j.1365-2745.2007.01280.x

Coomes, D.A., Allen, R.B., 2007b. Mortality and tree-size distributions in natural mixed-age forests. J. Ecol. 95, 27–40. https://doi.org/10.1111/j.1365-2745.2006.01179.x

D’Amato, A.W., Orwig, D.A., 2008. Stand and landscape-level disturbance dynamics in old-growth forests in Western Massachusetts. Ecol. Monogr. 78, 507–522. https://doi.org/10.1890/07-0593.1

Dani, K.G.S., Kodandaramaiah, U., 2018. Ageing in Trees: Role of Body Size Optimization in Demographic Senescence. Perspect. Plant Ecol. Evol. Syst. https://doi.org/10.1016/j.ppees.2018.10.002

Das, A.J., Stephenson, N.L., Davis, K.P., 2016. Why do trees die? Characterizing the drivers of background tree mortality. Ecology 97, 2616–2627. https://doi.org/10.1002/ecy.1497

De Frenne, P., 2023. Novel light regimes in European forests. Nat. Ecol. Evol. 8, 196–202. https://doi.org/10.1038/s41559-023-02242-2

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J., Ashcroft, M.B., Christiansen, D.M., Decocq, G., Pauw, K. De, Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klinges, D.H., Koelemeijer, I.A., Lembrechts, J.J., Marrec, R., Meeussen, C., Ogée, J., Tyystjärvi, V., Vangansbeke, P., Hylander, K., Frenne, P. De, 2021. Forest microclimates and climate change : Importance , drivers and future research agenda. Glob. Chang. Biol. 27, 2279–2297. https://doi.org/10.1111/gcb.15569

De Kroon, H., Huber, H., Stuefer, J.F., Van Groenendael, J.M., 2005. A modular concept of phenotypic plasticity in plants. New Phytol. 166, 73–82.

https://doi.org/10.1111/j.1469-8137.2004.01310.x

de Martonne, E., 1926. Aréisme et indice d'aridité. Bull. Assoc. Geogr. Fr. N°9, 3–5.

Di Filippo, A., Biondi, F., Maugeri, M., Schirone, B., Piovesan, G., 2012. Bioclimate and growth history affect beech lifespan in the Italian Alps and Apennines. Glob. Chang. Biol. 18, 960–972. https://doi.org/10.1111/j.1365-2486.2011.02617.x

Di Filippo, A., Biondi, F., Piovesan, G., Ziaco, E., 2017. Tree ring-based metrics for assessing old-growth forest naturalness. J. Appl. Ecol. 54, 737–749. https://doi.org/10.1111/1365-2664.12793

Di Filippo, A., Pederson, N., Baliva, M., Brunetti, M., Dinella, A., Kitamura, K., Knapp, H.D., Schirone, B., Piovesan, G., 2015. The longevity of broadleaf deciduous trees in Northern Hemisphere temperate forests: insights from tree-ring series. Front. Ecol. Evol. 3, 1–15. https://doi.org/10.3389/fevo.2015.00046

Diaci, J., Rozman, J., Rozman, A., 2020. Regeneration gap and microsite niche partitioning in a high alpine forest: Are Norway spruce seedlings more drought-tolerant than beech seedlings? For. Ecol. Manage. 455. https://doi.org/10.1016/j.foreco.2019.117688

Diaconu, D., Wassenberg, M., Spiecker, H., 2016. Variability of European beech wood density as influenced by interactions between tree-ring growth and aspect. For. Ecosyst. 3:6, 1–9. https://doi.org/10.1186/s40663-016-0065-8

Douglass, A.E., 1941. Crossdating in Dendrochronology. J. For. 39, 825–831.

Douglass, A.E., 1909. Weather Cycles in the Growth of Big Trees. Mon. Weather Rev. 37, 225–237.

Duncan, R.P., 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (Dacrycarpus dacrydioides). New Zeal. Nat. Sci. 16, 31–37.

Duncker, P.S., Barreiro, S.M., Hengeveld, G.M., Lind, T., Mason, W.L., Ambrozy, S., Spiecker, H., 2012. Classification of forest management approaches: A new conceptual framework and its applicability to European forestry. Ecol. Soc. 17. https://doi.org/10.5751/ES-05262-170451

Ellenberg, H., 1988. Vegetation Ecology of Central Europe, 4th Editio. ed. Cambridge University Press, Cambridge.

Ellenberg, H., Weber, H.E., Düll, R., Werner, W., Paulißen, D., 1991. Zeigerwerte der Pflanzen in Mitteleuropa, Scripta Ge. ed. Verlag Erich Goltze KG, Göttingen.

EU biodiversity strategy for 2030 : bringing nature back into our lives, 2021. https://doi.org/10.2779/677548

Fabian, D.K., Flatt, T., 2012. Life history evolution. Nat. Educ. Knowl. 3(10), 465–468. https://doi.org/10.1016/B978-0-12-383832-2.00066-9

Feldmann, E., Drößler, L., Hauck, M., Kucbel, S., Pichler, V., Leuschner, C., 2018. Canopy gap dynamics and tree understory release in a virgin beech forest, Slovakian Carpathians. For. Ecol. Manage. 415–416, 38–46. https://doi.org/10.1016/j.foreco.2018.02.022

Ferenčík, M., Svitok, M., Mikoláš, M., Hofmeister, J., Majdanová, L., Vostarek, O., Kozák, D., Bače, R., Begović, K., Běťák, J., Čada, V., Dušátko, M., Dvořak, D., Frankovič, M., Gloor, R., Janda, P., Kameniar, O., Kříž, M., Kunca, V., Markuljková, K., Ralhan, D., Rodrigo, R., Rydval, M., Pavlin, J., Pouska, V., Synek, M., Zemlerová, V., Svoboda, M., 2022. Spatial and temporal extents of natural disturbances differentiate deadwood-inhabiting fungal communities in spruce primary forest ecosystems. For. Ecol. Manage. 517, 1–10. https://doi.org/10.1016/j.foreco.2022.120272

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086

FOREST EUROPE, 2020. State of Europe’s Forests 2020.

Foster, J.R., Finley, A.O., D’Amato, A.W., Bradford, J.B., Banerjee, S., 2016. Predicting tree biomass growth in the temperate-boreal ecotone: Is tree size, age, competition, or climate response most important? Glob. Chang. Biol. 22, 2138–2151. https://doi.org/10.1111/gcb.13208

Fox, J., Weisberg, S., 2019. An R Companion to Applied Regression, Third edit. ed. Sage Publications, Thousand Oaks, CA.

Fox, J., Weisberg, S., 2018. Visualizing fit and lack of fit in complex regression models with predictor effect plots and partial residuals. J. Stat. Softw. 87, 1–27. https://doi.org/10.18637/jss.v087.i09

Franco, M., Silvertown, J., 1996. Life history variation in plants: an exploration of the fast-slow continuum hypothesis. Philos. Trans. R. Soc. London. Ser. B Biol. Sci. 351, 1341–1348. https://doi.org/10.1098/rstb.1996.0117

Franklin, J.F., Spies, T.A., Pelt, R. Van, Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155, 399–423. https://doi.org/10.1016/S0378-1127(01)00575-8

Frankovič, M., Janda, P., Mikoláš, M., Čada, V., Kozák, D., Pettit, J.L., Nagel, T.A., Buechling, A., Matula, R., Trotsiuk, V., Gloor, R., Dušátko, M., Kameniar, O., Vostarek, O., Lábusová, J., Ujházy, K., Synek, M., Begović, K., Ferenčík, M., Svoboda, M., 2020. Natural dynamics of temperate mountain beech-dominated primary forests in Central Europe. For. Ecol. Manage. 479, 118522. https://doi.org/10.1016/j.foreco.2020.118522

Fraver, S., White, A.S., 2005. Identifying growth releases in dendrochronological studies of forest disturbance. Can. J. For. Res. 35, 1648–1656. https://doi.org/10.1139/x05-092

Fraver, S., White, A.S., Seymour, R.S., 2009. Natural disturbance in an old-growth landscape of northern Maine, USA. J. Ecol. 97, 289–298. https://doi.org/10.1111/j.1365-2745.2008.01474.x

Frelich, L.E., Lorimer, C.G., 1991. Natural disturbance regimes in hemlock-hardwood forests of the upper great lakes region. Ecol. Monogr. 61, 145–164. https://doi.org/10.2307/1943005

Fritts, H.C., Swetnam, T.W., 1989. Dendroecology: A Tool for Evaluating Variations in Past and Present Forest Environments. Adv. Ecol. Res. 19, 111–188. https://doi.org/10.1016/S0065-2504(08)60158-0

Fritz, Ö., Heilmann-Clausen, J., 2010. Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (Fagus sylvatica). Biol. Conserv. 143, 1008–1016. https://doi.org/10.1016/j.biocon.2010.01.016

Gálhidy, L., Mihók, B., Hagyó, A., Rajkai, K., Standovár, T., 2006. Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a

Hungarian beech forest. Plant Ecol. 183, 133–145. https://doi.org/10.1007/s11258-005-9012-4

Gamborg, C., Larsen, J.B., 2003. “Back to nature” - A sustainable future for forestry? For. Ecol. Manage. 179, 559–571. https://doi.org/10.1016/S0378-1127(02)00553-4

Garbarino, M., Marzano, R., Shaw, J.D., Long, J.N., 2015. Environmental drivers of deadwood dynamics in woodlands and forests. Ecosphere 6. https://doi.org/10.1890/ES14-00342.1

Garnier, S., Ross, N., Rudis, R., Camargo, A.P., Scianini, M., Scherer, C., 2021. Rvision - Colorblind-Friendly Color Maps for R.

Geber, M.A., 2006. The Cost of Meristem Limitation in Polygonum arenastrum: Negative Genetic Correlations between Fecundity and Growth. Evolution (N. Y). 44, 799. https://doi.org/10.2307/2409547

Giesecke, T., Hickler, T., Kunkel, T., Sykes, M.T., Bradshaw, R.H.W., 2007. Towards an understanding of the Holocene distribution of Fagus sylvatica L. J. Biogeogr. 34, 118–131. https://doi.org/10.1111/j.1365-2699.2006.01580.x

Givnish, T.J., 1988. Adaptation to sun and shade: a whole-plant perspective. Aust. J. Plant Physiol. 15, 63–92. https://doi.org/10.1071/pp9880063

Global Forest Resources Assessment 2020: Main report, 2020. . Rome. https://doi.org/https://doi.org/10.4060/ca9825en

Gloor, R., Svitok, M., Mikoláš, M., Hofmeister, J., Halda, J., Janda, P., Sabatini, F.M., Zemanová, L., Buechling, A., Kozák, D., Ferenčík, M., Frankovič, M., Dušátko, M., Svoboda, M., 2024. Sustaining forest biodiversity: Exploring the effect of long-term natural disturbance dynamics on contemporary lichen communities in primary forest ecosystems. For. Ecosyst. 11. https://doi.org/10.1016/j.fecs.2024.100214

Glynn, C., Herms, D.A., Orians, C.M., Hansen, R.C., Larsson, S., 2007. Testing the growth-differentiation balance hypothesis: Dynamic responses of willows to nutrient availability. New Phytol. 176, 623–634. https://doi.org/10.1111/j.1469-8137.2007.02203.x

Gratani, L., 2014. Plant Phenotypic Plasticity in Response to Environmental Factors. Adv. Bot. 2014. https://doi.org/10.1155/2014/208747

Gravel, D., Canham, C.D., Beaudet, M., Messier, C., 2010. Shade tolerance, canopy gaps and mechanisms of coexistence of forest trees. Oikos 119, 475–484. https://doi.org/10.1111/j.1600-0706.2009.17441.x

Groover, A., 2017. Age-Related Changes in Tree Growth and Physiology. eLS 1–7. https://doi.org/10.1002/9780470015902.a0023924

Gutiérrez, A.G., Aravena, J.C., Carrasco-Farías, N. V., Christie, D.A., Fuentes, M., Armesto, J.J., 2008. Gap-phase dynamics and coexistence of a long-lived pioneer and shade-tolerant tree species in the canopy of an old-growth coastal temperate rain forest of Chiloé Island, Chile. J. Biogeogr. 35, 1674–1687. https://doi.org/10.1111/j.1365-2699.2008.01908.x

Handegard, E., Gjerde, I., Bollandsås, O.M., Storaunet, K.O., 2021. Identifying old Norway spruce and Scots pine trees by morphological traits and site characteristics. Scand. J. For. Res. 36, 550–562. https://doi.org/10.1080/02827581.2021.1996628

Harris, I., Osborn, T.J., Jones, P., Lister, D., 2020. Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. Sci. Data 7, 1–18. https://doi.org/10.1038/s41597-020-0453-3

Hartig, F., 2021. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Hartig, F., 2020. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Harvey, P.H., Zammuto, R.M., 1985. Patterns of mortality and age at first reproduction in natural populations of mammals. Nature 315, 319–320. https://doi.org/10.1038/315319a0

Herms, D.A., Mattson, W.J., 1992. The Dilemma of Plants: To Grow or Defend. J. Chem. Inf. Model. 67, 283–335. https://doi.org/10.1086/417659

Hirschmugl, M., Sobe, C., Di Filippo, A., Berger, V., Kirchmeir, H., Vandekerkhove, K., 2023. Review on the Possibilities of Mapping Old-Growth Temperate Forests by Remote Sensing in Europe. Environ. Model. Assess. 28, 761–785. https://doi.org/10.1007/s10666-023-09897-y

Hlásny, T., Zimová, S., Merganičová, K., Štěpánek, P., Modlinger, R., Turčáni, M., 2021. Devastating outbreak of bark beetles in the Czech Republic: Drivers, impacts, and management implications. For. Ecol. Manage. 490. https://doi.org/10.1016/j.foreco.2021.119075

Hobi, M.L., Ginzler, C., Commarmot, B., Bugmann, H., 2015. Gap pattern of the largest primeval beech forest of Europe revealed by remote sensing. Ecosphere 6. https://doi.org/10.1890/ES14-00390.1

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometrical J. 50, 346–363. https://doi.org/10.1002/bimj.200810425

Hupp, C.R., Osterkamp, W.R., 2013. Riparian vegetation and fluvial geomorphic processes. Geomorphology 14, 277–295. https://doi.org/10.1029/WS008

Ireland, K.B., Moore, M.M., Fulé, P.Z., Zegler, T.J., Keane, R.E., 2014. Slow lifelong growth predisposes Populus tremuloides trees to mortality. Oecologia 175, 847–859. https://doi.org/10.1007/s00442-014-2951-5

Issartel, J., Coiffard, C., 2011. Extreme longevity in trees: Live slow, die old? Oecologia 165, 1–5. https://doi.org/10.1007/s00442-010-1807-x

Izworska, K., Muter, E., Fleischer, P., Zielonka, T., 2022. Delay of growth release after a windthrow event and climate response in a light-demanding species (European larch Larix decidua Mill.). Trees - Struct. Funct. 36, 427–438. https://doi.org/10.1007/s00468-021-02218-4

Janda, P., Tepley, A.J., Schurman, J.S., Brabec, M., Nagel, T.A., Bače, R., Begovič, K., Chaskovskyy, O., Čada, V., Dušátko, M., Frankovič, M., Kameniar, O., Kozák, D., Lábusová, J., Langbehn, T., Málek, J., Mikoláš, M., Nováková, M.H., Svobodová, K., Synek, M., Teodosiu, M., Trotsiuk, V., Svoboda, M., 2019. Drivers of basal area variation across primary late-successional Picea abies forests of the Carpathian Mountains. For. Ecol. Manage. 435, 196–204. https://doi.org/10.1016/j.foreco.2018.12.045

Janda, P., Trotsiuk, V., Mikoláš, M., Bače, R., Nagel, T.A., Seidl, R., Seedre, M., Morrissey, R.C., Kucbel, S., Jaloviar, P., Jasík, M., Vysoký, J., Šamonil, P., Čada, V., Mrhalová, H., Lábusová, J., Nováková, M.H., Rydval, M., Matějů, L., Svoboda, M., 2017. The historical disturbance regime of mountain Norway spruce forests in the Western Carpathians and its influence on current forest structure and composition. For. Ecol. Manage. 388, 67–78.

https://doi.org/10.1016/j.foreco.2016.08.014

Janda, P., Ukhvatkina, O.N., Vozmishcheva, A.S., Omelko, A.M., Doležal, J., Krestov, P. V, Zhmerenetsky, A.A., Jan, J.S., 2021. Tree canopy accession strategy changes along the latitudinal gradient of temperate Northeast Asia. Glob. Ecol. Biogeogr. 1–11. https://doi.org/10.1111/geb.13259

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. Agric. For. Meteorol. 327. https://doi.org/10.1016/j.agrformet.2022.109236

Johnson, S.E., Abrams, M.D., 2009. Age class, longevity and growth rate relationships: Protracted growth increases in old trees in the eastern United States. Tree Physiol. 29, 1317–1328. https://doi.org/10.1093/treephys/tpp068

Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L.W., Schoennagel, T., Turner, M.G., 2016. Changing disturbance regimes, ecological memory, and forest resilience. Front. Ecol. Environ. 14, 369–378. https://doi.org/10.1002/fee.1311

Kahl, T., Arnstadt, T., Baber, K., Bässler, C., Bauhus, J., Borken, W., Buscot, F., Floren, A., Heibl, C., Hessenmöller, D., Hofrichter, M., Hoppe, B., Kellner, H., Krüger, D., Linsenmair, K.E., Matzner, E., Otto, P., Purahong, W., Seilwinder, C., Schulze, E.D., Wende, B., Weisser, W.W., Gossner, M.M., 2017. Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. For. Ecol. Manage. 391, 86–95. https://doi.org/10.1016/j.foreco.2017.02.012

Kahle, D., Wickham, H., 2013. ggmap: Spatial Visualization with ggplot2. R J. 5, 144–161.

Kameniar, O., Vostarek, O., Mikoláš, M., Svitok, M., Frankovič, M., Morrissey, R.C., Kozák, D., Nagel, T.A., Dušátko, M., Pavlin, J., Ferenčík, M., Keeton, W.S., Spînu, A.P., Petritan, I.C., Majdanová, L., Markuljaková, K., Roibu, C.-C., Gloor, R., Bače, R., Buechling, A., Synek, M., Rydval, M., Málek, J., Begović, K., Hofmeister, J., Rodrigo, R., Pettit, J.L., Fodor, E., Čada, V., Janda, P., Svoboda, M., 2023. Synchronised Disturbances in Spruce- and Beech-Dominated Forests Across the Largest Primary Mountain Forest Landscape in Temperate Europe. For. Ecol.

Manage. 537. https://doi.org/10.2139/ssrn.4139034

Kaplan, J.O., Krumhardt, K.M., Zimmermann, N., 2009. The prehistoric and preindustrial deforestation of Europe. Quat. Sci. Rev. 28, 3016–3034. https://doi.org/10.1016/j.quascirev.2009.09.028

Kašpar, J., Krůček, M., Král, K., 2024. The effects of solar radiation on daily and seasonal stem increment of canopy trees in European temperate old-growth forests. New Phytol. https://doi.org/10.1111/nph.19852

Keeling, H.C., Phillips, O.L., 2007. The global relationship between forest productivity and biomass. Glob. Ecol. Biogeogr. 16, 618–631. https://doi.org/10.1111/j.1466-8238.2007.00314.x

Keith, H., Kun, Z., Hugh, S., Svoboda, M., Mikoláš, M., Adam, D., Di Filippo, A., Dutcă, I., Garbarino, M., Horváth, F., Ivkovich, V., Jansons, Ā., Nagel, T.A., Panayotov, M., Pérez-Cruzado, C., Piovesan, G., Roibu, C.-C., Šamonil, P., Vostarek, O., Yermokhin, M., Zlatanov, T., Mackey, B., 2024. Carbon carrying capacity in primary forests shows potential for mitigation achieving the European Green Deal 2030 target. Commun. Earth Environ. 5, 1–14. https://doi.org/10.1038/s43247-024-01416-5

Keith, H., Mackey, B., Berry, S., Lindenmayer, D., Gibbons, P., 2010. Estimating carbon carrying capacity in natural forest ecosystems across heterogeneous landscapes: addressing sources of error. Glob. Chang. Biol. 16, 2971–2989. https://doi.org/10.1111/j.1365-2486.2009.02146.x

Keith, H., Mackey, B.G., Lindenmayer, D.B., 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world’s most carbon-dense forests. Proc. Natl. Acad. Sci. U. S. A. 106, 11635–11640. https://doi.org/10.1073/pnas.0901970106

Keren, S., Diaci, J., Motta, R., Govedar, Z., 2017. Stand structural complexity of mixed old-growth and adjacent selection forests in the Dinaric Mountains of Bosnia and Herzegovina. For. Ecol. Manage. 400, 531–541. https://doi.org/10.1016/j.foreco.2017.06.009

King, D.A., 2003. Allocation of above-ground growth is related to light in temperate deciduous saplings. Funct. Ecol. 17, 482–488. https://doi.org/10.1046/j.1365-2435.2003.00759.x

Kitajima, K., 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia 98, 419–428. https://doi.org/10.1007/BF00324232

Kleczewski, N.M., Herms, D.A., Bonello, P., 2010. Effects of soil type, fertilization and drought on carbon allocation to root growth and partitioning between secondary metabolism and ectomycorrhizae of Betula papyrifera. Tree Physiol. 30, 807–817. https://doi.org/10.1093/treephys/tpq032

Klopcic, M., Poljanec, A., Dolinar, M., Kastelec, D., Boncina, A., 2020. Ice-storm damage to trees in mixed Central European forests: Damage patterns, predictors and susceptibility of tree species. Forestry 93, 430–443. https://doi.org/10.1093/FORESTRY/CPZ068

Klopcic, M., Simoncic, T., Boncina, A., 2014. Comparison of regeneration and recruitment of shade-tolerant and light-demanding tree species in mixed uneven-aged forests: Experiences from the Dinaric region. Forestry 88, 552–563. https://doi.org/10.1093/forestry/cpv021

Kobe, R.K., Pacala, S.W., Silander Jr., J.A., 1995. Juvenile Tree Survivorship as a Component of Shade Tolerance. Ecol. Appl. 5, 517–532.

Koch, G.W., Stillet, S.C., Jennings, G.M., Davis, S.D., 2004. The limits to tree height. Nature 428, 851–854. https://doi.org/10.1038/nature02417

Kõrkjas, M., Remm, L., Lõhmus, A., 2021. Tree-related microhabitats on live Populus tremula and Picea abies in relation to tree age, diameter, and stand factors in Estonia. Eur. J. For. Res. 140, 1227–1241. https://doi.org/10.1007/s10342-021-01396-7

Körner, C., 2017. A matter of tree longevity. Science (80-.). 355, 130–131. https://doi.org/10.1126/science.aal2449

Körner, C., 2015. Paradigm shift in plant growth control. Curr. Opin. Plant Biol. 25, 107–114. https://doi.org/10.1016/j.pbi.2015.05.003

Korolyova, N., Buechling, A., Lieutier, F., Yart, A., Cudlín, P., Turčáni, M., Jakuš, R., 2022. Primary and secondary host selection by Ips typographus depends on Norway spruce crown characteristics and phenolic-based defenses. Plant Sci. 321. https://doi.org/10.1016/j.plantsci.2022.111319

Korpel', Š., 1995. Die Urwälder der Westkarpaten. Gustav Fischer Verlag, Stuttgart, Jena, New York.

Kozák, D., Mikoláš, M., Svitok, M., Bače, R., Paillet, Y., Larrieu, L., Nagel, T.A., Begovič, K., Čada, V., Diku, A., Frankovič, M., Janda, P., Kameniar, O., Keren, S., Kjučukov, P., Lábusová, J., Langbehn, T., Málek, J., Mikac, S., Morrissey, R.C., Nováková, M.H., Schurman, J.S., Svobodová, K., Synek, M., Teodosiu, M., Toromani, E., Trotsiuk, V., Vítková, L., Svoboda, M., 2018. Profile of tree-related microhabitats in European primary beech-dominated forests. For. Ecol. Manage. 429, 363–374. https://doi.org/10.1016/j.foreco.2018.07.021

Kozák, D., Svitok, M., Wiezik, M., Mikoláš, M., Thorn, S., Buechling, A., Hofmeister, J., Matula, R., Trotsiuk, V., Bače, R., Begovič, K., Čada, V., Dušátko, M., Frankovič, M., Horák, J., Janda, P., Kameniar, O., Nagel, T.A., Pettit, J.L., Pettit, J.M., Synek, M., Wieziková, A., Svoboda, M., 2021. Historical Disturbances Determine Current Taxonomic, Functional and Phylogenetic Diversity of Saproxylic Beetle Communities in Temperate Primary Forests. Ecosystems 24, 37–55. https://doi.org/10.1007/s10021-020-00502-x

Kozák, D., Svitok, M., Zemlerová, V., Mikoláš, M., Lachat, T., Larrieu, L., Paillet, Y., Buechling, A., Bače, R., Keeton, W.S., Vitková, L., Begovič, K., Čada, V., Dušátko, M., Ferenčík, M., Frankovič, M., Gloor, R., Hofmeister, J., Janda, P., Kameniar, O., Kníř, T., Majdanová, L., Mejstřik, M., Pavlin, J., Ralhan, D., Rodrigo, R., Roibu, C.-C., Synek, M., Vostarek, O., Svoboda, M., 2023. Importance of conserving large and old trees to continuity of tree-related microhabitats. Conserv. Biol. 37. https://doi.org/10.1111/cobi.14066

Krüger, K., Senf, C., Jucker, T., Pflugmacher, D., Seidl, R., 2024. Gap expansion is the dominant driver of canopy openings in a temperate mountain forest landscape. J. Ecol. https://doi.org/10.1111/1365-2745.14320

Kulakowski, D., Seidl, R., Holeksa, J., Kuuluvainen, T., Nagel, T.A., Panayotov, M., Svoboda, M., Thorn, S., Vacchiano, G., Whitlock, C., Wohlgemuth, T., Bebi, P., 2017. A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. For. Ecol. Manage. 388, 120–131. https://doi.org/10.1016/j.foreco.2016.07.037

Laanisto, L., Niinemets, Ü., 2015. Polytolerance to abiotic stresses: How universal is the shade-drought tolerance trade-off in woody species? Glob. Ecol. Biogeogr. 24, 571–

580. https://doi.org/10.1111/geb.12288

Landis, R.M., Peart, D.R., 2005. Early performance predicts canopy attainment across life histories in subalpine forest trees. Ecology 86, 63–72. https://doi.org/10.1890/03-0848

Landres, P.B., Morgan, P., Swanson, F.J., 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecol. Appl. 9, 1179–1188. https://doi.org/10.1890/1051-0761(1999)009[1179:OOTUON]2.0.CO;2

Lanner, R.M., 2002. Why do trees live so long? Ageing Res. Rev. 1, 653–671. https://doi.org/10.1016/S1568-1637(02)00025-9

Larson, D.W., 2001. The paradox of great longevity in a short lived tree species. Exp. Gerontol. 36, 651–673. https://doi.org/10.1016/S0531-5565(00)00233-3

Larson, D.W., Matthes, U., Gerrath, J.A., Larson, N.W.K., Gerrath, J.M., Nekola, J.C., Walker, G.L., Porembski Dand, S., Charlton, A., 2000. Evidence for the widespread occurrence of ancient forests on cliffs. J. Biogeogr. 27, 319–331. https://doi.org/10.1046/j.1365-2699.2000.00401.x

Larsson, L.A., 2015. CooRecorder and CDendro programs of the CooRecorder/CDendro package.

Lenth, R., 2022. Emmeans: estimated marginal means.

Lenth, R. V., 2019. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Lerdau, M., Litvak, M., Monson, R., 1994. Plant chemical defense: Monoterpenes and the growth-differentiation balance hypothesis. Trends Ecol. Evol. 9, 52–57. https://doi.org/10.1016/0169-5347(94)90269-0

Lertzman, K.P., Sutherland, G.D., Inselberg, A., Saunders, S.C., 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. Ecology 77, 1254–1270. https://doi.org/10.2307/2265594

Lestienne, M., Jamrichová, E., Kuosmanen, N., Diaconu, A.C., Schafstall, N., Goliáš, V., Kletetschka, G., Šulc, V., Kuneš, P., 2023. Development of high diversity beech forest in the eastern Carpathians. J. Biogeogr. 50, 699–714. https://doi.org/10.1111/jbi.14562

Leuschner, C., Ellenberg, H., 2017. Ecology of Central European Forests, Ecology of

Central European Forests. Springer International Publishing. https://doi.org/10.1007/978-3-319-43042-3

Leuschner, C., Meier, I.C., 2018. The ecology of Central European tree species: Trait spectra, functional trade-offs, and ecological classification of adult trees. Perspect. Plant Ecol. Evol. Syst. 33, 89–103. https://doi.org/10.1016/j.ppees.2018.05.003

Leverkus, A.B., Buma, B., Wagenbrenner, J., Burton, P.J., Lingua, E., Marzano, R., Thorn, S., 2021. Tamm review: Does salvage logging mitigate subsequent forest disturbances? For. Ecol. Manage. 481, 118721. https://doi.org/10.1016/j.foreco.2020.118721

Liang, Y., Gustafson, E.J., He, H.S., Serra-Diaz, J.M., Duveneck, M.J., Thompson, J.R., 2023. What is the role of disturbance in catalyzing spatial shifts in forest composition and tree species biomass under climate change? Glob. Chang. Biol. 29, 1160–1177. https://doi.org/10.1111/gcb.16517

Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., Comeau, P.G., 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. 29, 796–811. https://doi.org/10.1139/cjfr-29-6-796

Lin, J., Harcombe, P.A., Fulton, M.R., Hall, R.W., 2002. Sapling growth and survivorship as a function of light in a mesic forest of southeast Texas, USA. Oecologia 132, 428–435. https://doi.org/10.1007/s00442-002-0986-5

Lindenmayer, D.B., Laurance, W.F., 2017. The ecology, distribution, conservation and management of large old trees. Biol. Rev. 92, 1434–1458. https://doi.org/10.1111/brv.12290

Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., Likens, G.E., Banks, S.C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., Mcburney, L., Manning, A.D., Stein, J.A.R., 2014. New policies for old trees: Averting a global crisis in a keystone ecological structure. Conserv. Lett. 7, 61–69. https://doi.org/10.1111/conl.12013

Liu, Y., Walck, J.L., A., E.-K.Y., 2017. Roles of the Environment in Plant Life-History Trade- offs, in: Jimenez-Lopez, J.C. (Ed.), Advances in Seed Biology. IntechOpen, London, UK, pp. 3–23.

Loehle, C., 1988. Tree life history strategies: the role of defenses. Can. J. For. Res. 18, 209–222. https://doi.org/10.1139/x88-032

Lorimer, C.G., Frelich, L.E., 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Can. J. For. Res. 20, 651–663. https://doi.org/10.1139/x90-082

Lüdecke, D., Makows, D., Waggoner, P., 2020. Assessment of regression models performance.

Lusk, C., Smith, B., 1998. Life History Differences and Tree Species Coexistence in an Old-Growth New Zealand Rain Forest. Ecology 79, 795–806.

Máliš, F., Ujházy, K., Hederová, L., Ujházyová, M., Csölleová, L., Coomes, D.A., Zellweger, F., 2023. Microclimate variation and recovery time in managed and old-growth temperate forests. Agric. For. Meteorol. 342. https://doi.org/10.1016/j.agrformet.2023.109722

Marchand, W., Buechling, A., Rydval, M., Čada, V., Stegehuis, A.I., Fruleux, A., Hofmeister, J., Pavlin, J., Ralhan, D., Dušatko, M., Frankovič, M., Kozák, D., Roibu, C.-C., Chaskovskyy, O., Mikac, S., Zlatanov, T., Panayotov, M., Diku, A., Toromani, E., Svoboda, M., 2023. Accelerated growth rates of Norway spruce and European beech saplings from Europe’s temperate primary forests are related to warmer conditions. Agric. For. Meteorol. 329. https://doi.org/10.1016/j.agrformet.2022.109280

Marini, L., Økland, B., Jönsson, A.M., Bentz, B., Carroll, A., Forster, B., Grégoire, J.C., Hurling, R., Nageleisen, L.M., Netherer, S., Ravn, H.P., Weed, A., Schroeder, M., 2017. Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. Ecography (Cop.). 40, 1426–1435. https://doi.org/10.1111/ecog.02769

Martin-Benito, D., Pederson, N., Férriz, M., Gea-Izquierdo, G., 2021. Old forests and old carbon: A case study on the stand dynamics and longevity of aboveground carbon. Sci. Total Environ. 765, 142737. https://doi.org/10.1016/j.scitotenv.2020.142737

Martin-Benito, D., Pederson, N., Lanter, C., Köse, N., Doğan, M., Bugmann, H., Bigler, C., 2020. Disturbances and Climate Drive Structure, Stability, and Growth in Mixed Temperate Old-growth Rainforests in the Caucasus. Ecosystems 23, 1170–1185. https://doi.org/10.1007/s10021-019-00462-x

Martínez-Vilalta, J., López, B.C., Loepfe, L., Lloret, F., 2012. Stand- and tree-level determinants of the drought response of Scots pine radial growth. Oecologia 168, 877–888. https://doi.org/10.1007/s00442-011-2132-8

Marziliano, P.A., Tognetti, R., Lombardi, F., 2019. Is tree age or tree size reducing height increment in Abies alba Mill. at its southernmost distribution limit? Ann. For. Sci. 76. https://doi.org/10.1007/s13595-019-0803-5

Mašek, J., Tumajer, J., Rydval, M., Lange, J., Treml, V., 2021. Age and size outperform topographic effects on growth-climate responses of trees in two Central European coniferous forest types. Dendrochronologia 68. https://doi.org/10.1016/j.dendro.2021.125845

Mathaux, C., Mandin, J.P., Oberlin, C., Edouard, J.L., Gauquelin, T., Guibal, F., 2016. Ancient juniper trees growing on cliffs: Toward a long Mediterranean tree-ring chronology. Dendrochronologia 37, 79–88. https://doi.org/10.1016/j.dendro.2015.12.005

Matsushita, M., Takata, K., Hitsuma, G., Yagihashi, T., Noguchi, M., Shibata, M., Masaki, T., 2015. A novel growth model evaluating age-size effect on long-term trends in tree growth. Funct. Ecol. 29, 1250–1259. https://doi.org/10.1111/1365-2435.12416

Matthews, J.D., 1989. Silvicultural systems. Clarendon Press, Oxford, UK.

McCarroll, D., Loader, N.J., 2022. Stable Isotopes in Tree Rings, Quaternary Science Reviews, Tree Physiology. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-030-92698-4

McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. 13, 603–606. https://doi.org/10.1111/j.1654-1103.2002.tb02087.x

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? New Phytol. 178, 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark, J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G.C., Jackson, R.B., Johnson, D.J., Kueppers, L., Lichstein, J.W., Ogle, K., Poulter, B., Pugh, T.A.M., Seidl, R., Turner, M.G., Uriarte, M., Walker, A.P., Xu, C., 2020. Pervasive shifts in forest dynamics in a changing world. Science (80-.). 368, 1–10. https://doi.org/10.1126/science.aaz9463

McDowell, N.G., Fisher, R.A., Xu, C., et al., 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel – experiment framework. New Phytol. 200, 304–321. https://doi.org/10.1063/1.372164

Mcewan, R.W., Pederson, N., Cooper, A., Taylor, J., Watts, R., Hruska, A., 2014. Fire and gap dynamics over 300 years in an old-growth temperate forest. Appl. Veg. Sci. 17, 312–322. https://doi.org/10.1111/avsc.12060

Meigs, G.W., Morrissey, R.C., Bače, R., Chaskovskyy, O., Čada, V., Després, T., Donato, D.C., Janda, P., Lábusová, J., Seedre, M., Mikoláš, M., Nagel, T.A., Schurman, J.S., Synek, M., Teodosiu, M., Trotsiuk, V., Vítková, L., Svoboda, M., 2017. More ways than one: Mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways. For. Ecol. Manage. 406, 410–426. https://doi.org/10.1016/j.foreco.2017.07.051

Mencuccini, M., Martínez-Vilalta, J., Hamid, H.A., Korakaki, E., Vanderklein, D., 2007. Evidence for age- and size-mediated controls of tree growth from grafting studies. Tree Physiol. 27, 463–473. https://doi.org/10.1093/treephys/27.3.463

Mencuccini, M., Martínez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S., Michiels, B., 2005. Size-mediated ageing reduces vigour in trees. Ecol. Lett. 8, 1183–1190. https://doi.org/10.1111/j.1461-0248.2005.00819.x

Michaletz, S.T., Cheng, D., Kerkhoff, A.J., Enquist, B.J., 2014. Convergence of terrestrial plant production across global climate gradients. Nature 512, 39–43. https://doi.org/10.1038/nature13470

Mikoláš, M., Ujházy, K., Jasík, M., Wiezik, M., Gallay, I., Polák, P., Vysoký, J., Čiliak, M., Meigs, G.W., Svoboda, M., Trotsiuk, V., Keeton, W.S., 2019. Primary forest distribution and representation in a Central European landscape: Results of a large-scale field-based census. For. Ecol. Manage. 449, 117466. https://doi.org/10.1016/j.foreco.2019.117466

Mole, S., 1994. Trade-Offs and Constraints in Plant-Herbivore Defense Theory: A Life-

History Perspective. Oikos 71, 3–12. https://doi.org/10.2307/3546166

Motta, R., Alberti, G., Ascoli, D., Berretti, R., Bilic, S., Bono, A., Milic, C., Vojislav, D., Finsinger, W., Garbarino, M., Govedar, Z., Keren, S., Meloni, F., Ruffinatto, F., Nola, P., 2024. Old-growth forests in the Dinaric Alps of Bosnia-Herzegovina and Montenegro: a continental hot-spot for research and biodiversity. Front. For. Glob. Chang. 7, 1–16. https://doi.org/10.3389/ffgc.2024.1371144

Motta, R., Berretti, R., Castagneri, D., Dukić, V., Garbarino, M., Govedar, Z., Lingua, E., Maunaga, Z., Meloni, F., 2011. Toward a definition of the range of variability of central european mixed fagus-abies-picea forests: The nearly steady-state forest of lom (Bosnia and Herzegovina). Can. J. For. Res. 41, 1871–1884. https://doi.org/10.1139/x11-098

Mu, Y., Lindenmayer, D., Zheng, S., Yang, Y., Wang, D., Liu, J., 2023. Size-focused conservation may fail to protect the world’s oldest trees. Curr. Biol. 33, 1–9. https://doi.org/10.1016/j.cub.2023.09.046

Muffler, L., Schmeddes, J., Weigel, R., Barbeta, A., Beil, I., Bolte, A., Buhk, C., Holm, S., Schneider, L., Vitasse, Y., Kreyling, J., 2021. High plasticity in germination and establishment success in the dominant forest tree Fagus sylvatica across Europe. Glob. Ecol. Biogeogr. 1–14. https://doi.org/10.1111/geb.13320

Munné-Bosch, S., 2018. Limits to Tree Growth and Longevity. Trends Plant Sci. 23, 985–993. https://doi.org/10.1016/j.tplants.2018.08.001

Munné-Bosch, S., Alegre, L., 2004. Die and let live: Leaf senescence contributes to plant survival under drought stress. Funct. Plant Biol. 31, 203–216. https://doi.org/10.1071/FP03236

Nagel, T.A., Firm, D., Pisek, R., Mihelic, T., Hladnik, D., de Groot, M., Rozenbergar, D., 2017a. Evaluating the influence of integrative forest management on old-growth habitat structures in a temperate forest region. Biol. Conserv. 216, 101–107. https://doi.org/10.1016/j.biocon.2017.10.008

Nagel, T.A., Mikac, S., Dolinar, M., Klopcic, M., Keren, S., Svoboda, M., Diaci, J., Boncina, A., Paulic, V., 2017b. The natural disturbance regime in forests of the Dinaric Mountains : A synthesis of evidence. For. Ecol. Manage. 388, 29–42. https://doi.org/10.1016/j.foreco.2016.07.047

Nagel, T.A., Svoboda, M., Diaci, J., 2006. Regeneration patterns after intermediate wind disturbance in an old-growth Fagus-Abies forest in southeastern Slovenia. For. Ecol. Manage. 226, 268–278. https://doi.org/10.1016/j.foreco.2006.01.039

Nagel, T.A., Svoboda, M., Kobal, M., 2014. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. Ecol. Appl. 24, 663–679. https://doi.org/10.1890/13-0632.1

Nagel, T.A., Svoboda, M., Rugani, T., Diaci, J., 2010. Gap regeneration and replacement patterns in an old-growth Fagus-Abies forest of Bosnia-Herzegovina. Plant Ecol. 208, 307–318. https://doi.org/10.1007/s11258-009-9707-z

Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J. R. Soc. Interface 14. https://doi.org/10.1098/rsif.2017.0213

Nakashizuka, T., 2001. Species coexistence in temperate, mixed deciduous forests. Trends Ecol. Evol. 16, 205–210. https://doi.org/10.1016/S0169-5347(01)02117-6

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547.

Noyer, E., Lachenbruch, B., Dlouhá, J., Collet, C., Ruelle, J., Ningre, F., Fournier, M., 2017. Xylem traits in European beech (Fagus sylvatica L.) display a large plasticity in response to canopy release. Ann. For. Sci. 74, 1–11. https://doi.org/10.1007/s13595-017-0634-1

O’Hara, K.L., Ramage, B.S., 2013. Silviculture in an uncertain world: Utilizing multi-aged management systems to integrate disturbance. Forestry 86, 401–410. https://doi.org/10.1093/forestry/cpt012

Obeso, J.R., 2002. The costs of reproduction in plants. New Phytol. 155, 321–348. https://doi.org/10.1046/j.1469-8137.2002.00477.x

Omelko, A., Ukhvatkina, O., Zhmerenetsky, A., Sibirina, L., Petrenko, T., Bobrovsky, M., 2018. From young to adult trees: How spatial patterns of plants with different life strategies change during age development in an old-growth Korean pine-broadleaved forest. For. Ecol. Manage. 411, 46–66. https://doi.org/10.1016/j.foreco.2018.01.023

Orwig, D.A., Abrams, M.D., 1994. Contrasting radial growth and canopy recruitment patterns in Liriodendron tulipifera and Nyssa sylvatica: Gap-obligate versus gap-facultative tree species. Can. J. For. Res. 24, 2141–2149. https://doi.org/10.1139/x94-276

Panayotov, M., Gogushev, G., Tsavkov, E., Vasileva, P., Tsvetanov, N., Kulakowski, D., Bebi, P., 2017. Abiotic disturbances in Bulgarian mountain coniferous forests – An overview. For. Ecol. Manage. 388, 13–28. https://doi.org/10.1016/j.foreco.2016.10.034

Patacca, M., Lindner, M., Lucas-Borja, M.E., Cordonnier, T., Fidej, G., Gardiner, B., Hauf, Y., Jasinevičius, G., Labonne, S., Linkevičius, E., Mahnken, M., Milanovic, S., Nabuurs, G.J., Nagel, T.A., Nikinmaa, L., Panyatov, M., Bercak, R., Seidl, R., Ostrogović Sever, M.Z., Socha, J., Thom, D., Vuletic, D., Zudin, S., Schelhaas, M.J., 2023. Significant increase in natural disturbance impacts on European forests since 1950. Glob. Chang. Biol. 29, 1359–1376. https://doi.org/10.1111/gcb.16531

Pavanetto, N., Carmona, C.P., Laanisto, L., Niinemets, Ü., Puglielli, G., 2023. Trait dimensions of abiotic stress tolerance in woody plants of the Northern Hemisphere. Glob. Ecol. Biogeogr. 33, 1–14. https://doi.org/10.1111/geb.13788

Pavlin, J., Nagel, T.A., Svitok, M., Di Filippo, A., Mikac, S., Keren, S., Dikku, A., Toromani, E., Panayotov, M., Zlatanov, T., Frankovič, M., Buechling, A., Dušátko, M., Marchand, W., Mikoláš, M., Kozák, D., Rodrigo, R., Svoboda, M., 2024. Pathways and drivers of canopy accession across primary temperate forests of Europe. Sci. Total Environ. 906. https://doi.org/10.1016/j.scitotenv.2023.167593

Pavlin, J., Nagel, T.A., Svitok, M., Pettit, J.L., Begović, K., Mikac, S., Dikku, A., Toromani, E., Panayotov, M., Zlatanov, T., Haruta, O., Dorog, S., Chaskovskyy, O., Mikoláš, M., Janda, P., Frankovič, M., Rodrigo, R., Vostarek, O., Synek, M., Dušátko, M., Kníř, T., Kozák, D., Kameniar, O., Bače, R., Čada, V., Trotsiuk, V., Schurman, J.S., Saulnier, M., Buechling, A., Svoboda, M., 2021. Disturbance history is a key driver of tree life span in temperate primary forests. J. Veg. Sci. 32, 1–12. https://doi.org/10.1111/jvs.13069

Pearl, R., 1928. The Rate Of Living Theory. Alfred A. Knopf, New York, NY. https://doi.org/10.16309/j.cnki.issn.1007-1776.2003.03.004

Pellicone, G., Caloiero, T., Guagliardi, I., 2019. The De Martonne aridity index in

Calabria (Southern Italy). J. Maps 15, 788–796. https://doi.org/10.1080/17445647.2019.1673840

Peñuelas, J., Munné-Bosch, S., 2010. Potentially immortal? New Phytol. 187, 564–567. https://doi.org/10.1111/j.1469-8137.2010.03360.x

Pérez-Llorca, M., Munné-Bosch, S., 2021. Aging, stress, and senescence in plants: what can biological diversity teach us? GeroScience 43, 167–180. https://doi.org/10.1007/s11357-021-00336-y

Petit, R.J., Hampe, A., 2006. Some Evolutionary Consequences of Being a Tree. Annu. Rev. Ecol. Evol. Syst. 37, 187–214. https://doi.org/10.1146/annurev.ecolsys.37.091305.110215

Petritan, A.M., von Lüpke, B., Petritan, I.C., 2009. Influence of light availability on growth, leaf morphology and plant architecture of beech (Fagus sylvatica L.), maple (Acer pseudoplatanus L.) and ash (Fraxinus excelsior L.) saplings. Eur. J. For. Res. 128, 61–74. https://doi.org/10.1007/s10342-008-0239-1

Petritan, A.M., Von Lüpke, B., Petritan, I.C., 2007. Effects of shade on growth and mortality of maple (Acer pseudoplatanus), ash (Fraxinus excelsior) and beech (Fagus sylvatica) saplings. Forestry 80, 397–412. https://doi.org/10.1093/forestry/cpm030

Petrovska, R., Brang, P., Gessler, A., Bugmann, H., Hobi, M.L., 2021. Grow slowly, persist, dominate—Explaining beech dominance in a primeval forest. Ecol. Evol. 11, 10077–10089. https://doi.org/10.1002/ECE3.7800

Petrovska, R., Bugmann, H., Hobi, M.L., Ghosh, S., Brang, P., 2022. Survival time and mortality rate of regeneration in the deep shade of a primeval beech forest. Eur. J. For. Res. 141, 43–58. https://doi.org/10.1007/s10342-021-01427-3

Pettit, J.L., Pettit, J.M., Janda, P., Rydval, M., Čada, V., Schurman, J.S., Nagel, T.A., Bače, R., Saulnier, M., Hofmeister, J., Matula, R., Kozák, D., Frankovič, M., Turcu, D.O., Mikoláš, M., Svoboda, M., 2021. Both Cyclone-induced and Convective Storms Drive Disturbance Patterns in European Primary Beech Forests. J. Geophys. Res. Atmos. 126, 1–17. https://doi.org/10.1029/2020JD033929

Pickett, S.T.A., White, P.S., 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York, NY.

Piispanen, R., Heinonen, J., Valkonen, S., Mäkinen, H., Lundqvist, S.O., Saranpää, P., 2014. Wood density of Norway spruce in uneven-aged stands. Can. J. For. Res. 44, 136–144. https://doi.org/10.1139/cjfr-2013-0201

Piovesan, G., Biondi, F., 2021. On tree longevity. New Phytol. 231, 1318–1337. https://doi.org/10.1111/nph.17148

Piovesan, G., Biondi, F., Baliva, M., De Vivo, G., Marchianò, V., Schettino, A., Di Filippo, A., 2019a. Lessons from the wild: slow but increasing long-term growth allows for maximum longevity in European beech. Ecology 100, 1–4. https://doi.org/10.1002/ecy.2737

Piovesan, G., Biondi, F., Baliva, M., Dinella, A., Di Fiore, L., Marchiano, V., Presutti Saba, E., De Vivo, G., Schettino, A., Di Filippo, A., 2019b. Tree growth patterns associated with extreme longevity: Implications for the ecology and conservation of primeval trees in Mediterranean mountains. Anthropocene 26, 100199. https://doi.org/10.1016/j.ancene.2019.100199

Piovesan, G., Di Filippo, A., Alessandrini, A., Biondi, F., Schirone, B., 2005. Structure, dynamics and dendroecology of an old-growth Fagus forest in the Apennines. J. Veg. Sci. 16, 13–28. https://doi.org/10.1111/j.1654-1103.2005.tb02334.x

Piovesan, G., Lüttge, U., 2018. Tree growth dynamics during early ontogenetic stages in closed forests. Trees 32, 671–673. https://doi.org/10.1007/s00468-018-1664-5

Poorter, L., 1999. Growth responses of 15 rain-forest tree species to a light gradient: The relative importance of morphological and physiological traits. Funct. Ecol. 13, 396–410. https://doi.org/10.1046/j.1365-2435.1999.00332.x

Potapov, P., Hansen, M.C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., Smith, W., Zhuravleva, I., Komarova, A., Minnemeyer, S., Esipova, E., 2017. The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. Sci. Adv. 3, 1–13. https://doi.org/10.1126/sciadv.1600821

Pretzsch, H., 2020. The course of tree growth. Theory and reality. For. Ecol. Manage. 478, 118508. https://doi.org/10.1016/j.foreco.2020.118508

Pretzsch, H., Hilmers, T., Biber, P., Avdagić, A., Binder, F., Bončina, A., Bosela, M., Dobor, L., Forrester, D.I., Lévesque, M., Ibrahimspahić, A., Nagel, T.A., Río, M. Del, Sitkova, Z., Schütze, G., Stajić, B., Stojanović, D., Uhl, E., Zlatanov, T., Tognetti, R., 2020. Evidence of elevation-specific growth changes of spruce, fir, and beech in European mixed mountain forests during the last three centuries. Can. J. For. Res. 50, 689–703. https://doi.org/10.1139/cjfr-2019-0368

Prévost, M., Raymond, P., 2012. Effect of gap size, aspect and slope on available light and soil temperature after patch-selection cutting in yellow birch-conifer stands, Quebec, Canada. For. Ecol. Manage. 274, 210–221. https://doi.org/10.1016/j.foreco.2012.02.020

Pugh, T.A.M., Seidl, R., Liu, D., Lindeskog, M., Chini, L.P., Senf, C., 2024. The anthropogenic imprint on temperate and boreal forest demography and carbon turnover. Glob. Ecol. Biogeogr. 33, 100–115. https://doi.org/10.1111/geb.13773

Rajsnerová, P., Klem, K., Holub, P., Novotná, K., Večeřová, K., Kozáčiková, M., Rivas-Ubach, A., Sardans, J., Marek, M. V., Peñuelas, J., Urban, O., 2015. Morphological, biochemical and physiological traits of upper and lower canopy leaves of European beech tend to converge with increasing altitude. Tree Physiol. 35, 47–60. https://doi.org/10.1093/treephys/tpu104

Ralhan, D., Keith, H., Pavlin, J., Stegehuis, A.I., Marchand, W., Fruleux, A., Poláček, M., Svitok, M., Nagel, T.A., Mikoláš, M., Kozák, D., Buechling, A., Dušátko, M., Janda, P., Chaskovsky, O., Roibu, C.-C., Svoboda, M., 2023. Temperate Primary Forest Biomass Accumulates over Centuries-Long Time Frames. Ecosystems 26, 1685–1702. https://doi.org/10.1007/s10021-023-00858-w

Rathgeber, C.B.K., Cuny, H.E., Fonti, P., 2016. Biological basis of tree-ring formation: A crash course. Front. Plant Sci. 7. https://doi.org/10.3389/fpls.2016.00734

Ray-Mukherjee, J., Nimon, K., Mukherjee, S., Morris, D.W., Slotow, R., Hamer, M., 2014. Using commonality analysis in multiple regressions: A tool to decompose regression effects in the face of multicollinearity. Methods Ecol. Evol. 5, 320–328. https://doi.org/10.1111/2041-210X.12166

Rita, A., Bonanomi, G., Allevato, E., Borghetti, M., Cesarano, G., Mogavero, V., Rossi, S., Saulino, L., Zotti, M., Saracino, A., 2021. Topography modulates near-ground microclimate in the Mediterranean Fagus sylvatica treeline. Sci. Rep. 11, 1–14. https://doi.org/10.1038/s41598-021-87661-6

Roberts, M.R., 2004. Response of the herbaceous layer to natural disturbance in North

American forests. Can. J. Bot. 82, 1273–1283. https://doi.org/10.1139/B04-091

Rodrigo, R., Pettit, J.L., Matula, R., Kozák, D., Bače, R., Pavlin, J., Janda, P., Mikoláš, M., Nagel, T.A., Schurman, J., Trotsiuk, V., Vostarek, O., Frankovič, M., Pettit, J.M., Buechling, A., Čada, V., Begovič, K., Chaskovskyy, O., Teodosiu, M., Saulnier, M., Dušátko, M., Kníř, T., Kameniar, O., Málek, J., Synek, M., Gloor, R., Svoboda, M., 2022. Historical mixed-severity disturbances shape current diameter distributions of primary temperate Norway spruce mountain forests in Europe. For. Ecol. Manage. 503. https://doi.org/10.1016/j.foreco.2021.119772

Rollinson, C.R., Alexander, M.R., Dye, A.W., Moore, D.J.P., Pederson, N., Trouet, V., 2021. Climate sensitivity of understory trees differs from overstory trees in temperate mesic forests. Ecology 102, 1–11. https://doi.org/10.1002/ecy.3264

Roskilly, B., Keeling, E., Hood, S., Giuggiola, A., Sala, A., 2019. Conflicting functional effects of xylem pit structure relate to the growth-longevity trade-off in a conifer species. Proc. Natl. Acad. Sci. U. S. A. 116, 15282–15287. https://doi.org/10.1073/pnas.1900734116

Rötheli, E., Heiri, C., Bigler, C., 2012. Effects of growth rates, tree morphology and site conditions on longevity of Norway spruce in the northern Swiss Alps. Eur. J. For. Res. 131, 1117–1125. https://doi.org/10.1007/s10342-011-0583-4

Roženbergar, D., Pavlin, J., Nagel, T.A., 2020. Short term survival and crown rebuilding of European broadleaf tree species following a severe ice storm. Can. J. For. Res. 50, 1131–1137. https://doi.org/10.1139/cjfr-2020-0063

Ryan, M.G., Yoder, B.J., 1997. Hydraulic limits to tree height and tree growth: What keeps trees from growing beyond a certain height? Bioscience 47, 235–242. https://doi.org/10.2307/1313077

Rydval, M., Druckenbrod, D.L., Svoboda, M., Trotsiuk, V., Janda, P., Mikoláš, M., Čada, V., Bače, R., Teodosiu, M., Wilson, R., 2018. Influence of sampling and disturbance history on climatic sensitivity of temperature-limited conifers. The Holocene 28, 1574–1587. https://doi.org/10.1177/0959683618782605

Sabatini, F.M., Bluhm, H., Kun, Z., Aksenov, D., Atauri, J.A., Buchwald, E., Burrascano, S., Cateau, E., Diku, A., Duarte, I.M., Fernández López, Á.B., Garbarino, M., Grigoriadis, N., Horváth, F., Keren, S., Kitenberga, M., Kiš, A., Kraut, A., Ibisch, P.L., Larrieu, L., Lombardi, F., Matovic, B., Melu, R.N., Meyer, P., Midteng, R., Mikac, S., Mikoláš, M., Mozgeris, G., Panayotov, M., Pisek, R., Nunes, L., Ruete, A., Schickhofer, M., Simovski, B., Stillhard, J., Stojanovic, D., Szwagrzyk, J., Tikkanen, O.-P., Toromani, E., Volosyanchuk, R., Vrška, T., Waldherr, M., Yermokhin, M., Zlatanov, T., Zagidullina, A., Kuemmerle, T., 2021. European primary forest database v2.0. Sci. Data 8, 1–15. https://doi.org/10.1038/s41597-021-00988-7

Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., Verkerk, P.J., Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horváth, F., Garbarino, M., Grigoriadis, N., Lombardi, F., Marques Duarte, I., Meyer, P., Midteng, R., Mikac, S., Mikoláš, M., Motta, R., Mozgeris, G., Nunes, L., Panayotov, M., Ódor, P., Ruete, A., Simovski, B., Stillhard, J., Svoboda, M., Szwagrzyk, J., Tikkanen, O.P., Volosyanchuk, R., Vrska, T., Zlatanov, T., Kuemmerle, T., 2018. Where are Europe's last primary forests? Divers. Distrib. 24, 1426–1439. https://doi.org/10.1111/ddi.12778

Salguero-Gómez, R., Jones, O.R., Jongejans, E., Blomberg, S.P., Hodgson, D.J., Mbeau-Ache, C., Zuidema, P.A., De Kroon, H., Buckley, Y.M., 2016. Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. Proc. Natl. Acad. Sci. U. S. A. 113, 230–235. https://doi.org/10.1073/pnas.1506215112

Salzer, M., Baisan, C., 2013. Dendrochronology of the "Currey Tree," in: Ameridendro 2013: Second American Dendrochronology Conference. Tucson, Arizona, United States of America.

Saulnier, M., Schurman, J.S., Vostarek, O., Rydval, M., Pettit, J.L., Trotsiuk, V., Janda, P., Bače, R., Björklund, J., Svoboda, M., 2020. Climatic drivers of Picea growth differ during recruitment and interact with disturbance severity to influence rates of canopy replacement. Agric. For. Meteorol. 287. https://doi.org/10.1016/j.agrformet.2020.107981

Schneider, H.M., 2022. Characterization, costs, cues and future perspectives of phenotypic plasticity. Ann. Bot. 130, 131–148. https://doi.org/10.1093/aob/mcac087

Schnitzler, A., 2014. Towards a new European wilderness: Embracing unmanaged forest growth and the decolonisation of nature. Landsc. Urban Plan. 126, 74–80.

https://doi.org/10.1016/j.landurbplan.2014.02.011

Schulman, E., 1954. Longevity under adversity in conifers. Science (80-.). 119, 883–884. https://doi.org/10.1126/science.119.3103.883-a

Schurman, J., Janda, P., Rydval, M., Mikolaš, M., Svoboda, M., Babst, F., 2024. Climate-competition tradeoffs shape the range limits of European beech and Norway spruce along elevational gradients across the Carpathian Mountains. Ecography (Cop.). 2024. https://doi.org/10.1111/ecog.06715

Schurman, J.S., Babst, F., Björklund, J., Rydval, M., Bače, R., Čada, V., Janda, P., Mikolaš, M., Saulnier, M., Trotsiuk, V., Svoboda, M., 2019. The climatic drivers of primary Picea forest growth along the Carpathian arc are changing under rising temperatures. Glob. Chang. Biol. 25, 3136–3150. https://doi.org/10.1111/gcb.14721

Schurman, J.S., Trotsiuk, V., Bače, R., Čada, V., Fraver, S., Janda, P., Kulakowski, D., Labusova, J., Mikoláš, M., Nagel, T.A., Seidl, R., Synek, M., Svobodová, K., Chaskovskyy, O., Teodosiu, M., Svoboda, M., 2018. Large-scale disturbance legacies and the climate sensitivity of primary Picea abies forests. Glob. Chang. Biol. 24, 2169–2181. https://doi.org/10.1111/gcb.14041

Schuster, R., Oberhuber, W., 2013. Age-dependent climate-growth relationships and regeneration of Picea abies in a drought-prone mixed-coniferous forest in the Alps. Can. J. For. Res. 43, 609–618. https://doi.org/10.1139/CJFR-2012-0426

Sedmáková, D., Sedmák, R., Bosela, M., Ježík, M., Blaženec, M., Hlásny, T., Marušák, R., 2019. Growth-climate responses indicate shifts in the competitive ability of European beech and Norway spruce under recent climate warming in East-Central Europe. Dendrochronologia 54, 37–48. https://doi.org/10.1016/j.dendro.2019.02.001

Sedmáková, D., Sedmák, R., Kúdela, P., Ďurica, P., Saniga, M., Jaloviar, P., Kucbel, S., 2022. Divergent growth responses of healthy and declining spruce trees to climatic stress: a case study from the Western Carpathians. Dendrochronologia 76. https://doi.org/10.1016/j.dendro.2022.126023

Seibold, S., Bässler, C., Brandl, R., Gossner, M.M., Thorn, S., Ulyshen, M.D., Müller, J., 2015. Experimental studies of dead-wood biodiversity - A review identifying global gaps in knowledge. Biol. Conserv. 191, 139–149. https://doi.org/10.1016/j.biocon.2015.06.006

Seidl, R., Honkaniemi, J., Aakala, T., Aleinikov, A., Angelstam, P., Bouchard, M., Boulanger, Y., Burton, P.J., De Grandpré, L., Gauthier, S., Hansen, W.D., Jepsen, J.U., Jõgiste, K., Kneeshaw, D.D., Kuuluvainen, T., Lisitsyna, O., Makoto, K., Mori, A.S., Pureswaran, D.S., Shorohova, E., Shubnitsina, E., Taylor, A.R., Vladimirova, N., Vodde, F., Senf, C., 2020. Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems. Ecography (Cop.). 43, 967–978. https://doi.org/10.1111/ecog.04995

Seidl, R., Schelhaas, M.J., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. Nat. Clim. Chang. 4, 806–810. https://doi.org/10.1038/nclimate2318

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyer, C.P.O., 2017. Forest disturbances under climate change. Nat. Clim. Chang. 7, 395–402. https://doi.org/10.1038/nclimate3303

Seidl, R., Turner, M.G., 2022. Post-disturbance reorganization of forest ecosystems in a changing world. Proc. Natl. Acad. Sci. U. S. A. 119, 1–10. https://doi.org/10.1073/pnas.2202190119

Senf, C., Müller, J., Seidl, R., 2019. Post-disturbance recovery of forest cover and tree height differ with management in Central Europe. Landsc. Ecol. 34, 2837–2850. https://doi.org/10.1007/s10980-019-00921-9

Senf, C., Pflugmacher, D., Zhiqiang, Y., Sebald, J., Knorn, J., Neumann, M., Hostert, P., Seidl, R., 2018. Canopy mortality has doubled in Europe's temperate forests over the last three decades. Nat. Commun. 9. https://doi.org/10.1038/s41467-018-07539-6

Senf, C., Seidl, R., 2021a. Storm and fire disturbances in Europe: distribution and trends. Glob. Chang. Biol. 1–15. https://doi.org/10.1111/gcb.15679

Senf, C., Seidl, R., 2021b. Post-disturbance canopy recovery and the resilience of Europe's forests. Glob. Ecol. Biogeogr. 1–12. https://doi.org/10.1111/geb.13406

Senf, C., Seidl, R., 2021c. Mapping the forest disturbance regimes of Europe. Nat. Sustain. 4, 63–70. https://doi.org/10.1038/s41893-020-00609-y

Sillett, S.C., Van Pelt, R., Carroll, A.L., Kramer, R.D., Ambrose, A.R., Trask, D., 2015. How do tree structure and old age affect growth potential of california redwoods? Ecol. Monogr. 85, 181–212. https://doi.org/10.1890/14-1016.1

Silvertown, J., Franco, M., Perez-Ishiwara, R., 2001. Evolution of senescence in iteroparous perennial plants. Evol. Ecol. Res. 3, 393–412.

Solberg, S., Dobbertin, M., Reinds, G.J., Lange, H., Andreassen, K., Fernandez, P.G., Hildingsson, A., de Vries, W., 2009. Analyses of the impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: A stand growth approach. For. Ecol. Manage. 258, 1735–1750. https://doi.org/10.1016/j.foreco.2008.09.057

Sommerfeld, A., Senf, C., Buma, B., D’Amato, A.W., Després, T., Díaz-Hormazábal, I., Fraver, S., Frelich, L.E., Gutiérrez, Á.G., Hart, S.J., Harvey, B.J., He, H.S., Hlásny, T., Holz, A., Kitzberger, T., Kulakowski, D., Lindenmayer, D., Mori, A.S., Müller, J., Paritsis, J., Perry, G.L.W., Stephens, S.L., Svoboda, M., Turner, M.G., Veblen, T.T., Seidl, R., 2018. Patterns and drivers of recent disturbances across the temperate forest biome. Nat. Commun. 9. https://doi.org/10.1038/s41467-018-06788-9

Speer, J., 2010. Fundamentals of tree-ring research. https://doi.org/10.1002/gea.20357

Speer, J.H., 2012. Fundamentals of Tree Ring Research, Reprint ed. ed. University of Arizona Press, Tucson, Arizona, United States of America.

Speer, J.H., Swetnam, T.W., Wickman, B.E., Youngblood, A., 2001. Changes in pandora moth outbreak dynamics during the past 622 years. Ecology 82, 679–697. https://doi.org/10.1890/0012-9658(2001)082[0679:CIPMOD]2.0.CO;2

Stahl, U., Voigt, W., Wirth, C., Kattge, J., Dickie, J., Reu, B., Ogle, K., 2013. Whole-plant trait spectra of North American woody plant species reflect fundamental ecological strategies. Ecosphere 4, 1–28. https://doi.org/10.1890/es13-00143.1

Stan, A.B., Daniels, L.D., 2014. Growth releases across a natural canopy gap-forest gradient in old-growth forests. For. Ecol. Manage. 313, 98–103. https://doi.org/10.1016/j.foreco.2013.11.004

Stan, A.B., Daniels, L.D., 2010. Growth releases of three shade-tolerant species following canopy gap formation in old-growth forests. J. Veg. Sci. 21, 74–87. https://doi.org/10.1111/j.1654-1103.2009.01120.x

Stancioiu, P.T., O'hara, K.L., 2006. Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania. Eur. J. For. Res. 125, 151–162. https://doi.org/10.1007/s10342-005-0069-3

Standovár, T., Kenderes, K., 2003. A review on natural stand dynamics in Beechwoods of East Central Europe. Appl. Ecol. Environ. Res. 1, 19–46. https://doi.org/10.15666/aeer/01019046

Stearns, S.C., 2000. Life history evolution: Successes, limitations, and prospects. Naturwissenschaften 87, 476–486. https://doi.org/10.1007/s001140050763

Stephenson, N.L., van Mantgem, P.J., Bunn, A.G., Bruner, H., Harmon, M.E., O'Connell, K.B., Urban, D.L., Franklin, J.F., 2011. Causes and implications of the correlation between forest productivity and tree mortality rates. Ecol. Monogr. 81, 527–555. https://doi.org/10.1890/10-1077.1

Stoffel, M., Perret, S., 2006. Reconstructing past rockfall activity with tree rings: Some methodological considerations. Dendrochronologia 24, 1–15. https://doi.org/10.1016/j.dendro.2006.04.001

Stritih, A., Senf, C., Seidl, R., Grêt-Regamey, A., Bebi, P., 2021. The impact of land-use legacies and recent management on natural disturbance susceptibility in mountain forests. For. Ecol. Manage. 484. https://doi.org/10.1016/j.foreco.2021.118950

Studhalter, R.A., 1956. Early History of Crossdating. Tree-Ring Bull. 21, 31–35.

Sturtevant, B.R., Bissonette, J.A., Long, J.N., Roberts, D.W., 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecol. Appl. 7, 702–712. https://doi.org/10.1890/1051-0761(1997)007[0702:CWDAAF]2.0.CO;2

Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B., Thomas, C.D., 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. Oikos 120, 1–8. https://doi.org/10.1111/j.1600-0706.2010.18270.x

Sultan, S.E., 2000. Phenotypic plasticity for plant development, function and life history. Trends Plant Sci. 5, 537–542. https://doi.org/10.1016/S1360-1385(00)01797-0

Svoboda, M., Janda, P., Bače, R., Fraver, S., Nagel, T.A., Rejzek, J., Mikoláš, M., Douda, J., Boublík, K., Šamonil, P., Čada, V., Trotsiuk, V., Teodosiu, M., Bouriaud, O., Biriş, A.I., Sýkora, O., Uzel, P., Zelenka, J., Sedlák, V., Lehejček, J., 2014. Landscape-level variability in historical disturbance in primary Picea abies mountain forests of the Eastern Carpathians, Romania. J. Veg. Sci. 25, 386–401. https://doi.org/10.1111/jvs.12109

Synek, M., Janda, P., Mikoláš, M., Nagel, T.A., Schurman, J.S., Pettit, J.L., Trotsiuk, V., Morrissey, R.C., Bače, R., Čada, V., Brang, P., Bugmann, H., Begovič, K., Chaskovskyy, O., Dušátko, M., Frankovič, M., Kameniar, O., Kníř, T., Kozák, D., Langbehn, T., Málek, J., Rodrigo, R., Saulnier, M., Teodosiu, M., Vostarek, O., Svoboda, M., 2020. Contrasting patterns of natural mortality in primary Picea forests of the Carpathian Mountains. For. Ecol. Manage. 457. https://doi.org/10.1016/j.foreco.2019.117734

Taeroe, A., Koning, J.H.C. De, Löf, M., Tolvanen, A., Heiðarsson, L., 2019. Recovery of temperate and boreal forests after windthrow and the impacts of salvage logging . A quantitative review. For. Ecol. Manage. 446, 304–316. https://doi.org/10.1016/j.foreco.2019.03.048

Thiele, C., Hirschfeld, G., 2021. cutpointr : Improved Estimation and Validation of Optimal Cutpoints in R. J. Stat. Softw. 98, 1–27. https://doi.org/10.18637/jss.v098.i11

Thom, D., Sommerfeld, A., Sebald, J., Hagge, J., Müller, J., Seidl, R., 2020. Effects of disturbance patterns and deadwood on the microclimate in European beech forests. Agric. For. Meteorol. 291, 108066. https://doi.org/10.1016/j.agrformet.2020.108066

Trotsiuk, V., Svoboda, M., Janda, P., Mikolaš, M., Bace, R., Rejzek, J., Samonil, P., Chaskovskyy, O., Korol, M., Myklush, S., 2014. A mixed severity disturbance regime in the primary Picea abies (L.) Karst. forests of the Ukrainian Carpathians. For. Ecol. Manage. 334, 144–153. https://doi.org/10.1016/j.foreco.2014.09.005

Trotsiuk, V., Svoboda, M., Weber, P., Pederson, N., Klesse, S., Janda, P., Martin-Benito, D., Mikolaš, M., Seedre, M., Bace, R., Mateju, L., Frank, D., 2016. The legacy of disturbance on individual tree and stand-level aboveground biomass accumulation and stocks in primary mountain Picea abies forests. For. Ecol. Manage. 373, 108–

115. https://doi.org/10.1016/j.foreco.2016.04.038

Tumajer, J., Altman, J., Štěpánek, P., Treml, V., Doležal, J., Cienciala, E., 2017. Increasing moisture limitation of Norway spruce in Central Europe revealed by forward modelling of tree growth in tree-ring network. Agric. For. Meteorol. 247, 56–64. https://doi.org/10.1016/j.agrformet.2017.07.015

Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. Ecology 91, 2833–2849. https://doi.org/10.1890/10-0097.1

Turner, M.G., Baker, W.L., Peterson, C.J., Peet, R.K., 1998. Factors influencing succession: Lessons from large, infrequent natural disturbances. Ecosystems 1, 511–523. https://doi.org/10.1007/s100219900047

Turner, M.G., Seidl, R., 2023. Novel Disturbance Regimes and Ecological Responses. Annu. Rev. Ecol. Evol. Syst. 54, 63–83. https://doi.org/10.1146/annurev-ecolsys-110421-101120

Ujházy, K., Hederová, L., Máliš, F., Ujházyová, M., Bosela, M., Čiliak, M., 2017. Overstorey dynamics controls plant diversity in age-class temperate forests. For. Ecol. Manage. 391, 96–105. https://doi.org/10.1016/j.foreco.2017.02.010

Valen, L. Van, 1975. Life, Death, and Energy of a Tree. Biotropica 7, 259–269. https://doi.org/10.2307/2989738

Valladares, F., Chico, J., Aranda, I., Balaguer, L., Dizengremel, P., Manrique, E., Dreyer, E., 2002. The greater seedling high-light tolerance of Quercus robur over Fagus sylvatica is linked to a greater physiological plasticity. Trees - Struct. Funct. 16, 395–403. https://doi.org/10.1007/s00468-002-0184-4

Valladares, F., Laanisto, L., Niinemets, Ü., Zavala, M.A., 2016. Shedding light on shade: ecological perspectives of understorey plant life. Plant Ecol. Divers. 9, 237–251. https://doi.org/10.1080/17550874.2016.1210262

Valladares, F., Niinemets, Ü., 2008. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. Annu. Rev. Ecol. Evol. Syst. 39, 237–257. https://doi.org/10.1146/annurev.ecolsys.39.110707.173506

Vandekerkhove, K., Meyer, P., Kirchmeir, H., Piovesan, G., Hirschmugl, M., Larrieu, L., Kozák, D., Mikoláš, M., Nagel, T.A., Schmitt, C., Blumröder, J., 2022. Old-growth criteria and indicators for beech forests (Fageta). LIFE-PROGNOSES -

Work Package 1.11.

Vandekerkhove, K., Vanhellemont, M., Vrška, T., Meyer, P., Tabaku, V., Thomaes, A., Leyman, A., De Keersmaeker, L., Verheyen, K., 2018. Very large trees in a lowland old-growth beech (Fagus sylvatica L.) forest: Density, size, growth and spatial patterns in comparison to reference sites in Europe. For. Ecol. Manage. 417, 1–17. https://doi.org/10.1016/j.foreco.2018.02.033

Vašíčková, I., Šamonil, P., Král, K., Fuentes Ubilla, A.E., Daněk, P., Adam, D., Král, K., Daněk, P., Adam, D., 2019. Driving factors of the growth response of Fagus sylvatica L. to disturbances: A comprehensive study from Central-European old-growth forests. For. Ecol. Manage. 444, 96–106. https://doi.org/10.1016/j.foreco.2019.04.018

Veblen, T.T., 1986. Treefalls and the coexistence of conifers in subalpine forests of the central Rockies. Ecology 67, 644–649. https://doi.org/10.2307/1937688

Veen, P., Fanta, J., Raev, I., Biriş, I.A., de Smidt, J., Maes, B., 2010. Virgin forests in Romania and Bulgaria: Results of two national inventory projects and their implications for protection. Biodivers. Conserv. 19, 1805–1819. https://doi.org/10.1007/s10531-010-9804-2

Vinod, N., Slot, M., McGregor, I.R., Ordway, E.M., Smith, M.N., Taylor, T.C., Sack, L., Buckley, T.N., Anderson-Teixeira, K.J., 2022. Thermal sensitivity across forest vertical profiles: patterns, mechanisms, and ecological implications. New Phytol. https://doi.org/10.1111/nph.18539

Violle, C., Garnier, E., Navas, M.-L., Fortunel, C., Vile, D., Kazakou, E., Hummel, I., 2007. Let the concept of trait be functional! Oikos 116, 882–892. https://doi.org/10.1111/j.2007.0030-1299.15559.x

Walker, A.P., De Kauwe, M.G., Bastos, A., Belmecheri, S., Georgiou, K., Keeling, R.F., McMahon, S.M., Medlyn, B.E., Moore, D.J.P., Norby, R.J., Zaehle, S., Anderson-Teixeira, K.J., Battipaglia, G., Brienen, R.J.W., Cabugao, K.G., Cailleret, M., Campbell, E., Canadell, J.G., Ciais, P., Craig, M.E., Ellsworth, D.S., Farquhar, G.D., Fatichi, S., Fisher, J.B., Frank, D.C., Graven, H., Gu, L., Haverd, V., Heilman, K., Heimann, M., Hungate, B.A., Iversen, C.M., Joos, F., Jiang, M., Keenan, T.F., Knauer, J., Körner, C., Leshyk, V.O., Leuzinger, S., Liu, Y., MacBean, N., Malhi, Y., McVicar, T.R., Penuelas, J., Pongratz, J., Powell, A.S., Riutta, T., Sabot, M.E.B., Schleucher, J., Sitch, S., Smith, W.K., Sulman, B., Taylor, B., Terrer, C., Torn, M.S., Treseder, K.K., Trugman, A.T., Trumbore, S.E., van Mantgem, P.J., Voelker, S.L., Whelan, M.E., Zuidema, P.A., 2021. Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO2. New Phytol. 229, 2413–2445. https://doi.org/10.1111/nph.16866

Walters, M.B., Reich, P.B., 1996. Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. Ecology 77, 841–853. https://doi.org/10.2307/2265505

Wang, L., Cui, J., Jin, B., Zhao, J., Xu, H., Lu, Z., Li, W., Li, X., Li, L., Liang, E., Rao, X., Wang, S., Fu, C., Cao, F., Dixon, R.A., Lin, J., 2020. Multifeature analyses of vascular cambial cells reveal longevity mechanisms in old Ginkgo biloba trees. Proc. Natl. Acad. Sci. U. S. A. 117, 2201–2210. https://doi.org/10.1073/pnas.1916548117

West, G.B., Enquist, B.J., Brown, J.H., 2009. A general quantitative theory of forest structure and dynamics. Proc. Natl. Acad. Sci. U. S. A. 106, 1–48. https://doi.org/10.1073/pnas.0812294106

Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199, 213–227. https://doi.org/10.1023/A:1004327224729

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant ecological strategies: Some leading dimensions of variation between species. Annu. Rev. Ecol. Syst. 33, 125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452

Whitmore, T.C., 1989. Canopy Gaps and the Two Major Groups of Forest Trees. Ecology 70, 536–538. https://doi.org/10.2307/1940195

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis.

Wilke, C.O., 2020. cowplot: Streamlined Plot Theme and Plot Annotations for “ggplot2.”

Will, R.E., Wilson, S.M., Zou, C.B., Hennessey, T.C., 2013. Increased vapor pressure deficit due to higher temperature leads to greater transpiration and faster mortality during drought for tree seedlings common to the forest-grassland ecotone. New Phytol. 200, 366–374. https://doi.org/10.1111/nph.12321

Wojciechowska, N., Marzec-Schmidt, K., Kalemba, E.M., Ludwików, A., Bagniewska-Zadworna, A., 2020. Seasonal senescence of leaves and roots of populus trichocarpa-is the scenario the same or different? Tree Physiol. 40, 987–1000. https://doi.org/10.1093/TREEPHYS/TPAA019

Wong, C.M., Lertzman, K.P., 2001. Errors in estimating tree age: implications for studies of stand dynamics. Can. J. For. Res. 31, 1262–1271. https://doi.org/10.1139/cjfr-31-7-1262

Woods, K.D., 2008. Living long by staying small: stem layering as an adaptive life-history trait in shade-tolerant tree seedlings. Can. J. For. Res. 38, 480–487. https://doi.org/10.1139/x07-136

Wright, E.F., Canham, C.D., Coates, K.D., 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. Can. J. For. Res. 30, 1571–1580. https://doi.org/10.1139/cjfr-30-10-1571

Wright, E.F., Coates, K.D., Canham, C.D., Bartemucci, P., 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. Can. J. For. Res. 28, 871–886. https://doi.org/10.1139/cjfr-28-6-871

Wyka, T., Robakowski, P., Zytkowiak, R., 2007. Acclimation of leaves to contrasting irradiance in juvenile trees differing in shade tolerance. Tree Physiol. 27, 1293–1306. https://doi.org/10.1093/treephys/27.9.1293

Yamaguchi, D.K., 1991. A simple method for cross-dating increment cores from living trees. Can. J. For. Res. 21, 414–416. https://doi.org/10.1139/x91-053

Yasuda, Y., Utsumi, Y., Tashiro, N., Koga, S., Fukuda, K., 2018. Cessation of annual apical growth and partial death of cambium in stem of Abies sachalinensis under intensive shading. J. Plant Res. 131, 261–269. https://doi.org/10.1007/s10265-017-0984-7

Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., Van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Máliš, F., Macek, M., Malicki, M., Naaf, T., Nagel, T.A., Ortmann-Ajkai, A., Petřík, P., Pielech, R., Reczyńska, K., Schmidt, W., Standovár, T., Świerkosz, K., Teleki, B., Vild, O., Wulf, M., Coomes, D., 2020. Forest microclimate dynamics drive plant responses to warming. Science (80-.). 368, 772–775. https://doi.org/10.1126/science.aba6880

Zhang, Y.L., Moser, B., Li, M.H., Wohlgemuth, T., Lei, J.P., Bachofen, C., 2020. Contrasting leaf trait responses of conifer and broadleaved seedlings to altered resource availability are linked to resource strategies. Plants 9. https://doi.org/10.3390/plants9050621

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R, Journal of Chemical Information and Modeling. Springer Science & Business Media, New York, NY. https://doi.org/https://doi.org/10.1007/978-0-387-87458-6

9. SUPPLEMENTARY MATERIAL

Table S1. Stand characteristics and composition of collected cores used in the life span analysis

					N of cores			
Landscape	Stand	N of plots	Mean altitude [m]	Share of broadleaves	*Abies a.*	*Acer p.*	*Fagus s.*	*Picea a.*
BEECH		437			**1343**	**220**	**7411**	**720**
Albania					68	0	629	0
	Curai i Epperm	14	1141	1.00	0	0	362	0
	Lumi i Gashit	14	1375	0.92	68	0	267	0
Bulgaria					33	4	696	0
	Boatin	14	1328	1.00	0	0	261	0
	Steneto	14	1314	0.98	0	0	171	0
	Steneto 2	14	1347	0.91	33	4	264	0
Croatia					240	42	1611	270
	Corkova Uvala	10	1009	0.70	36	13	137	7
	Cudinka	10	1119	0.52	61	11	115	28
	Ramino Korito	16	892	0.99	15	1	357	0
	Risnjak	14	1000	0.37	43	3	41	25
	Rjecica	14	679	0.95	1	7	182	13
	Smrceve Doline	14	1411	0.64	62	1	474	154
	Smrceve Doline 2	8	1448	0.77	22	6	305	43
South Romania Beech					567	40	1493	180
	Arpasul	14	1121	0.52	194	8	196	63
	Belia	14	1227	0.61	81	15	262	87
	Boia Mica	14	1192	0.85	52	2	310	4
	Izvoarle Nerei	14	1113	0.96	0	0	239	0
	Sebesu	14	1165	0.87	82	4	330	4
	Ucea Mare	14	1052	0.72	158	11	156	22
North Romania Beech					191	9	534	38
	Bistra valley	14	1063	0.81	80	1	183	15

	Criva	14	1011	0.84	68	4	165	9
	Paulic	12	1013	0.91	43	4	186	14
East Slovakia Beech					49	13	1174	0
	Havesova	14	641	1.00	0	1	158	0
	Stuzica 1	14	920	0.98	4	1	236	0
	Stuzica 2	14	938	0.96	16	3	211	0
	Stuzica 3	14	968	0.93	22	5	343	0
	Vihorlat	14	817	0.86	7	3	226	0
Central Slovakia Beech					195	112	1274	232
	Klenovsky vepor	12	1189	0.51	25	28	103	53
	Kornietova	14	1143	0.60	20	20	235	57
	Kundracka	7	1086	0.72	22	5	76	34
	Obrstin	6	901	0.71	17	5	91	2
	Polana S	20	1147	0.73	20	41	255	38
	Sramkova	14	1043	0.69	50	0	232	30
	Sutovska	14	1026	0.84	41	13	282	18
SPRUCE		534			**15**	**16**	**7**	**10868**
Central Slovakia Spruce					1	13	7	3614
	Bielovodska dolina	12	1342	0.01	0	0	0	302
	Bystra	16	1408	0.06	0	0	0	329
	Dumbier	17	1495	0.02	0	0	0	491
	Hlina	14	1440	0.07	0	0	0	271
	Janosikova Kolkaren	25	1300	0.04	0	0	0	348
	Javorova	8	1441	0.00	0	0	0	205
	Koprova dolina	12	1437	0.03	0	0	0	232
	Osobita	14	1367	0.03	0	1	0	324
	Pilsko	12	1329	0.00	0	0	0	235
	Polana	11	1373	0.10	1	12	7	243
	Smrekovica	11	1385	0.03	0	0	0	221
	Ticha dolina	16	1410	0.04	0	0	0	262

	Zadne medodoly	7	1508	0.02	0	0	0	151
North Romania Spruce					0	0	0	2215
	Calimani 1	20	1589	0.02	0	0	0	294
	Calimani 2	19	1565	0.03	0	0	0	270
	Calimani 3	20	1574	0.04	0	0	0	392
	Giumalau 1	29	1400	0.00	0	0	0	356
	Giumalau 2	29	1449	0.00	0	0	0	482
	Giumalau 3	22	1459	0.02	0	0	0	421
South Romania Spruce					14	3	0	2891
	Arpaselu	12	1522	0.01	0	0	0	231
	Arpasul S	14	1459	0.04	3	0	0	273
	Belia S	12	1473	0.01	2	0	0	324
	Boia Mica S	11	1463	0.04	2	0	0	288
	Capra	12	1574	0.07	0	2	0	334
	Doamnei	12	1523	0.04	2	0	0	278
	Sambata	12	1499	0.01	1	0	0	275
	Ucea Mare S	12	1466	0.02	3	0	0	269
	Ucisoara	12	1426	0.04	1	1	0	338
	Vistea Mare	12	1468	0.03	0	0	0	281
Ukraine					0	0	0	2148
	Gropha 1	19	1380	0.03	0	0	0	440
	Gropha 2	15	1354	0.01	0	0	0	330
	Gropha 3	15	1322	0.03	0	0	0	325
	Syvulya 1	20	1427	0.01	0	0	0	456
	Syvulya 2	15	1358	0.01	0	0	0	321
	Syvulya 3	15	1304	0.03	0	0	0	276
		971			**1358**	**236**	**7418**	**11588**

Table S2. All variables used in the mixed models for the life span analyses with the mean value of the variable per species (first value) and its range (values in parentheses). For the variable forest type only both possible values are listed.

	Abies alba	*Acer pseudoplatanus*	*Fagus sylvatica*	*Picea abies*
Disturbance severity [%]	46.1(19-100)	49.0 (19-98)	50.1 (15-100)	41.9 (13-100)
Disturbance year	1872 (1707-1999)	1887 (1744-1998)	1871 (1694-2000)	1875 (1659-1999)
Early growth [mm year-1]	1.173 (0.164-4.650)	1.761 (0.414-3.818)	0.930 (0.072-5.117)	1.582 (0.085-6.273)
Maximum growth [mm year-1]	2.527 (0.567-8.023)	2.759 (0.920-5.511)	2.147 (0.387-7.957)	2.504 (0.359-8.666)
Minimum growth [mm year-1]	0.321 (0.020-2.106)	0.526 (0.020-2.949)	0.275 (0.010-3.104)	0.566 (0.020-3.234)
Number of releases	0.62 (0-5)	0.65 (0-3)	1.04 (0-6)	0.66 (0-5)
Latitude [˚]	46.21 (42.49-49.19)	47.40 (42.74-49.27)	46.15 (42.36-49.19)	47.63 (44.77-49.52)
Northness	0.016 (-1, 1)	0.009 (-1, 1)	-0.010 (-1, 1)	0.170 (-1, 1)
Slope [˚]	30.3 (2-48)	28.5 (11-44)	25.9 (2-45)	29.1 (4-52)
Mean temperature of vegetation season [˚C]	11.6 (9.0-15.0)	11.14 (9.0-15.0)	11.7 (9.0-15.0)	9.05 (8-15)
Forest type	/	/	/	Spruce, beech

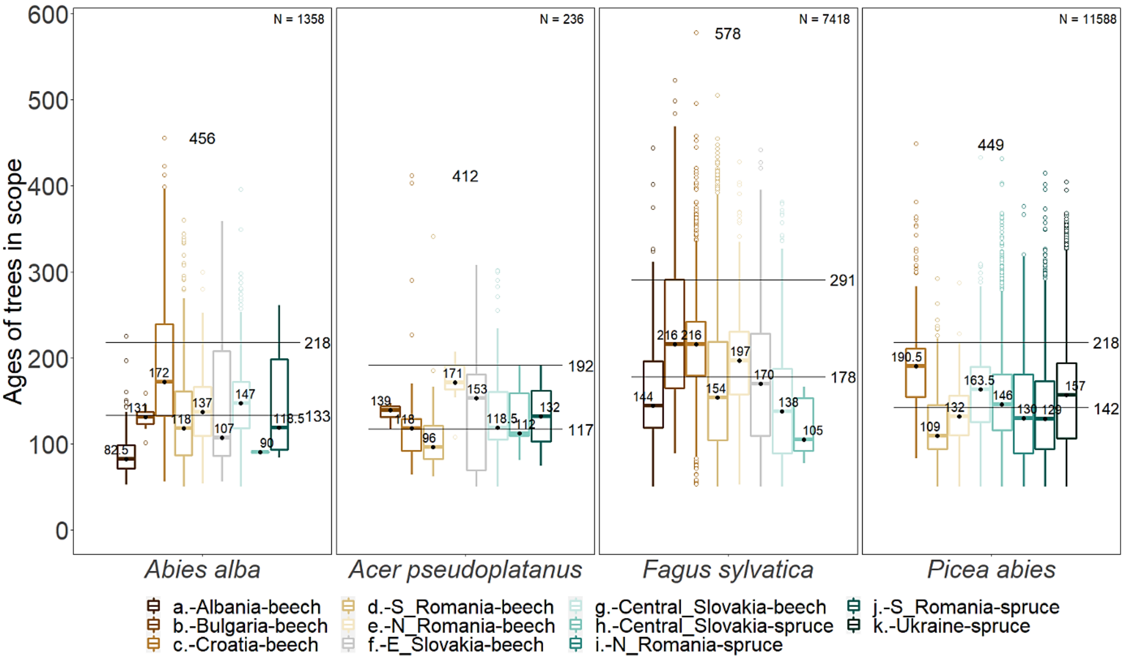

Figure S1. The age distributions of all the included trees based on the species and landscape. Lower lines indicate the median age of all the included cores per species, while the upper lines indicate the 90th percentile of ages per species. The numbers above the dots indicate species-specific medians of age per landscape, while the upper-middle number in each of the frames indicates maximum recorded species-specific ages, and the number of cores included per species is indicated in the upper right corner of each frame.

Table S3. Tukey’s pairwise comparisons of estimated marginal means of the oldest trees among the four species. Est. – estimate of the difference, SE – standard error, p – probability. Significant differences are displayed in bold.

Pairwise comparison	Est.	SE	p
Abies alba - Acer pseudoplatanus	0.05	0.03	0.340
Abies alba - Fagus sylvatica	**-0.15**	**0.01**	**<0.001**
Abies alba - Picea abies	**0.06**	**0.02**	**0.001**
Acer pseudoplatanus - Fagus sylvatica	**-0.21**	**0.03**	**<0.001**
Acer pseudoplatanus - Picea abies	0.01	0.03	0.989
Fagus sylvatica - Picea abies	**0.22**	**0.02**	**<0.001**

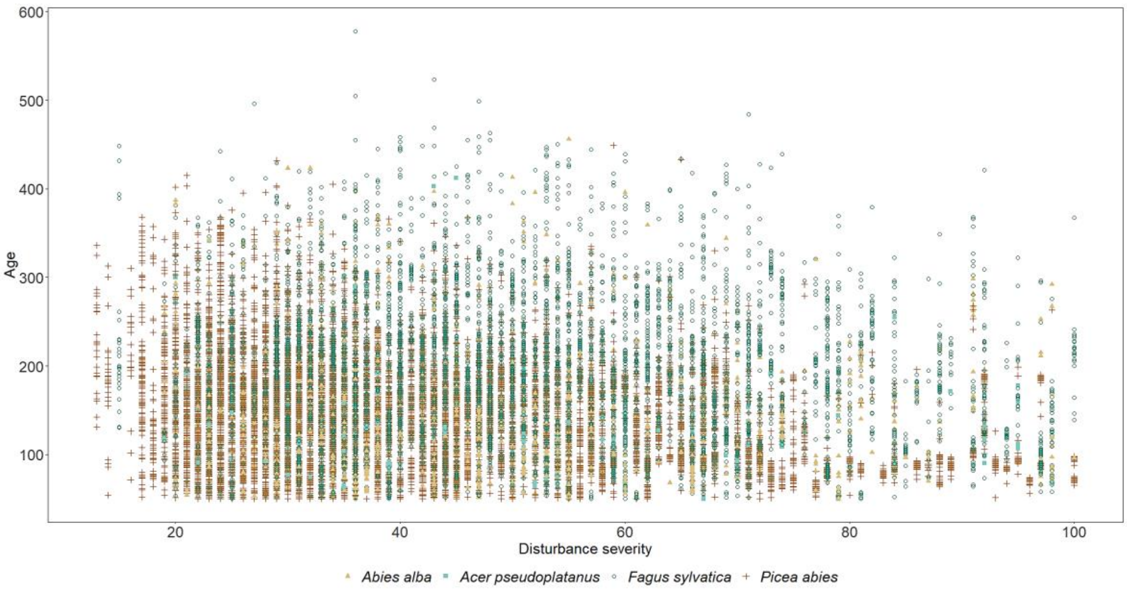

Figure S2. Relationship between age and severity of the most severe event on the plot

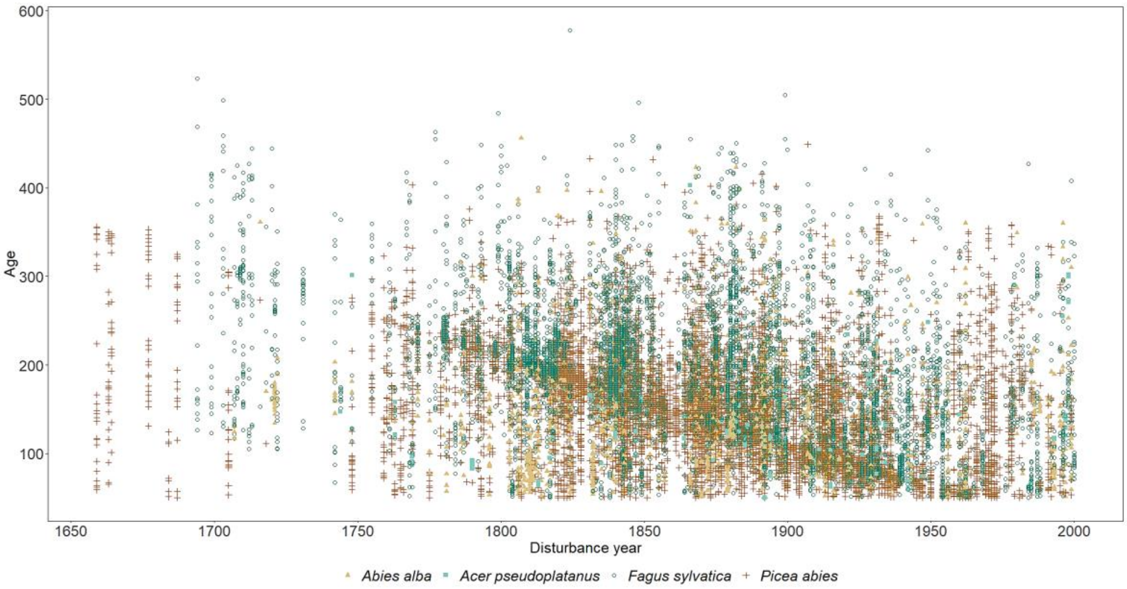

Figure S3. Relationship between age and the year of the most severe disturbance event on the plot

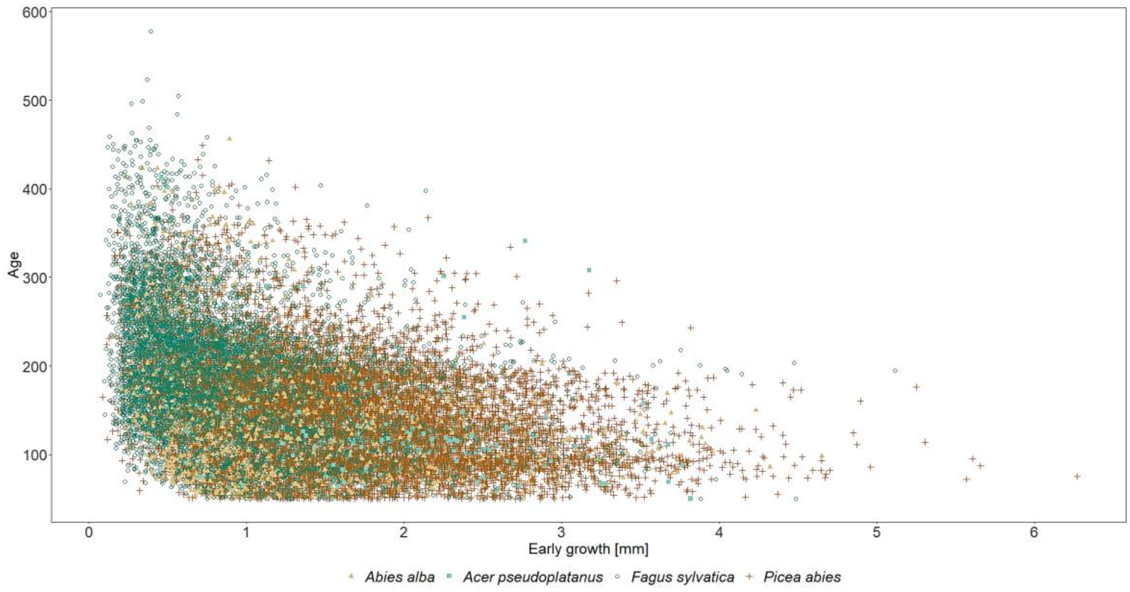

Figure S4. Relationship between age and average growth increment in the first 50 years

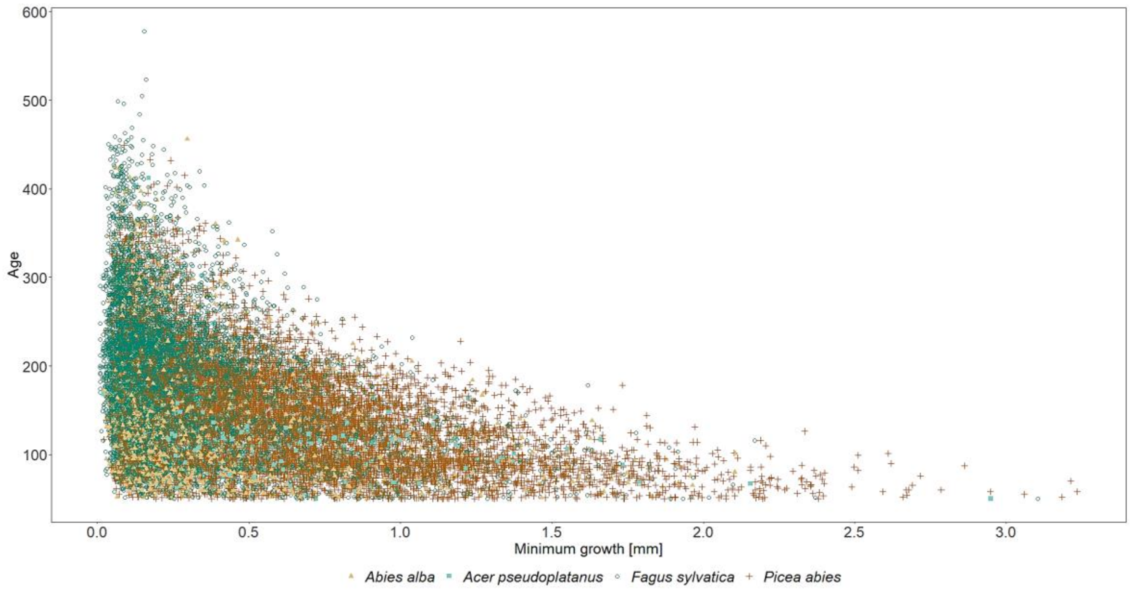

Figure S5. Relationship between age and minimum 10-year running mean of growth increment

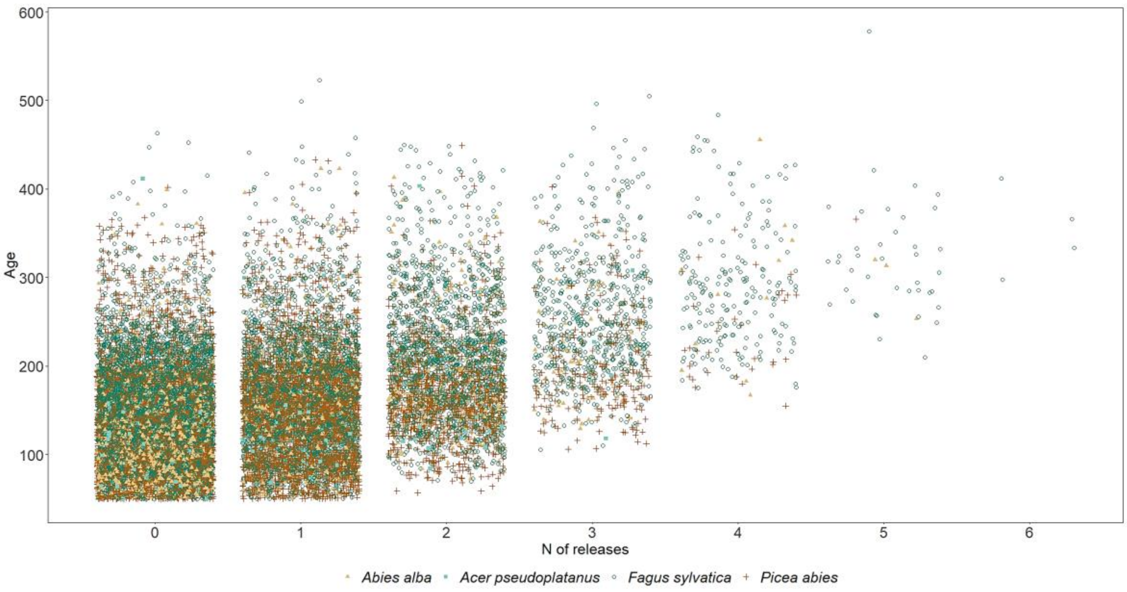

Figure S6. Relationship between age and the number of release events identified per core

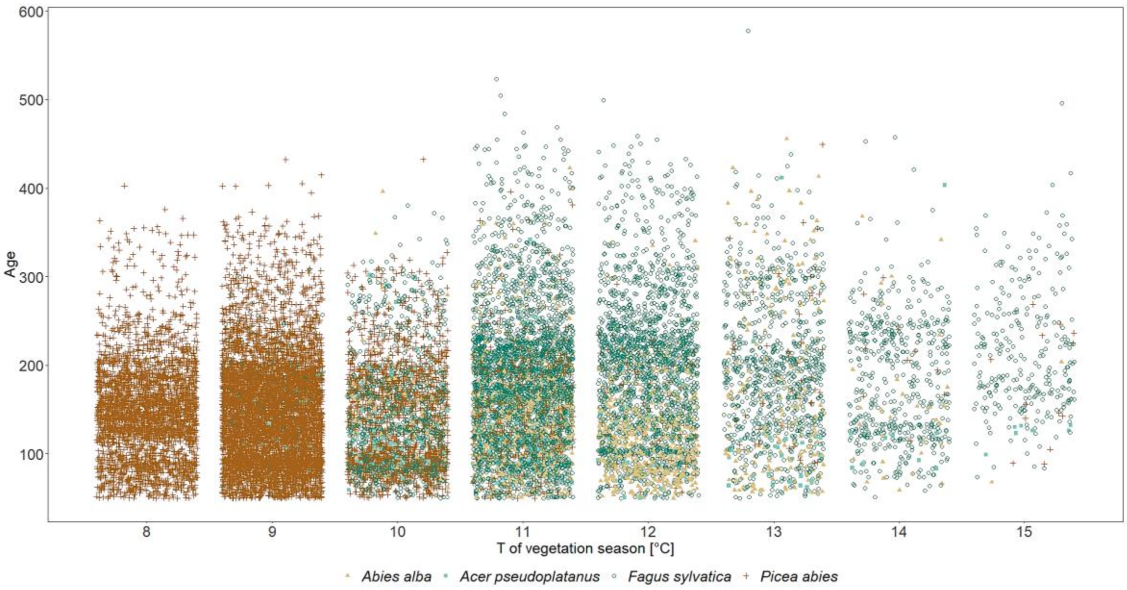

Figure S7. Relationship between age and the average temperature of the vegetation season

Table S4. Characteristics of stands included in the canopy accession patterns drivers analyses

Forest type	Country	Stand	Sampling year	N of plots	Average altitude (m)	Average annual T (° C)	Average annual precipitation (mm)
Mixed beech	Albania	Curraj i Eperm	2016	14	1141	6.9	1157
		Lumi i Gashit	2016	14	1373	8.3	1043
	Bosnia and Herzegovina	Perucica 1	2016	14	1293	6.5	1193
		Perucica 2	2016	14	1176	6.5	1193
		Perucica 3	2016	14	1118	6.5	1193
	Bulgaria	Boatin	2017	14	1319	8.6	676
		Steneto 1	2017	14	1321	8.2	715
		Steneto 2	2017	14	1357	8.2	715
	Croatia	Corkova Uvala	2015	10	1009	7.7	1552
		Cudinka	2015	10	1119	7.5	1477
		Ramino Korito	2015	16	896	11.7	1174
		Risnjak	2015	14	1000	8.6	1669
		Rjecica	2015	14	679	7.5	1477
		Smrceve Doline 1	2015	14	1411	11.5	1319
		Smrceve Doline 2	2015	8	1453	11.5	1319
	Romania	Arpasul	2014	14	1116	6.8	766
		Belia	2014	14	1232	6.8	766
		Bistra valley	2016	14	1063	5.3	887
		Boia Mica	2014	14	1194	8.3	690
		Criva	2015	14	1007	5.3	888
		Izvoarle Nerei	2017	14	1104	8.1	848
		Paulic	2015	8	1015	5.3	888
		Sebesu	2014	14	1164	8.3	690
		Ucea Mare	2014	8	1010	6.8	766
	Slovakia	Havesova	2015	13	634	6.9	810
		Klenovsky Vepor	2019	13	1190	5.1	941
		Kornietova	2014	14	1141	5.5	1004
		Kundracka	2018	7	1090	5.7	1067
		Obrstin	2014	6	901	5.5	979
		Padva	2019	6	1159	5.6	979
		Polana	2015	20	1146	5.4	963
		Skalna Alpa	2019	8	1164	5.6	979
		Sramkova	2014	14	1036	5.6	1066
		Stuzica 1	2015	14	923	6.3	848
		Stuzica 2	2015	14	937	6.3	848
		Stuzica 3	2015	14	967	6.3	848
		Sutovska	2014	12	1065	5.6	1066
		Vihorlat	2022	21	780	8.2	794
Spruce	Romania	Arpasul	2012	6	1415	6.8	766
		Belia	2013	12	1483	6.8	766
		Boia Mica	2013	11	1467	8.3	690
		CAL3-Cajmrsk	2011	4	1632	3.8	874
		CAL3-Cocos	2011	5	1567	3.8	874
		CAL3-Dragus	2011	6	1585	3.8	874
		CAL3-Kota1618	2011	6	1504	3.8	874
		Capra	2013	12	1574	6.8	766

	Doamnei	2012	12	1519	6.8	766
	Giumalau 2	2011	24	1417	3.8	874
	Giumalau 3	2011	6	1435	3.8	874
	Sambata	2012	12	1498	6.8	766
	Ucea Mare	2012	12	1458	6.8	766
	Ucisoara	2013	12	1427	6.8	766
	Vistea Mare	2012	12	1468	6.8	766
Slovakia	Bielovodska dolina	2014	13	1345	4.0	973
	Bystra	2013	14	1410	5.1	940
	Dumbier	2013	17	1495	5.1	940
	Hlina	2013	16	1438	5.0	1075
	Janosikova Kolkaren	2013	24	1307	5.6	1066
	Javorova	2013	8	1439	4.0	972
	Koprova dolina	2014	13	1431	5.0	1075
	Osobita	2014	14	1368	5.0	1075
	Pilsko	2013	12	1328	6.7	1002
	Polana	2017	11	1375	5.5	980
	Smrekovica	2013	11	1385	5.5	979
	Ticha dolina	2013	16	1410	5.0	1075
	Zadne Medodoly	2013	7	1508	4.0	972
Ukraine	Gropha 1	2012	19	1377	4.7	945
	Gropha 2	2012	15	1353	4.7	945
	Gropha 3	2012	13	1314	4.7	945
	Syvulya 1	2012	15	1430	5.8	848
	Syvulya 2	2012	15	1357	5.8	848

Table S5. Species-specific parameters and threshold values for open-canopy recruitment, release detection, and canopy accession DBH threshold (DBHc). The early growth thresholds and canopy accession DBH threshold (DBHc) were identified as optimal cutpoints by minimising the absolute difference between sensitivity and specificity: *Abies* (OC = 1.509, sensitivity = 0.67, specificity = 0.66, AUC = 0.71), *Acer* (OC = 2.244, sensitivity = 0.72, specificity = 0.71, AUC = 0.79), *Fagus* (OC = 1.095, sensitivity = 0.62, specificity = 0.62, AUC = 0.67), *Picea* (OC = 1.748, sensitivity = 0.60, specificity = 0.60, AUC = 0.65), Others (OC = 1.855, sensitivity = 0.73, specificity = 0.75, AUC = 0.81), and DBHc (OC = 250.6, sensitivity = 0.92, specificity = 0.92, AUC = 0.98).

	Early growth rate threshold (mm)	Absolute increment threshold (mm)	DBHc (mm)
Abies alba	1.509	0.710	251
Acer pseudoplatanus	2.244	0.726	251
Fagus sylvatica	1.095	0.544	251
Picea abies	1.748	0.527	251
Others	1.855	0.734	251

Table S6. Variables used in the mixed models for the canopy accession drivers analyses with the mean value of the variable per species (first value) and its range (values in parentheses).

	Abies alba	*Acer pseudoplatanus*	*Fagus sylvatica*	*Picea abies* MB	*Picea abies* S
DMI	62.073 (37.75-89.77)	66.209 (45.51-88.26)	56.595 (36.31-89.77)	62.000 (37.75-89.77)	58.769 (37.76-71.61)
PDIR (MJ cm^{-2} yr^{-1})	0.755 (0.33-1.00)	0.707 (0.40-0.97)	0.766 (0.33-1.01)	0.812 (0.35-1.00)	0.682 (0.27-0.99)
Disturbance severity (%)	25.82 (10.0-67.1)	34.76 (10.2-71.0)	30.01 (10.0-71.0)	28.52 (10.0-58.3)	30.48 (10.1-82.8)
Disturbance timing (y)	49.61 (0-206)	11.56 (0-92)	52.83 (0-238)	30.31 (0-155)	30.18 (0-271)
Cumulative disturbance severity (%)	34.93 (10.0-92.1)	23.32 (10.0-74.0)	43.31 (10.0-117.9)	36.09 (10.0-79.1)	38.91 (10.1-106.7)
Number of disturbance events	1.57 (1-4)	1.20 (1-3)	1.93 (1-5)	1.61 (1-4)	1.75 (1-5)

Table S7. Tukey's pairwise comparisons of estimated marginal means of the canopy accession modes distributions (a); time to first release (b); time to DBHc (c); and the number of releases (d) of the dominant species.

(a) Canopy accession modes

Pairwise comparison	Est.	SE	p
Abies a. - *Acer p.*	-0.29	0.25	0.783
Abies a.* - *Fagus s.	**0.98**	**0.11**	**<0.001**
Abies a. - *Picea a.* MB	-0.18	0.15	0.769
***Abies a.* - *Picea a.* S**	**-1.02**	**0.18**	**<0.001**
Acer p.* - *Fagus s.	**1.26**	**0.24**	**<0.001**
Acer p. - *Picea s.* MB	0.11	0.26	0.993
Acer p. - *Picea a.* S	-0.73	0.28	0.064
***Fagus s.* - *Picea a.* MB**	**-1.15**	**0.13**	**<0.001**
***Fagus s.* - *Picea a.* S**	**-2.00**	**0.16**	**<0.001**
***Picea a.* MB - *Picea a.* S**	**-0.84**	**0.20**	**<0.001**

(b) Time to first release

Pairwise comparison	Est.	SE	p
Abies a.* - *Acer p.	**0.68**	**0.11**	**<0.001**
Abies a. - *Fagus s.*	0.07	0.04	0.331
***Abies a.* - *Picea a.* MB**	**0.17**	**0.06**	**0.029**
***Abies a.* - *Picea a.* S**	**0.57**	**0.06**	**<0.001**
Acer p.* - *Fagus s.	**-0.61**	**0.10**	**<0.001**
***Acer p.* - *Picea s.* MB**	**-0.51**	**0.11**	**<0.001**
Acer p. - *Picea a.* S	-0.11	0.11	0.860
Fagus s. - *Picea a.* MB	0.10	0.05	0.257
***Fagus s.* - *Picea a.* S**	**0.50**	**0.05**	**<0.001**
***Picea a.* MB - *Picea a.* S**	**0.40**	**0.07**	**<0.001**

(c) Time to DBHc

Pairwise comparison	Est.	SE	p
Abies a.* - *Acer p.	**0.23**	**0.04**	**<0.001**
Abies a.* - *Fagus s.	**-0.21**	**0.02**	**<0.001**
***Abies a.* - *Picea a.* MB**	**0.24**	**0.02**	**<0.001**
***Abies a.* - *Picea a.* S**	**0.28**	**0.05**	**<0.001**
Acer p.* - *Fagus s.	**-0.44**	**0.04**	**<0.001**
Acer p. - *Picea s.* MB	0.01	0.04	1.000
Acer p. - *Picea a.* S	0.05	0.06	0.956
***Fagus s.* - *Picea a.* MB**	**0.45**	**0.02**	**<0.001**
***Fagus s.* - *Picea a.* S**	**0.49**	**0.05**	**<0.001**
Picea a. MB - *Picea a.* S	0.04	0.06	0.954

(d) Number of releases

Pairwise comparison	Est.	SE	p
Abies a. - *Acer p.*	0.23	0.14	0.514
Abies a.* - *Fagus s.	**-0.42**	**0.05**	**<0.001**
Abies a. - *Picea a.* MB	0.11	0.09	0.678
***Abies a.* - *Picea a.* S**	**0.42**	**0.07**	**<0.001**
Acer p.* - *Fagus s.	**-0.65**	**0.14**	**<0.001**
Acer p. - *Picea s.* MB	-0.11	0.15	0.946
Acer p. - *Picea a.* S	0.19	0.15	0.701
***Fagus s.* - *Picea a.* MB**	**0.53**	**0.07**	**<0.001**
***Fagus s.* - *Picea a.* S**	**0.84**	**0.06**	**<0.001**
***Picea a.* MB - *Picea a.* S**	**0.30**	**0.09**	**0.008**

Est. – estimate of the difference, SE – standard error, p – probability. Significant differences are displayed in bold.

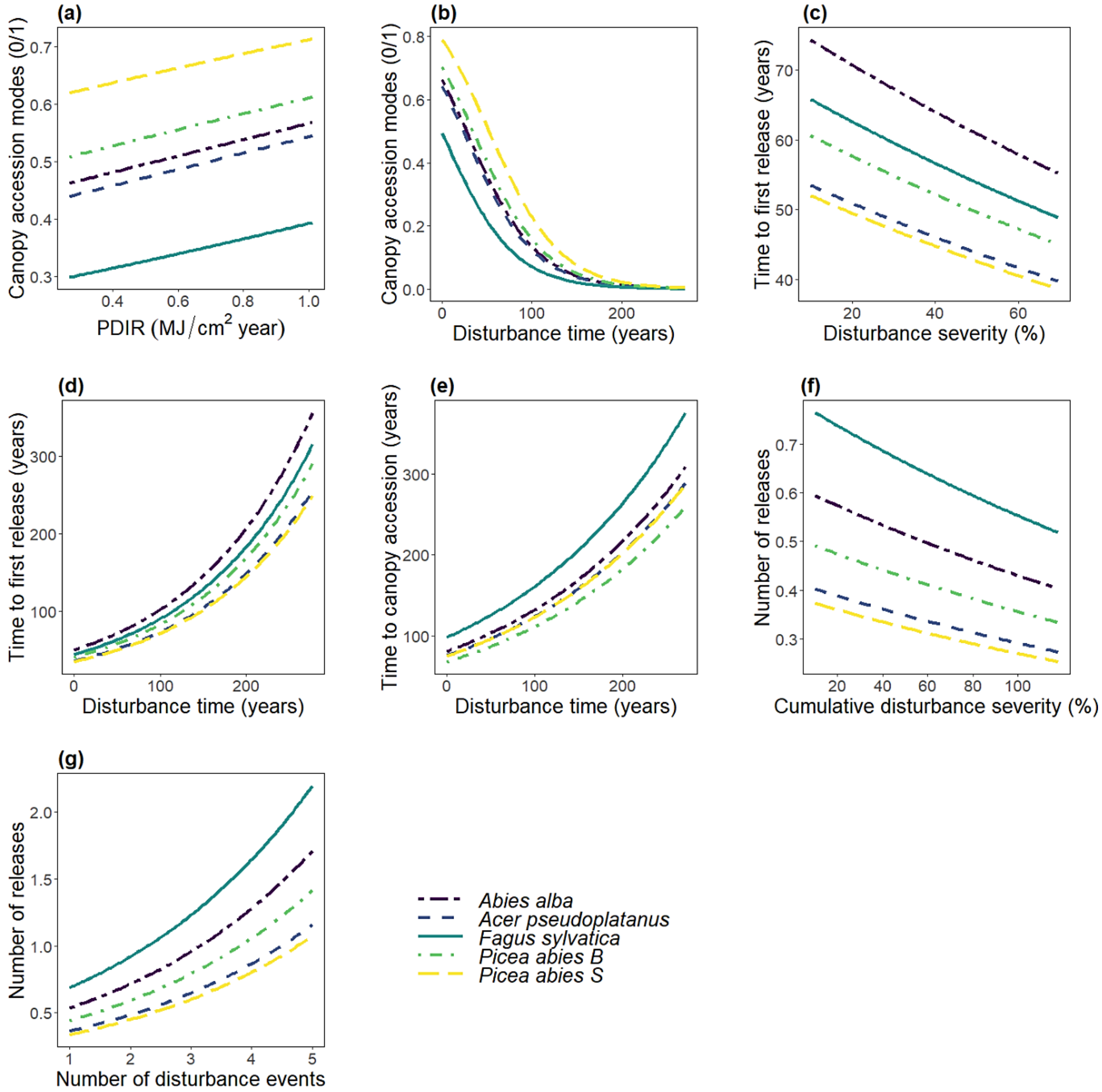

Figure S8. Predictions of significant effects and all the species based on generalized linear mixed models examining the drivers of canopy accession modes (a, b); time to fist release (c, d); time to reach DBHc (canopy accession) (e); and number of releases (f, g). The partial relationships between focal variables are displayed with keeping the other variables in the models constant. Further details of the models are displayed in Table 2.

Table S8. Tukey’s pairwise comparisons of estimated marginal means of the minimum growth (a); maximum growth (b); minimum BAI (c); and maximum BAI (d) of the dominant species.

(a) Minimum growth

Pairwise comparison	Est.	SE	p
Abies a. - Acer p.	**-0.32**	**0.08**	**0.001**
Abies a. - Fagus s.	**0.53**	**0.03**	**<0.001**
***Abies a. - Picea a.* MB**	**-0.39**	**0.05**	**<0.001**
***Abies a. - Picea a.* S**	**-0.47**	**0.09**	**<0.001**
Acer p. - Fagus s.	**0.84**	**0.08**	**<0.001**
Acer p. - Picea s. MB	-0.07	0.08	0.912
Acer p. - Picea a. S	-0.15	0.11	0.637
***Fagus s. - Picea a.* MB**	**-0.92**	**0.04**	**<0.001**
***Fagus s. - Picea a.* S**	**-1.00**	**0.08**	**<0.001**
Picea a. MB - *Picea a.* S	-0.08	0.09	0.900

(b) Maximum growth

Pairwise comparison	Est.	SE	p
Abies a. - Acer p.	-0.01	0.03	0.998
Abies a. - Fagus s.	**0.18**	**0.01**	**<0.001**
***Abies a. - Picea a.* MB**	**-0.12**	**0.02**	**<0.001**
Abies a. - Picea a. S	0.04	0.04	0.867
Acer p. - Fagus s.	**0.20**	**0.03**	**<0.001**
***Acer p. - Picea s.* MB**	**-0.11**	**0.03**	**0.010**
Acer p. - Picea a. S	0.05	0.05	0.848
***Fagus s. - Picea a.* MB**	**-0.31**	**0.02**	**<0.001**
***Fagus s. - Picea a.* S**	**-0.14**	**0.04**	**0.004**
***Picea a.* MB - *Picea a.* S**	**0.16**	**0.04**	**0.002**

(c) Minimum BAI

Pairwise comparison	Est.	SE	p
Abies a. - Acer p.	-0.25	0.11	0.178
Abies a. - Fagus s.	**0.77**	**0.05**	**<0.001**
***Abies a. - Picea a.* MB**	**-0.35**	**0.06**	**<0.001**
Abies a. - Picea a. S	-0.11	0.12	0.871
Acer p. - Fagus s.	**1.02**	**0.11**	**<0.001**
Acer p. - Picea s. MB	-0.10	0.12	0.907
Acer p. - Picea a. S	0.14	0.15	0.894
***Fagus s. - Picea a.* MB**	**-1.13**	**0.06**	**<0.001**
***Fagus s. - Picea a.* S**	**-0.88**	**0.11**	**<0.001**
Picea a. MB - *Picea a.* S	0.24	0.12	0.268

(d) Maximum BAI

Pairwise comparison	Est.	SE	p
Abies a. - Acer p.	0.20	0.04	**<0.001**
Abies a. - Fagus s.	**0.26**	**0.02**	**<0.001**
Abies a. - Picea a. MB	-0.07	0.02	0.062
***Abies a. - Picea a.* S**	**0.23**	**0.04**	**<0.001**
Acer p. - Fagus s.	0.06	0.04	0.554
***Acer p. - Picea s.* MB**	**-0.26**	**0.04**	**<0.001**
Acer p. - Picea a. S	0.03	0.06	0.990
***Fagus s. - Picea a.* MB**	**-0.33**	**0.02**	**<0.001**
Fagus s. - Picea a. S	-0.03	0.04	0.928
***Picea a.* MB - *Picea a.* S**	**0.29**	**0.05**	**<0.001**

Est. – estimate of the difference, SE – standard error, p – probability. Significant differences are displayed in bold.

Table S9. Overview of the studied stands and cores include in the analyses of duration and growth rates during releases

Region	Stand	N of plots	Mean altitude [m]	Mean T [°C]	EQ [°C*1000/mm]	N of cores
Fagus sylvatica						**611**
Western Carpathians						
	Klenovsky Vepor	3	1245	5.10	16.26	5
	Kornietova	8	1158	5.45	15.03	26
	Kundracka	2	1098	5.47	14.41	6
	Obrstin	3	890	5.42	15.65	16
	Padva	6	1173	5.46	15.67	18
	Polana	3	1260	5.28	15.28	11
	Skalna Alpa	2	1129	5.51	16.05	7
	Sramkova	9	1052	5.55	14.67	27
	Sutovska	9	1012	5.53	14.63	33
Eastern Slovakia						
	Havesova	1	633	6.79	20.93	4
	Stuzica 1	8	921	6.20	19.68	52
	Stuzica 2	6	1002	6.23	19.83	34
	Stuzica 3	12	958	6.24	19.94	105
	Vihorlat	7	812	8.08	23.35	26
Eastern Carpathians						
	Bistra valley	7	1036	5.11	17.17	30
	Criva	8	977	5.14	17.36	21
	Paulic	1	961	5.01	16.82	1
Southern Carpathians						
	Arpasul	11	1102	6.71	21.90	45
	Belia	4	1243	6.71	21.70	8
	Boia Mica	10	1180	8.13	26.27	45
	Izvoarle Nerei	1	1105	7.88	20.79	4
	Sebesu	9	1122	8.16	26.77	76
	Ucea Mare	3	946	6.74	22.19	11
Picea abies						**902**
Western Carpathians						
	Bielovodska dolina	6	1334	3.90	13.92	18
	Bystra	12	1408	5.03	15.72	51
	Dumbier	3	1522	5.02	15.62	10
	Hlina	12	1436	4.92	13.72	36
	Janosikova Kolkaren	17	1310	5.48	14.28	66
	Javorova	1	1475	3.88	13.89	5
	Koprova dolina	5	1450	4.95	13.52	17
	Osobita	7	1351	4.90	13.57	39
	Pilsko	6	1337	5.52	14.30	18
	Polana	10	1380	5.24	14.74	38
	Smrekovica	3	1385	5.33	15.23	5
	Ticha dolina	11	1424	4.92	13.81	38

	Zadne Medodoly	4	1518	3.87	13.84	15
Eastern Carpathians						
	Calimani 1	2	1580	3.64	16.50	4
	Calimani 2	1	1554	3.64	16.05	3
	Calimani 3	5	1493	3.61	15.43	9
	Giumalau 1	10	1399	3.66	16.09	38
	Giumalau 2	3	1415	3.68	16.46	23
	Gropha1	13	1375	4.57	16.00	62
	Gropha2	7	1350	4.55	15.75	41
	Gropha3	4	1307	4.55	15.64	10
	Syvulya1	11	1432	5.74	19.29	34
	Syvulya2	11	1390	5.75	19.62	55
Southern Carpathians						
	Arpasul	4	1381	6.71	21.64	12
	Belia	9	1483	6.66	21.32	34
	Boia Mica	9	1446	8.12	26.35	37
	Capra	12	1558	6.71	21.84	54
	Doamnei	6	1477	6.71	21.79	30
	Sambata	5	1525	6.67	21.30	17
	Ucea Mare	4	1499	6.71	21.59	27
	Ucisoara	5	1423	6.69	21.50	21
	Vistea Mare	8	1444	6.69	21.81	35

Table S10. Summary of generalized linear mixed models with the lowest AIC score per species and response variable combination examining the effect of select parameters on average growth during release (a) and duration of the release event (b) for beech and spruce.

a)	*Fagus sylvatica*					*Picea abies*				
Parameter	Est.	SE	t	p	R^2_m [%]	Est.	SE	t	p	R^2_m [%]
(Intercept)	**0.54**	**0.03**	**18.23**	**<0.001**		**0.69**	**0.02**	**27.45**	**<0.001**	**/**
Disturbance severity	**0.13**	**0.02**	**7.06**	**<0.001**	**10.37**	**0.06**	**0.01**	**4.49**	**<0.001**	**2.37**
EQ	0.03	0.03	1.08	0.282	/	-0.03	0.02	-1.29	0.197	/
PDIR	**-0.05**	**0.02**	**-2.62**	**0.009**	**0.53**	0.01	0.01	0.36	0.721	/
Age at release onset	/	/	/	/	/	**-0.08**	**0.01**	**-7.55**	**<0.001**	**6.16**
DBH at release onset	**0.09**	**0.02**	**5.70**	**<0.001**	**4.18**	/	/	/	/	/
Calendar year at release onset	**0.06**	**0.02**	**3.94**	**<0.001**	**2.43**	**0.04**	**0.01**	**3.54**	**<0.001**	**1.50**
$\tau_{00\ \mathrm{tree}}$	0.01					0.02				
$\tau_{00\ \mathrm{plot}}$	0.02					0.01				
$\tau_{00\ \mathrm{stand}}$	0.01					0.01				
R^2_m [%]	19.65					9.94				
R^2_c [%]	44.34					41.19				
Observations	642					916				

b)	*Fagus sylvatica*					*Picea abies*				
Parameter	Est.	SE	t	p	R^2_m [%]	Est.	SE	t	p	R^2_m [%]
(Intercept)	**3.21**	**0.02**	**148.58**	**<0.001**	**/**	**3.20**	**0.03**	**118.73**	**<0.001**	**/**
Disturbance severity	-0.03	0.02	-1.61	0.107	/	-0.01	0.02	-0.48	0.628	/
EQ	-0.02	0.02	-1.01	0.315	/	0.04	0.03	1.34	0.179	/
PDIR	0.02	0.02	0.79	0.428	/	0.01	0.02	0.29	0.772	/
DBH at release onset	**-0.40**	**0.02**	**-20.78**	**<0.001**	**48.05**	**-0.39**	**0.01**	**-27.27**	**<0.001**	**45.98**
$\tau_{00\ \mathrm{tree}}$	0.00					0.00				
$\tau_{00\ \mathrm{plot}}$	0.02					0.01				
$\tau_{00\ \mathrm{stand}}$	0.00					0.01				
R^2_m [%]	50.70					45.99				
R^2_c [%]	56.34					53.48				
Observations	642					916				

Results show estimates of the regression coefficients (Est.), standard errors (SE), z- values (t), and probabilities (p) of respective explanatory variables used in the models. Variances of random effects levels ($\tau00$), marginal determination coefficients (R^2_m), and conditional determination coefficients (R^2_c) are additionally displayed. All significant model parameters ($p < 0.05$) are signified in bold.