Czech University of Life Sciences Prague

Faculty of Forestry and Wood Sciences

Department of Forest Ecology

Structure, dynamics, and disturbances in the primary forests of eastern and southeastern Europe

Doctoral Thesis

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Ph.D. THESIS ASSIGNMENT

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Forestry Engineering
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Structure, dynamics, and disturbances in the primary forests of eastern and southeastern Europe

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Objectives of thesis

Natural disturbances play a significant role in shaping forest structural dynamics, influencing stand structural heterogeneity, biomass, and overall forest functioning. The legacy of these disturbances can have a profound impact on current forest structure, affecting how we interpret the drivers of forest dynamics. Structural attributes such as tree size distributions, including diameter at breast height (DBH) and age distributions, are critical indicators of forest dynamics. In primary temperate forests, these attributes reflect the cumulative effects of historical disturbances and ongoing environmental changes. Understanding these dynamics is essential for assessing forest resilience and predicting future changes in forest structure and ecosystem functioning. Quantifying disturbance regimes is imperative to assess their impact on present forest structural heterogeneity. Hence, the primary goal of this dissertation is to explore the impact of past disturbances on forest structural attributes—specifically DBH and age distributions—across primary temperate mountain forests in Europe, particularly in the Carpathian Mountains. The specific objectives of this dissertation are:
1. To analyze how historical mixed-severity disturbances shape current diameter distributions of primary temperate Norway spruce mountain forests in Europe.
2. To investigate the influence of past disturbances on present tree size distributions in European primary beech-dominated forests.
3. To examine how past disturbances have shaped stand age distributions in primary European temperate mountain forests.

Methodology

To achieve the objectives of this dissertation, a network of permanent research plots was utilized, established using a stratified random design across the Carpathian Mountains, encompassing regions in Slovakia, Romania, and Ukraine. The dataset included more than 500 permanent sample plots. Disturbance regimes at both the plot and stand levels were reconstructed with a focus on severity and timing, using a tree-ring approach. These disturbance regimes were then analyzed at both the plot and stand scales. A two-parameter Weibull function was applied to characterize DBH and age distributions, enabling the identification of distribution shapes such as negative exponential, unimodal, bimodal, and negatively skewed distributions.

Linear mixed-effects models (LMMs) and linear modeling (LM) were employed to assess the impact of disturbance regimes on forest structure, particularly in terms of age and DBH distributions. In these models, distribution shapes were used as response variables, while disturbance regime parameters (timing and severity) were treated as explanatory variables. The ”visreg” R package was used for visualizing model outputs, and the ”sjPlot” R package was utilized for model summaries and parameter extraction. All statistical analyses were conducted using the R programming language and environment for statistical computing.

The proposed extent of the thesis

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Keywords

Past disturbances; dendrochronology; dendroecology; forest structure; forest dynamics; tree size distribution; primary forests; Weibull distribution; mixed-modelling; linear modelling; Norway spruce forest; European beech forests; Carpathians Mountains

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DECLARATION OF INDEPENDENCE

I hereby declare that this PhD. Thesis, titled “Structure, dynamics, and disturbances in the primary forests of eastern and southeastern 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 the direct supervision of my supervisor.

I agree with the disclosure of this PhD. Thesis in accordance with the Czech Law Act (Act No. 111.1998 Coll. Sb.) regardless of the Defense of this results.

September 30, 2024, Prague

Signature

SUMMARY

Forest structure, including tree size distributions such as diameter at breast height (DBH) and age distributions, is a critical indicator of ecological change and forest dynamics. In primary temperate forests, these structural attributes reflect the cumulative effects of historical disturbances and ongoing environmental shifts. Understanding these dynamics is essential for assessing forest resilience and predicting future changes in forest structure and ecosystem functioning. The primary goal of this dissertation is to explore the impact of past disturbances on forest structural attributes—specifically DBH and age distributions—across primary temperate mountain forests in Europe, particularly in the Carpathian Mountains. This dissertation is divided into three major papers.

The first paper focuses on how historical mixed-severity disturbances have shaped the DBH distribution in Norway spruce-dominated forests in the Carpathian Mountains. Using a dendroecological dataset from 339 plots across 28 stands (7,845 trees), a linear mixed-effects model was performed to analyze the impact of disturbance parameters, including disturbance severity, timing, and recent disturbances, on DBH distribution. The analysis revealed that historical disturbances had a strong and significant effect on the current diameter distribution shapes at the plot level. High-severity disturbances were associated with unimodal diameter distributions, whereas low-severity disturbances resulted in reverse J-shaped distributions. These findings have important implications for forest management, particularly in terms of tree size heterogeneity, biomass storage, and productivity.

The second paper examines the impact of past disturbance severity, including the most recent and maximum disturbance severities, and timing, such as time since the last disturbance and time since the maximum disturbance, on present tree size distributions in beech-dominated forests in the Carpathians. The study utilized a dataset from the REMOTE Network, which includes 238 permanent sample plots across 23 stands (11,755 live trees) in Slovakia and Romania. A two-parameter Weibull function was fitted at the plot level, and linear mixed modeling was applied. The analysis revealed that mixed-severity disturbances historically shaped these forests, with significant variability in both severity and timing observed across different spatial scales. The

interaction between the time since the last disturbance and the maximum disturbance severity was identified as the most influential factor driving current tree size distributions. These findings highlight the complex dynamics governing forest ecosystems and suggest that shifts towards more moderate-severity disturbances, as predicted by climate change scenarios, could increase structural complexity at both stand and landscape levels.

The third paper investigates the impact of past disturbance regimes on stand-level age distributions in temperate mountain forests across the Carpathian Mountains. Data from 21,727 trees sampled across 590 plots (500 m², 1000 m², 1500 m²) within 55 stands in Romania (23 stands), Slovakia (27 stands), and Ukraine (5 stands) were analyzed. The study examined the influence of disturbance parameters—including maximum and most recent disturbance severities, time since the last disturbance, and time since the maximum disturbance—on stand age distributions across different forest types (beech and spruce) and regions. The results reveal significant variability in age distributions across the Carpathians, with spruce forests exhibiting greater variability compared to the more stable age distributions observed in beech forests. Based on the Akaike Information Criterion, among the disturbance parameters analyzed, time since the last disturbance emerged as the most influential factor, significantly affecting the Weibull shape parameter, which characterizes the stand age distribution. In contrast, the severity of disturbances—both recent and maximum—showed minimal impact on age distribution, suggesting that while disturbances occur, their timing rather than intensity most profoundly influences forest structure. These findings highlights the importance of incorporating temporal aspects of disturbance into forest management practices to ensure the sustainability and resilience of these temperate mountain forests.

This dissertation highlights the profound impact that historical disturbances have had on the structural dynamics of primary temperate forests in the Carpathian Mountains. Across all three studies, it is evident that the severity and timing of past disturbances have shaped the present diameter and age distributions of Norway spruce- and beech-dominated forests. High-severity disturbances tend to create simpler, unimodal distributions, while low-severity disturbances maintain more complex, reverse J-shaped distributions, indicating greater structural heterogeneity. These findings underscore the importance of considering both historical disturbance legacies and future climate

change scenarios in forest management strategies. By understanding how past disturbances influence present forest structure, we can better predict and manage the resilience and sustainability of these critical ecosystems in the face of ongoing environmental changes. Tailored management approaches that account for regional and ecological differences will be essential for preserving the diversity, productivity, and stability of Europe's mountain forests

Keywords:

Past disturbances; dendrochronology; dendroecology; forest structure; forest dynamics; tree size distribution; primary forests; weibull distribution; mixed-modelling; Norway spruce forest; European beech forests; Carpathians mountains

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I am also deeply grateful to Biliran Province State University in the Philippines for granting me the study leave that allowed me to pursue my PhD abroad. This opportunity has given me a broader perspective on forestry research and helped me better understand my role in forestry education as a faculty member of the Department of Forest Science.

This journey would not have been possible without the love and support of my family and friends. Thank you for your unwavering encouragement, patience, and understanding. Your belief in me has been a constant source of strength, carrying me through the most challenging moments of this journey. To my friends and colleagues, both near and far, thank you for being my sounding boards, my cheerleaders, and my sources of laughter and joy. Your companionship and encouragement have made this journey more manageable and enjoyable.

To everyone who has played a part in this journey, I am profoundly grateful. This accomplishment is as much yours as it is mine, and I am deeply thankful for the support, guidance, and encouragement I have received along the way.

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LIST OF ABBREVIATIONS

AIC - Akaike Information Criterion
ANOVA - Analysis of Variance
BA - Basal Area
BALM -Basal Area Larger than the Mean
BIC - Bayesian Information Criterion
CI - Confidence Interval
DBH - Diameter at Breast Height
ECDF- Empirical Cumulative Distribution Function
GIS - Geographic Information System
GLM - Generalized Linear Model
GPS - Global Positioning System
H - Height (of trees)
ICC – Intraclass Correlation Coefficient
LME - Linear Mixed Effects
LM - Linear Model
R^2 - Coefficient of Determination
SD - Standard Deviation
SE - Standard Error
TSI- Tree Size Inequality

PREFACE

My passion for forestry was nurtured in the Philippines, where I pursued both my bachelor's and first master's degrees in Forestry at Visayas State University, Philippines. I was fortunate to receive the Department of Science and Technology–Accelerated Science and Technology Human Resource Development Program (DOST-ASTHRDP) scholarship, which allowed me to pursue my master's studies and deepen my knowledge in this field. Building on this foundation, I later earned a second master's degree in Forest Sciences and Forest Ecology at the University of Göttingen, Germany, supported by a DAAD postgraduate scholarship. This educational journey, backed by the German Academic Exchange Service, reflects my deep commitment to advancing education and research in forest science.

I have been fortunate to conduct research in diverse forest ecosystems, including the tropical rainforests of the Philippines, the tropical dry forests of Ecuador, and the Caspian forests of Iran. My growing interest in forestry research motivated me to pursue a PhD, and completing this dissertation marks a significant milestone in my academic and professional development. This work has not only deepened my understanding of forest sciences but also shaped my perspective on the complex interactions between natural and human-induced changes in forest ecosystems. I hope that the findings of this research will contribute to ongoing efforts in forest conservation and management.

During my PhD journey, I had the incredible experience of conducting fieldwork in the Carpathian and Dinaric mountains, both located in Europe. This dissertation is the culmination of several years of research, driven by my deep interest in the impact of historical disturbances on forest structure. My journey began with a curiosity about how forests evolve over time, which led me to explore the primary temperate forests of Europe.

All of this has been driven by my passion for forestry, research, and teaching, with a focus on enhancing the understanding and preservation of natural environments. Through my academic and fieldwork endeavors, I strive to inspire others in the field of forest science and contribute to sustainable forestry practices worldwide.

Between Mountains and Memory

Steeped in the silence of these hills,
The land speaks in a quiet tongue.
Mountains hold their memories close,
As I gather them, one by one.

1. INTRODUCTION

1.1 FOREST STRUCTURE AND HISTORICAL DISTURBANCES IN PRIMARY TEMPERATE FORESTS

The structure of primary temperate forests is shaped by a combination of biological, environmental, and historical influences. Forest structure refers to the spatial arrangement of trees, including their size, density, species composition, and vertical layering. In these forests, which have experienced little human interference, natural events such as windthrow, fire, insect infestations, and diseases play major roles in their structural development (Seidl et al., 2017). To fully understand current forest conditions, it is necessary to examine both the present-day patterns and the historical disturbances that have shaped them over time (Ruiz-Benito et al., 2014).

Historical disturbances are critical in defining the composition and structure of temperate forests. These disturbances, which can vary in frequency and intensity, create openings in the canopy that allow sunlight to penetrate, promoting understory growth and the regeneration of trees (Thom & Seidl, 2016). Mixed-severity disturbances, where different areas of the forest are affected to varying degrees, often result in a mosaic of tree sizes and ages, contributing to the forest's structural complexity (Seidl et al., 2017). This heterogeneity supports a wide range of species and ecological processes, thus fostering biodiversity and ecosystem resilience (Ruiz-Benito et al., 2014).

Frequent disturbances, such as windthrow and insect outbreaks, impact forest structure differently than less frequent, high-severity events like large wildfires or severe storms. These more intense disturbances can significantly alter the landscape, often resetting successional stages by removing large numbers of trees and creating opportunities for pioneer species to establish (Thom & Seidl, 2021). While forests may eventually return to their original composition, some disturbance regimes can lead to long-term shifts in species dominance and overall forest dynamics (Ruiz-Benito et al., 2014).

Tree size and age distribution are key indicators of a forest's disturbance history. Primary temperate forests often display an uneven-aged structure, where older, larger trees dominate the canopy and younger trees grow in gaps created by past disturbances

(Seidl et al., 2017). Dendrochronology, or tree ring analysis, is a valuable method for reconstructing disturbance histories, offering insights into the timing, frequency, and severity of past events (Thom & Seidl, 2016). This technique provides detailed records of how natural disturbances have shaped forest structure over time.

Vertical stratification, or the layering of vegetation from the forest floor to the canopy, is another important feature of primary temperate forests. This stratification is influenced by the frequency and intensity of disturbances. For instance, frequent, low-intensity disturbances help maintain an open understory, whereas infrequent, high-severity events lead to dense regeneration in the understory (Seidl et al., 2017). These vertical layers affect light penetration, habitat availability, and species diversity, which in turn influence the overall health and functioning of the forest ecosystem (Ruiz-Benito et al., 2014).

Disturbances play a crucial role in shaping the successional trajectory of forests, determining how they recover and evolve over time. In primary temperate forests, succession can take centuries, with pioneer species being gradually replaced by late-successional species as the forest matures (Thom & Seidl, 2016). The frequency and severity of disturbances influence the pace and direction of this process. Frequent, small-scale disturbances promote continuous regeneration, while larger, more intense disturbances can reset successional stages, allowing for new forest development (Seidl et al., 2017).

Climate change is increasingly affecting forest structure and disturbance regimes. Rising temperatures and changes in precipitation patterns are expected to increase the frequency and intensity of storms, wildfires, and pest outbreaks. These shifts could alter the composition and structure of temperate forests, making them more susceptible to large-scale transformations (Thom & Seidl, 2021). Understanding past disturbances can provide a useful baseline for predicting how these ecosystems might respond to future environmental changes (Ruiz-Benito et al., 2014).

In forest management, efforts to preserve primary temperate forests often aim to mimic natural disturbance regimes to maintain biodiversity and ecosystem function. By promoting uneven-aged forest structures, conserving coarse woody debris, and supporting natural regeneration processes, managers can help preserve the ecological integrity of these forests (Ruiz-Benito et al., 2014). However, with human-induced climate change altering disturbance patterns, traditional management practices may face challenges, as emerging disturbance regimes do not always align with historical ones (Thom & Seidl, 2021).

In summary, the structure of primary temperate forests is deeply influenced by their disturbance history. The interplay between various disturbance types and intensities over time has created a diverse mosaic of tree sizes, ages, and species. As climate change continues to modify disturbance regimes, understanding the historical context of these natural events will be essential for developing effective conservation and management strategies to maintain the complexity and resilience of these forests (Seidl et al., 2017).

1.2 IMPORTANCE OF PRIMARY MOUNTAIN FORESTS IN EUROPE

Europe's primary mountain forests are among the most ecologically significant and biodiverse ecosystems on the continent. These forests, having experienced minimal human interference, serve as crucial habitats for a wide variety of plant and animal species, many of which are rare or endemic. Protecting these forests is vital for preserving biodiversity, as they offer safe havens for species vulnerable to habitat loss and fragmentation. For instance, research indicates that these primary forests are essential for maintaining mountain bird diversity, emphasizing their role as biodiversity hotspots (Wu et al., 2016). Beyond supporting wildlife, these forests contribute to the overall ecological health of the planet by maintaining balance within ecosystems.

Beyond their biodiversity importance, primary mountain forests play a crucial role in climate regulation at both local and regional levels. They help influence microclimates by storing carbon, preventing soil erosion, and managing water cycles. The dense canopy of these forests stabilizes humidity and minimizes temperature fluctuations, which is particularly vital in mountainous areas with extreme climatic conditions (Price et al., 2016). Additionally, the forest floor acts like a natural sponge, soaking up rainfall and reducing runoff, which helps prevent landslides and maintains water quality in surrounding areas. As climate change continues to affect ecosystems worldwide, the role of these forests in climate regulation becomes increasingly critical.

The structural complexity and diversity within primary mountain forests also contribute to their resilience in the face of disturbances. With their diverse species compositions and old-growth characteristics, these forests recover more effectively from natural events such as storms, fires, and pest outbreaks. Research shows that primary forests are more resilient to disturbances than managed forests, which often lack the complexity required for natural recovery (Pavlin et al., 2021). The presence of old trees, deadwood, and diverse undergrowth supports a variety of species and provides key ecosystem services like nutrient cycling and habitats for specialized organisms (Kozak et al., 2018).

These forests are also culturally significant, having played an essential role in the lives of mountain communities for centuries. Many local populations have historically depended on these forests for sustainable timber production, non-timber forest products, and traditional medicinal practices. The cultural heritage tied to these forests is deeply intertwined with local traditions, making their conservation not only an environmental concern but also a socio-cultural imperative (Malek et al., 2015). With increasing pressures from urbanization and industrialization, it is crucial to integrate these cultural values into forest conservation strategies to ensure their long-term protection.

In the face of climate change, the conservation of primary mountain forests takes on an even greater significance. As climate patterns shift, these forests may serve as critical refuges for species migrating in response to changing environmental conditions. The unique microhabitats within primary forests can provide safe spaces for species that struggle in more altered landscapes (Elkin et al., 2013). Additionally, protecting these forests plays a key role in global climate mitigation efforts, as they act as significant carbon sinks. By preserving and restoring these ecosystems, we can enhance carbon sequestration and help combat greenhouse gas emissions (Kun et al., 2020).

In summary, Europe’s primary mountain forests are invaluable for their role in conserving biodiversity, regulating climate, enhancing ecosystem resilience, preserving cultural heritage, and mitigating climate change. Their protection is essential not only for the species that inhabit them but also for the health of the planet and the well-being of future generations. To ensure the survival of these ecosystems, we must strengthen efforts to safeguard them from human activities and climate change, allowing them to continue thriving for a sustainable future.

1.3 TREE SIZE DISTRIBUTION (DBH AND AGE) AS INDICATORS OF CARBON STORAGE, BIODIVERSITY, AND FOREST FUNCTION

Tree size distribution, particularly diameter at breast height (DBH) and age, plays a crucial role in evaluating a forest's potential for carbon sequestration, biodiversity, and overall ecological function. The link between tree size and carbon storage is well-established, with larger trees, typically having higher DBH, contributing disproportionately to carbon sequestration compared to smaller ones. Studies show that forests with a greater proportion of large, mature trees have a higher capacity for carbon storage due to their accumulated biomass over time (Lutz et al., 2018). As trees grow older and increase in size, their ability to sequester carbon grows, making DBH and age important factors in forest carbon models. This highlights the importance of protecting mature forests, which are essential for climate change mitigation efforts.

Tree size distribution is also closely tied to biodiversity, as forests with a variety of tree sizes, including both large, mature trees and smaller, younger trees, support more diverse ecosystems. The structural diversity within these forests creates multiple niches that allow different species to thrive, ranging from understory plants to animals in the canopy. Forest stands with uneven DBH distributions and a mix of tree age classes tend to provide more varied habitats, thereby enhancing biodiversity (Poorter et al., 2015). Larger trees contribute to habitat complexity by providing features like cavities for birds and mammals, while younger trees support a range of plant and animal species through vertical stratification. This diversity of tree sizes is key to maintaining ecological balance and resilience in forest ecosystems.

In terms of forest function, the distribution of tree sizes and ages influences vital ecological processes such as nutrient cycling and water retention. Larger, older trees play a critical role in stabilizing forest ecosystems by maintaining soil integrity and regulating water cycles. These trees are essential for long-term forest health, often acting as keystone species. A diverse mix of tree ages and sizes increases forest resilience to disturbances, such as windthrow or insect outbreaks, by providing structural complexity that helps buffer against ecosystem collapse (Chave et al., 2009).

This structural diversity is especially important in the context of climate change, where forests are increasingly facing extreme weather events and shifting environmental conditions.

Understanding tree size distribution is vital for effective forest management, particularly in the face of climate change. By focusing on DBH and age, forest managers can enhance carbon sequestration, conserve biodiversity, and maintain critical ecosystem services. Management practices that promote the growth of larger trees and the preservation of old-growth forests can significantly increase a forest's carbon storage capacity. Moreover, maintaining a diverse age structure within forests can improve their resilience to disturbances, ensuring the continued provision of services such as habitat, water filtration, and carbon storage. These practices are essential for the long-term sustainability of forest ecosystems.

Statistical models like the Weibull distribution are useful tools for accurately assessing tree size distributions within forests. The two-parameter Weibull function is particularly effective in modeling these distributions, as it can adapt to various shapes that represent the ecological dynamics of forest stands (Zhang et al., 2001). By using such models, researchers and forest managers can gain valuable insights into forest structure, allowing for more informed decisions on conservation and management strategies. This quantitative approach deepens our understanding of how tree size and age distributions relate to broader ecological processes and forest health.

In conclusion, tree size distribution, particularly in terms of DBH and age, is a key indicator of a forest's carbon sequestration potential, biodiversity, and ecological function. The importance of maintaining structurally complex forests with a variety of tree sizes is clear, as it enhances resilience and carbon storage capacity. In the face of climate change and habitat loss, prioritizing the conservation and management of forests with diverse tree size distributions is essential for ensuring the sustainability of these ecosystems. Further research should continue exploring the relationships between tree size, age, and ecological processes, providing insights for more effective forest management and conservation efforts.

1.4 HISTORICAL DISTURBANCES AND ITS IMPACT ON CURRENT DIAMETER DISTRIBUTIONS

Global change has had a marked impact on disturbance severity and frequency in European forests (Panayotov et al., 2011; Seidl et al., 2014). These changing natural disturbances play a critical role in regulating forest structure and ecosystem dynamics at scales ranging from small patches to landscapes (Pickett and White 1985; Turner, 2010) and are among the most important natural processes that affect forest structure, composition, and functioning (Mitchell, 2013). Because forest disturbances have the ability to disproportionately impact susceptible tree cohorts (e.g. large trees are susceptible to windthrow and bark beetle attack; Canham et al. 2001; Coomes and Allen 2007), the size distribution of trees will almost certainly be impacted by increasing forest disturbance severities. This will undoubtedly impact the forest legacy, but the ultimate direction of that legacy remains uncertain (Panayotov et al., 2011; Seidl et al. 2014). However, understanding the essential role of natural disturbance in shaping the present forest structure is crucial to forest sustainability (i.e. future recruitment, resistance, and resilience), and will have important implications for guiding appropriate management strategies in forests increasingly impacted by disturbance (Seidl et al. 2014).

Any process that encourages the rise of a single cohort of trees will impact the future legacy of a forest by influencing the possibility of future recruitment and ongoing mortality (Oliver and Larson 1996; Coomes and Allen 2007). The presence of a dominant cohort within a forest can be identified through the analysis of size class distributions of trees (Coomes and Allen 2007). Thus, Franklin et al. (2002) and Coomes and Allen (2007) have shown that size class distributions are influenced by competition, disturbance, and senescence. Because Coomes and Allen (2007) focus much discussion on how disturbance induced mortality can influence the demography of trees and their subsequent diameter distributions, we focus here on the mechanism by which disturbance legacies impact forest sustainability. For example, we anticipate that low severity disturbance regimes will open small canopy gaps in a heterogenous spatial pattern. This will allow for continuous pulses of recruitment as gaps open and as mortality remains stable across size classes (Coomes and Allen 2007). The resulting diameter distribution of this disturbance regime will approach the famous reverse J-shaped distribution (Figure 1a) which represents an uneven aged stand that is highly resistant to mortality of one specific cohort (Niklas et al., 2003; Meyer, 1952; Westphal et al., 2006). Conversely, high severity disturbance will likely impact susceptible trees (e.g. large trees) reducing the diversity of size classes, encouraging a dense canopy under which recruitment may be reduced (Figure 1c). Thus, past forest disturbance regimes must be accounted for when postulating the future direction of a forest stand.

Torresan et al. (2020) suggested that maintaining the tree size heterogeneity (i.e. close to reverse J-shaped distributions), enhances stand productivity. Similarly, stand structural complexity such as tree DBH diversity was strongly related to aboveground biomass on a large-scale ecosystem (Ali et al., 2019). The present study investigates stand structural attributes (e.g. diameter distributions), linking past disturbances and their impacts on current and future forest trajectory. This will enable forest managers and policy makers to have a better understanding on forest changes that have occurred, the environmental context they occurred in, and anticipate future changes under different disturbance scenarios as they are predicted by a growing body of research (Panayotov et al., 2011; Mitchell 2013; Seidl et al., 2014). Also, because DBH is related to tree volume and carbon storage, we can speculate that natural disturbances have a long-lasting effect on ecosystem services and functioning such as biomass storage and stand productivity (Mensah et al., 2020, Torresan et al. 2020).

Norway spruce (*Picea abies* (L.) Karst.) is one of the most important tree species of the Carpathian Mountains, Alps, and the Balkan Mountains (Panayotov et al., 2011). Unmanaged Norway spruce mountain forests are limited in quantity in continental Europe and the majority of these forests are located in the Carpathian Mountains (Panayotov et al., 2011), which represents one of the largest mountain forest ecosystem in Europe (Holeksa et al., 2017; Kulakowski et al., 2017). Because the Carpathian Mountains span greater than 1,500 km, the extensive forests within the Carpathian Mountains offer an ideal opportunity to study forest dynamics of Norway spruce forests as impacted by past disturbances. However, previous studies have focused on old-growth and protected forest with a lesser focus on primary, unmanaged forests and the interactions between natural disturbances (D'Amato et al., 2008; Fraver et al., 2008; Panayotov et al., 2011). In order to better understand the dynamics of

Norway spruce forest, we compiled a large dataset to capture the long-lasting influences of past disturbances across a myriad of forest disturbance regimes.

Here, we hypothesized that disturbance severity and timing would have a strong influence on the current diameter distribution. The main objective of this study was to investigate how past disturbances influence the shape of current diameter distributions of primary Norway spruce-dominated forests on the plot-level. Our specific objectives were to address the following questions: (i) Do historical disturbances influence the shape of current diameter distributions, and (ii) which aspects of disturbance severity, or timing are most responsible for influencing the shape of current diameter distributions?

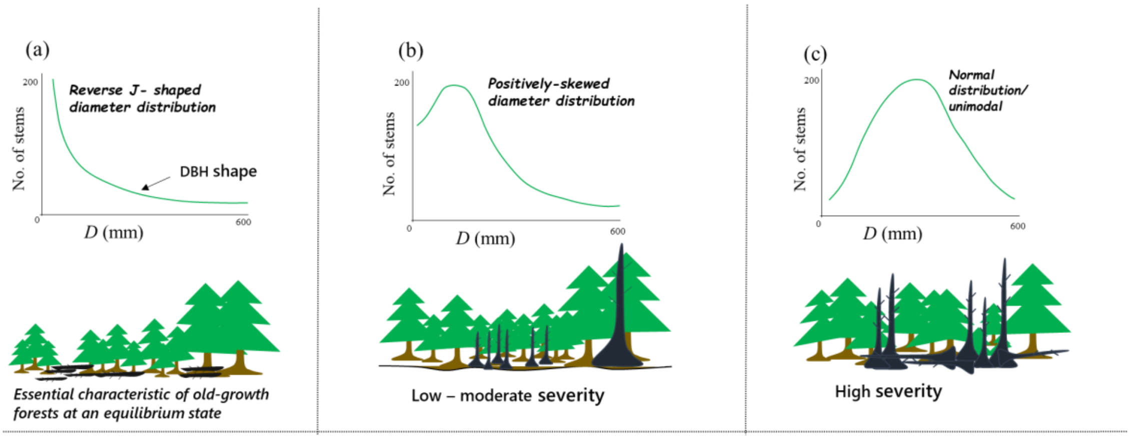

Figure 1. Conceptual figure illustrating how historical disturbance severity influences the current diameter distribution shapes. Panel (a) shows a forest stand in a state of equilibrium which follows the reverse J-shaped diameter distribution. This stand is not subject to large-, high-severity disturbance. Our premise that each forest stand follows uneven-aged populations, and the forest development phases follows Franklin et al. (2002). (b) Low – moderate severity disturbances create small-scale dynamics associated with small-sized gap dynamics killing select trees especially of sensitive cohorts (Holeksa et al., 2017). The resulting diameter distribution is positively skewed. (c) High severity disturbance kills all trees except those highly resistant to disturbance (Coomes and Allen, 2007). The resulting diameter distribution is unimodal.

1.5 PAST DISTURBANCE AND ITS IMPACT ON PRESENT TREE SIZE DISTRIBUTION

Global change has the potential to increase the severity and frequency of disturbances in European forests, affecting their structure and dynamics from small patches to entire landscapes (Panayotov et al., 2011; Seidl et al., 2014; Vacek et al., 2023). These disturbances play a crucial role in regulating forest ecosystem dynamics and are vital for forest structure and functioning (Mitchell, 2013). Understanding the role of natural disturbances is essential for maintaining demographic equilibrium in forests, influencing recruitment, mortality, and guiding management strategies in environments increasingly affected by these events (Seidl et al., 2014).

Large trees are particularly vulnerable to disturbances such as windthrow and bark beetle attacks, which can profoundly influence tree size distribution and the forest legacy (Canham et al., 2001; Coomes and Allen, 2007). The emergence of a dominant tree cohort, identifiable through size class distributions, significantly shapes the forest's future legacy (Oliver and Larson, 1996). These distributions, altered by competition, disturbance, and senescence, affect tree size distributions (Franklin et al., 2002; Coomes and Allen, 2007). Disturbances, ranging from low to high severity, contribute to structural complexity by creating a mosaic of different forest patches, each at varying stages of succession and development (Meigs et al., 2017). Therefore, understanding past disturbance regimes is essential for predicting the future dynamics of forest stand structures.

Coomes and Allen (2007) emphasized how disturbance-induced mortality influences tree demography and subsequent tree size distributions. Our conceptual model shows that mixed-severity disturbances create complex tree size patterns (Figure 2). These disturbances generate a heterogeneous forest structure by affecting tree mortality and regeneration patterns. We focus on how past disturbance legacies affect present forest tree size distributions, suggesting that low-severity disturbance regimes create small, spatially heterogeneous canopy gaps, enabling continuous recruitment pulses while maintaining stable mortality across size classes (Figure 2b).

Moderate-severity disturbances, such as windstorms, often lead to small-scale dynamics with small-sized gaps, primarily affecting sensitive cohorts (Holeksa et al., 2017). In contrast, high-severity disturbances typically impact large, vulnerable trees, reducing size class diversity and fostering a dense canopy that may limit recruitment (Figure 2d). High-severity disturbances can reduce size class diversity and potentially lead to denser canopies that suppress recruitment (Coomes and Allen, 2007; Rodrigo et al., 2022). A mixed-severity disturbance regime, dominated by moderate disturbances, can maintain tree size heterogeneity and structural complexity at both stand and landscape levels, potentially enhancing stand productivity and improving ecosystem services such as biomass storage and carbon sequestration (Larsary et al., 2021; Torresan et al., 2020; Yun et al., 2018).

Tree size heterogeneity, such as reverse J-shaped distributions, is associated with enhanced stand productivity (Torresan et al., 2020; Panayotov et al., 2011). Similarly, stand structural complexity strongly correlates with aboveground biomass on a large-scale ecosystem (Larsary et al., 2021; Ali et al., 2019; Yuan et al., 2018). The long-term effects of disturbances on ecosystem services, such as biomass storage and productivity, underscore the importance of acknowledging disturbance legacies in forest management (Mensah et al., 2020; Torresan et al., 2020). Recent investigations of Norway spruce forests reveal that low-severity disturbances create small canopy gaps, facilitating continuous recruitment and stable mortality across size classes, thus supporting a reverse J-shaped diameter distribution indicative of an uneven-aged stand resilient to cohort-specific mortality (Panayotov et al., 2015 Rodrigo et al., 2022).

Thus, this research aims to explore how past disturbances shape present tree size distributions in European beech-dominated forests. By linking historical disturbance patterns to present forest structure (proxied by tree size distributions), this allows us to identify the long-term impacts of past disturbances and their role in forest development, thereby informing effective forest management and conservation practices (Panayotov et al., 2011; Mitchell, 2013; Seidl et al., 2014). We hypothesize that the severity and timing of past disturbances substantially impact tree size distributions in European beech forests. Specifically, this research aims to (1) assess how disturbance severity and timing have shaped present tree size distributions both at the plot and stand levels, and (2) identify the role of mixed-severity disturbances in significantly impacting these tree size distributions.

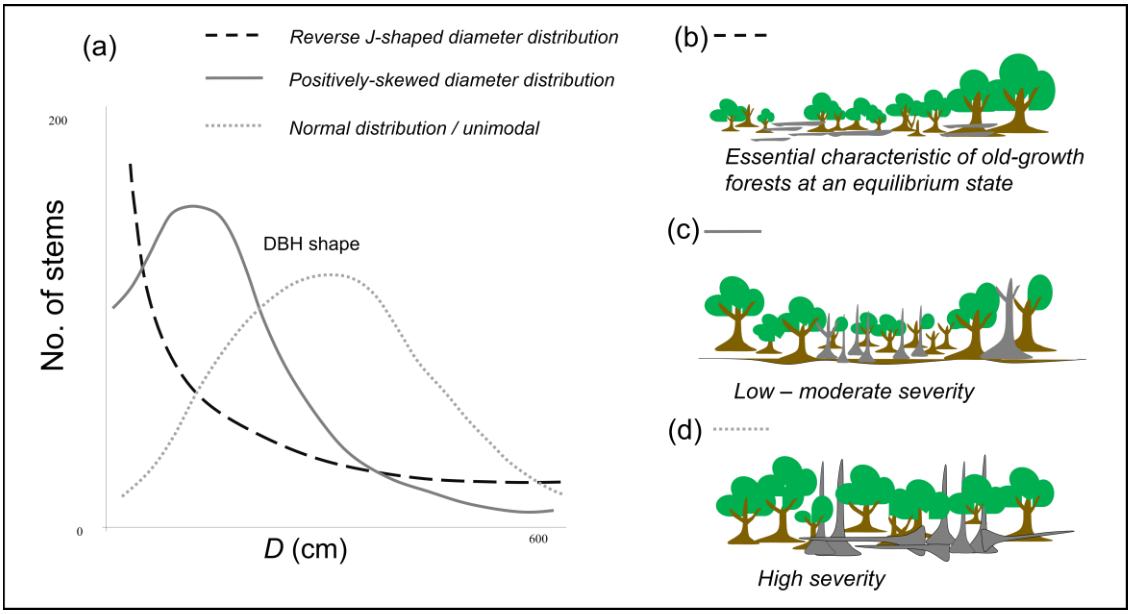

Figure 2. (a) Conceptual figure illustrating how past disturbance severity influences the current tree size distribution shapes modified with permission from Rodrigo et al. (2022). **(b)**This stand was not subject to large, high-severity disturbances. Each forest stand follows uneven-aged populations and development phases as per Franklin et al. (2002). **(c)** Low to moderate severity disturbances create small-scale dynamics with small-sized gaps, killing select trees, especially sensitive cohorts (Holeksa et al., 2017), resulting in a positively skewed diameter distribution. **(d)** High severity disturbances kill all but highly resistant trees (Coomes and Allen, 2007), resulting in a unimodal diameter distribution.

1.6 THE IMPACT OF PAST DISTURBANCES ON AGE DISTRIBUTION IN EUROPEAN TEMPERATE MOUNTAIN FORESTS

Mountain forests, particularly those in temperate regions of Europe, are currently experiencing significant transformations driven by a complex interplay of climate change, land-use alterations, and natural disturbances (Dale et al., 2001; Kulakowski et al., 2017; Kulakowski et al., 2012). These forests, often charaterized by a mix of species such as European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*), serve as crucial biodiversity reservoirs and provide essential ecosystem services. However, the resilience and structural integrity of these forests are increasingly threatened by the cumulative effects of various disturbances, including fires, windstorms, insect outbreaks, and avalanches (Kulla, 2023; Bolte et al., 2009). Understanding the historical and contemporary patterns of age distribution within these forests is essential for devising effective conservation and management strategies, particularly as these patterns are indicative of past disturbance regimes and their ongoing impacts on forest structure (Lindenmayer and Laurence, 2017; Turner and Seidl et al., 2023).

Historical disturbances have left an indelible mark on the age distribution and structural composition of European temperate primary forests (Bradford et al., 2008; Seidl et al., 2011). The legacy of these past events is evident in the current forest structures, where variations in age distribution reflect the intensity and frequency of disturbances that occurred decades or even centuries ago (Kozak et al., 2021; Čada et al., 2016). The resulting age structures can either stabilize or destabilize over time, depending on the severity and recurrence of disturbances (Pan et al., 2011; Vlam et al., 2017). For instance, stable age distributions are often flat or monotonically decreasing, suggesting a forest in equilibrium with its disturbance regime (Figure 3). In contrast, forests with irregular or unimodal age distributions may indicate a recent or ongoing shift in disturbance patterns, which could have significant implications for forest dynamics and biodiversity (Frelich, 2002; Correia et al., 2017).

In the Carpathian Mountains, a key region for studying European temperate primary forests, the interplay between past disturbances and current forest age structures provides valuable insights into the resilience and adaptability of these ecosystems. These forests, dominated by species like European beech and Norway spruce, have been shaped by centuries of natural and anthropogenic disturbances. Quantitative reconstructions of past disturbance events, including their severity, patch size, and spatial distribution, offer a crucial baseline for assessing the sustainability of these ecosystems under current and future environmental conditions (Čada et al., 2020; Turner et al., 2003; Seidl et al., 2011). The ability of these forests to maintain their ecological functions, such as carbon sequestration and biodiversity support, hinges on understanding how past disturbances have influenced their age distribution patterns.

The conservation and management of European mountain forests are increasingly focused on maintaining and enhancing their resilience in the face of global change.

This includes recognizing the importance of forest structure, particularly age distribution, as a critical parameter in assessing the impacts of disturbances and climate change (Seidl et al., 2017; Ruiz-Benito et al., 2017; Ruiz-Benito et al., 2014). Forests with diverse age structures may be more resilient to future disturbances, as they can better buffer against the loss of particular age cohorts and maintain essential ecosystem functions (Vangi et al., 2024a; Vangi et al., 2024b). Conversely, forests with skewed or homogenized age structures may be more vulnerable to the compounded effects of ongoing disturbances and climate change, underscoring the need for adaptive management practices that consider historical disturbance legacies (Kiel, 2024).

Hence, this present study of age distribution patterns in relation to past disturbances in European temperate primary mountain forests is crucial for understanding the long-term dynamics of these ecosystems. By examining the historical impacts of disturbances on forest structure, researchers can better predict how these forests will respond to future environmental changes. This knowledge is essential for developing conservation strategies that not only preserve the biodiversity and ecosystem services provided by these forests but also enhance their resilience in a rapidly changing world. As global change accelerates, the insights gained from studying these patterns will be invaluable for ensuring the sustainability of Europe's mountain forests. Specifically, we aim to address two main research questions: (1) What is the extent of age variability in European temperate primary mountain forests? and (2) How do historical disturbance parameters influence stand age distributions in these forests?

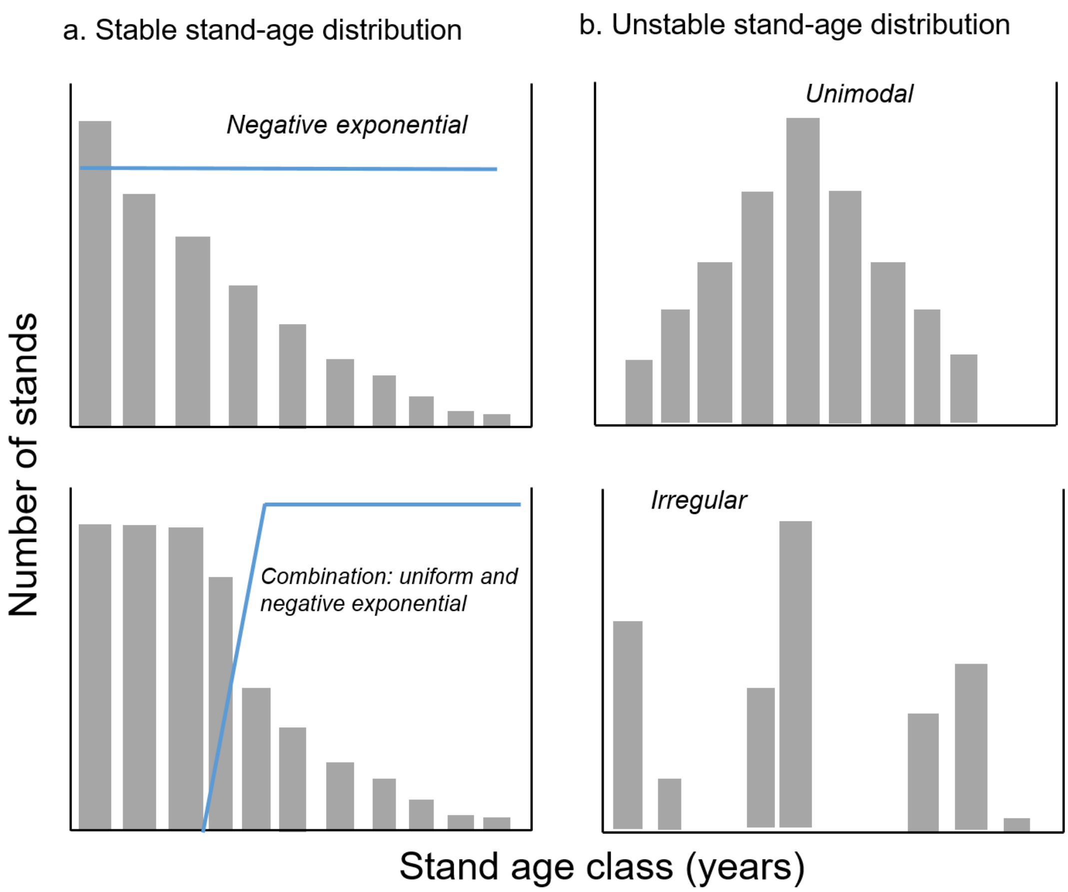

Figure 3. Frelich's theory on stable age distributions: Age structures may stabilize or destabilize over time depending on the severity and frequency of disturbances. Stable age distributions, characterized by flat or monotonically decreasing patterns, suggest a forest in equilibrium with its disturbance regime. In contrast, irregular or unimodal age distributions may reflect recent or ongoing shifts in disturbance patterns, with potential implications for forest dynamics and biodiversity (Frelich, 2002).

2. LITERATURE REVIEW

2.1 FOREST DYNAMICS REGIME IN TEMPERATE FORESTS

For more than two decades, forest principles have been integrated into various international policies and agreements, particularly within the framework of sustainable forest management (SFM). These international forest principles were first formulated during the United Nations Conference on Environment and Development (UNCED) in Rio de Janeiro in 1992 (Holvoet and Muys, 2004). There is a growing global concern regarding forest conservation and management, especially in the context of climate change. Several authors have pointed out that climate change is likely to alter natural disturbance regimes, posing significant negative impacts on forest ecosystems and their functioning (Turner, 2010; Dale et al., 2001; Easterling et al., 2000). Similarly, natural disturbances are recognized as key drivers of forest ecosystem dynamics (Svoboda et al., 2012). Seidl et al. (2017) reviewed various studies published since 1990, covering a wide range of significant forest disturbance agents (e.g., fire, wind, insects), and concluded that climate change could substantially modify future forest disturbance regimes on a global scale.

Additionally, several researchers have emphasized that disturbances can disrupt forest structure, composition, and ecosystem functioning by altering resource availability and the physical environment (Pickett and White, 1985). Lindner et al. (2010) further highlighted that changes in disturbance regimes are expected to be among the most profound impacts of climate change on forest ecosystems and their functioning in the coming decades. Natural disturbances, therefore, have pervasive direct and indirect effects on forest ecosystems worldwide, influencing the goods and services these ecosystems provide.

In Europe, disturbance agents such as snow, ice, wind, and insects are prevalent, with wind disturbance being the most significant (Seidl et al., 2017). For example, in the summer of 1983, a severe thunderstorm caused moderate to severe damage to a 12-hectare old-growth forest in Slovenia, dominated by *Fagus sylvatica* and *Abies alba* (Nagel et al., 2006). Seidl et al. (2014) reported that windstorms and bark beetle outbreaks have become the dominant disturbance regimes in Europe, with projections indicating that they could damage 60 million m^3 of wood annually between 2021 and 2030. These species are crucial for European forestry and require immediate conservation management efforts. Norway spruce, the most widespread and economically important tree species in Europe (Brus et al., 2011), is particularly vulnerable to windstorms and European bark beetle (*Ips typographus*) outbreaks (Overbeck and Schmidt, 2012). Similarly, *Fagus sylvatica L.*, or European beech, is one of the most important and widespread broadleaved trees in Europe (Durrant et al., 2016).

Studies have shown that wind disturbances are often followed by bark beetle outbreaks, leading to significant mortality in spruce forests across Europe (Figure 4; Wermelinger, 2004; Mezei et al., 2014). For instance, a windstorm in 2004 in Tatra National Park, Slovakia, damaged 12,000 hectares of forest in a single event (Mezei et al., 2014). Historical records and dendroecological reconstructions, as documented by Čada et al. (2016) and Svoboda et al. (2012), indicate that forests in the Bohemian Forest have been shaped by windstorms and bark beetle outbreaks dating back to 1760. Despite these disturbances, the old-growth forest still accounted for 26% of the region by 1880 (Bruna et al., 2013). Similar patterns of disturbances have also been observed in Yellowstone National Park and the southwestern United States, where wildfires and bark beetle outbreaks have significantly influenced forest dynamics (Turner et al., 2003; Noss et al., 2006).

However, Janda et al. (2017) noted that the long-term effects of disturbances are still poorly understood. They emphasized that the disturbance history of landscapes is rarely considered in forest management, despite its relevance to many ecosystem processes and the concept of "close to nature" management. This current research seeks to address this gap by providing baseline information on the influence of past natural disturbances on the structure and functioning of the remaining forests in eastern and southeastern Europe.

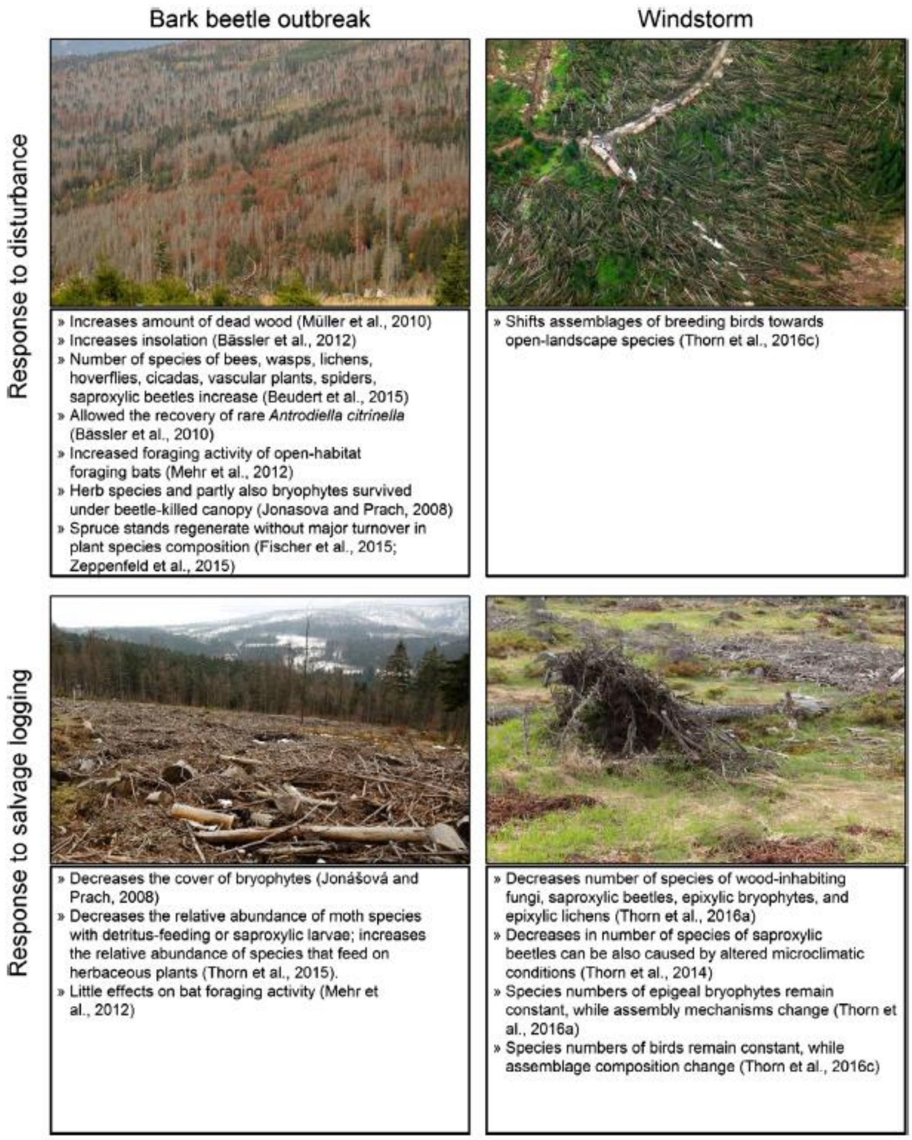

Figure 4. The windstorm Kyrill and extensive outbreaks of the European spruce bark beetle (*Ips typographus*) in the Bavarian Forest National Park, Germany, and the Šumava National Park, Czech Republic, have significantly altered forest structure and species composition (Thorn et al., 2017).

In a study conducted by Nagel et al. (2006) on regeneration patterns influenced by wind disturbances in southern Slovenia, it was suggested that intermediate wind disturbances can have long-lasting and distinctive effects on stand structure and composition. Similarly, recent research on an old-growth sub-alpine *Picea abies* stand in the Bohemian Forest provides strong evidence of the impact of wind disturbances on forest structure. Historically, this forest was shaped by infrequent, moderate to high-severity natural disturbances (Svoboda et al., 2012). While natural disturbances clearly influence forest stand characteristics, there is still a limited number of studies specifically examining the effects of these disturbances on forest structure and composition, especially in relation to different forest types (e.g., spruce, beech, and mixed-broadleaf forests).

Meigs et al. (2017) further reported that mixed-severity disturbance regimes are prevalent in temperate forests worldwide, yet significant uncertainties remain regarding the variability in disturbance-mediated structural development pathways. Although much research has been conducted on the influence of disturbances on forest structure, questions persist about how varying disturbance severity and timing affect forest structural complexity, particularly in systems characterized by severe disturbances (Svoboda et al., 2014).

Evaluating the impact of historical disturbances not only provides a crucial baseline for understanding how future changes in disturbance regimes might affect forests but also informs post-disturbance management and helps quantify forest resilience (Seidl et al., 2016). The implications of this understanding are significant, especially concerning decisions related to salvage logging and replanting, which have important consequences for biodiversity (Thorn et al., 2016; Fritz et al., 2008) and the provisioning of ecosystem services (Thom and Seidl, 2016). Therefore, understanding how forest structure and composition have been shaped by past natural disturbances is essential for informed management strategies in the context of a changing climate.

2.2 DISTURBANCE HISTORY AND ITS IMPACT ON FOREST STRUCTURE

Natural disturbances strongly influence the dynamics of forest ecosystems, as noted by Pickett and White (1985) and Turner (2010). As discussed earlier, these disturbances are prevalent worldwide and have both direct and indirect effects on forest ecosystem functioning, which in turn affects the goods and services that forests provide. According to Čada et al. (2013), understanding forest dynamics is crucial for effective forest management, particularly in the context of "close to nature" management. Similarly, characterizing the structure of old-growth forests is essential for providing forest managers with the necessary information to make informed decisions (Silver et al., 2013). Laginha Pinto Correia et al. (2017) emphasized that forest structure is a key indicator of biodiversity in temperate and boreal forests. Additionally, several authors have pointed out that understanding how forest structure and composition respond to past disturbances can provide insights into future resilience to climate-driven changes in disturbance regimes (Tepley and Veblen, 2015; Kneeshaw et al., 2011; Kulakowski et al., 2017).

One effective strategy for characterizing forest structure is by examining the dynamics of diameter distributions. Diameter distribution is widely used to assess disturbances within forests (Baker et al., 2005; Coomes and Allen, 2007), describe successional pathways and structural development (Zenner, 2005), predict future forest stand structure (Westphal et al., 2006), and evaluate potential forest sustainability based on structure (Rubin et al., 2006; Wang et al., 2009). Pommerening and Särkkä (2013) highlighted that understanding diameter distributions in detail enhances our knowledge of forest dynamics, particularly how different levels and scales of natural disturbances influence stand development processes. Janda et al. (2017) also noted that current forest structure and composition can provide insights into the impacts of past climate-driven disturbances.

Tree diameter diversity and height diversity are generally characterized as aspects of stand structural complexity (Wang et al., 2011; Ali et al., 2016), with height class and canopy cover density linked to forest stand structural development (Harper et al., 2003). Height-diameter equations are critical for understanding forest dynamics and estimating forest biomass and carbon stocks (Mensah et al., 2016). These variables, such as diameter or height, are widely used in growth prediction models and are essential for describing and understanding forest structure, which is directly relevant to forest ecosystem functioning (Ali, 2019). Therefore, analyzing the dynamics of diameter distributions in relation to historical disturbances is crucial for improving our understanding of forest dynamics and informing sustainable forest management practices.

Similarly, Xu et al. (2018) emphasized that forest stand variables such as height, basal area, and stand age are critical for sustainable forest management. This suggests that these variables are essential for effective forest management strategies. Laginha Pinto Correia et al. (2017) also pointed out that forest age structure is a critical component in forest management, as highlighted by the Montréal Process (Montréal Process Working

Group, 2015), which includes countries focused on the conservation and sustainable management of temperate and boreal forests. However, Laginha Pinto Correia et al. (2017) cautioned that stand age should not be used as the sole indicator of ecosystem sustainability; instead, it should be complemented by cover type and stand height. Xu et al. (2018) similarly emphasized that stand age is a fundamental variable in forest management, although it is not always readily available.

In the context of biodiversity, Chapin et al. (1996) argued that age structure targets alone may not capture all facets of biodiversity and should be supplemented or even replaced by other indicators of ecosystem sustainability. However, Harper et al. (2003) found that age class significantly influenced Shannon’s diversity within deciduous and mixed wood stands, supporting previous findings on the influence of forest age on tree structural diversity. Despite these findings, Laginha Pinto Correia et al. (2017) proposed that forest age structure, when combined with cover type and stand height, can help achieve a balance between forest exploitation, ecosystem function, and environmental conservation. Rubin et al. (2006) also discussed the relationship between age and tree diameter, which can influence the shape of diameter distributions. Thus, stand age, tree diameter, and height are interrelated and essential for understanding forest dynamics, ecosystem functioning, and sustainable forest management.

Rempel et al. (2016) further explained that stand structure is largely driven by stand age, which affects tree height, volume, carbon accumulation, and both vertical and horizontal complexity. These variables are vital for understanding forest ecosystem functioning. Consequently, this research aims to provide significant information that can inform future management strategies, particularly in addressing natural disturbances and enhancing forest resilience.

2.3 FOREST STRUCTURE AS AN INDICATOR OF ECOSYSTEM CHANGE

In recent years, forest health and sustainability have garnered significant attention within the context of sustainable forest management and the pursuit of the Sustainable Development Goals (SDGs). One of the most commonly used and well-studied variables in forest ecological studies is the frequency distribution of tree diameter classes (Zhang, 2001; Leak, 2002). Diameter distributions play a crucial role in silvicultural practices (McElhinny et al., 2005), as they provide insights into diameter size classes, age structure (Pan et al., 2011), and regeneration strategies (Westphal et al., 2006). Several researchers have utilized tree diameter distribution to characterize structural features in virgin forests across Europe (Westphal et al., 2006; Bradford et al., 2008).

Moreover, diameter distributions, which are graphs depicting the density of trees across 5various diameter classes (Figure 5), can indicate whether the density of smaller trees in a forest is sufficient to replace the current population of larger trees (Rubin et al., 2006). This makes diameter distribution a valuable tool for assessing potential forest sustainability. As a result, diameter distribution has become a key attribute for the management and conservation of biodiversity in forests (McElhinny et al., 2005).

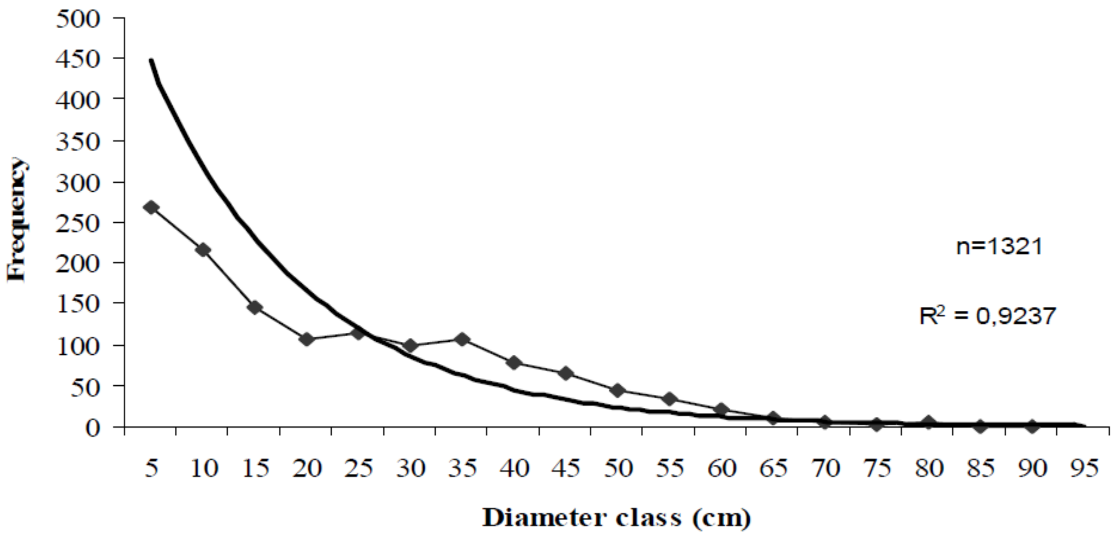

Figure 5. An example of diameter distribution pulled from Swedish beech dominated landscape (n=530) (Churski, 2006).

Different diameter distributions have been used to describe the structure of uneven-aged forests in Europe. For over a century, the reverse J-shaped curve, or the negative exponential relationship between tree density and diameter, has traditionally been considered a key characteristic of old-growth forests in an equilibrium state. However, various findings, particularly from North America, suggest that other forms of diameter distributions may also characterize old-growth forests (Westphal et al., 2006). These alternative distributions, often referred to as negative exponential distributions (Figure 6), have been studied extensively.

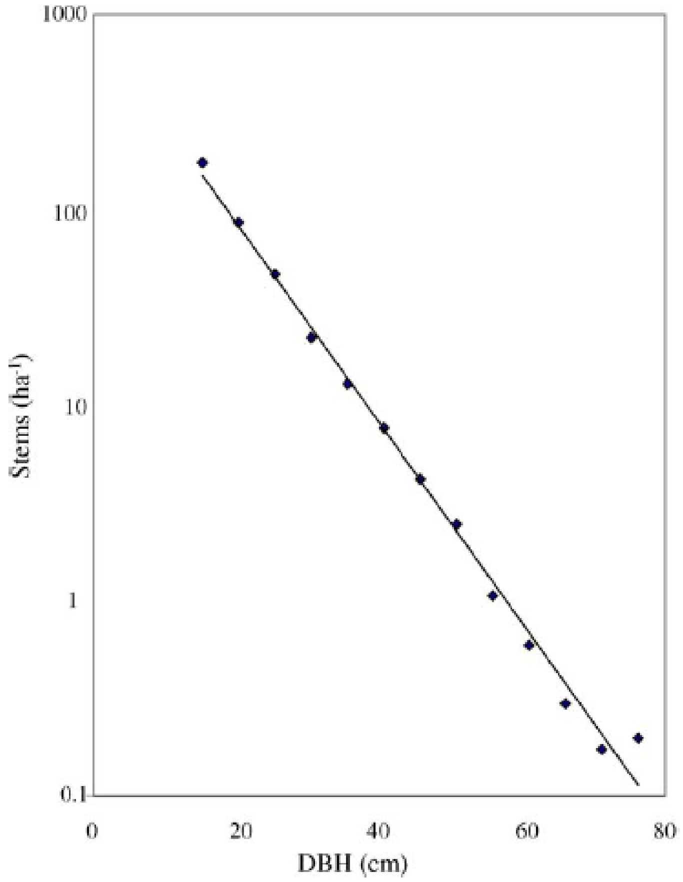

Figure 6. A negative exponential diameter distribution from a forest survey of New Hamsphire Redrawn with permission from Meyer (1952) (Rubin et al., 2006).

Schmelz and Lindsey (1965) demonstrated a negative exponential model when investigating 19 old-growth hardwood stands in Indiana. Similarly, Lorimer (1980), in his study of mixed-species virgin forests in eastern North America, found irregular diameter distributions that aligned with the negative exponential model. Leak (1996) confirmed these findings, reporting a negative exponential diameter distribution in an old-growth northern hardwood stand. Early analyses of virgin beech forests in the Eastern Carpathian Mountains by Roth (1932), as cited by Westphal et al. (2006), also described a smoothly and uniformly descending diameter curve. Likewise, Leibundgut (1993), also cited by Westphal et al. (2006), observed a reverse J-shaped diameter distribution, forming a straight line when plotted on a semi-logarithmic scale, in three adjacent virgin beech forest stands in Serbia. Tabaku (1999), cited by Westphal et al. (2006), described the diameter distributions of three Albanian virgin beech forests as a selection curve, implying a monotonically descending, reverse J-shaped form.

However, Westphal et al. (2006) challenged the notion that the reverse J-shaped curve is universally applicable, revealing that this model is not the only one suitable for describing diameter distributions in virgin beech forests. Their analysis of nine virgin beech forests (*Fagus sylvatica*) in southeastern Europe suggested that other forms of diameter distributions might also be indicative of forests in equilibrium. These findings call into question the previous assumption that the J-shaped curve is the most applicable diameter distribution for indicating a forest in equilibrium. Similarly, Gove et al. (2008) supported these findings, arguing that the quintessential reverse J-shaped model is not the only widely accepted and applicable model for describing the structure of uneven-aged forests. They introduced the concept of the rotated sigmoid form (Figure 7), characterized by a slight to pronounced plateau or even a mild hump in the mid-diameter range.

These studies suggest that there is no clear consensus on the type of diameter distribution characteristic of unmanaged primary forests in southern and southeastern Europe, where many of the continent's remnant forests are located. This highlights the complexity and variability of forest structures in these regions, challenging the traditional models used to describe them.

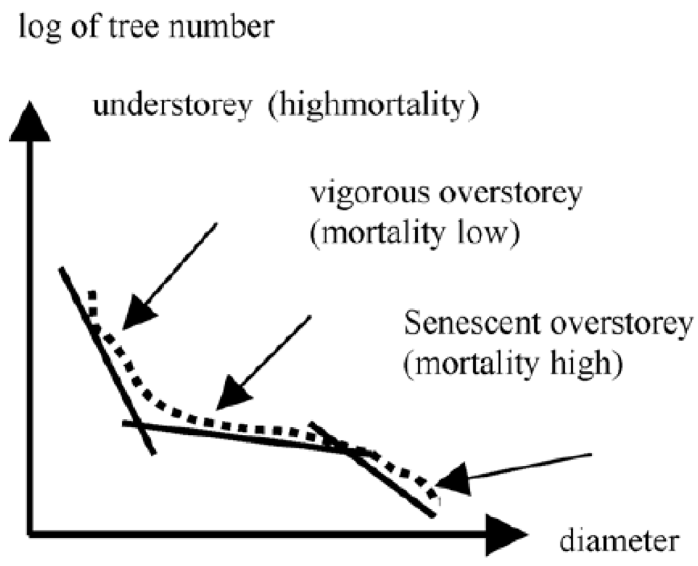

Figure 7. Hypothetical diameter distribution following Goff and West (1975) and showing three distinct growth and mortality rates. The dashed line shows that rotated sigmoid form of the diameter distribution (Westphal et al., 2006).

Diameter distribution can also provide insights into the age structure of a forest. Previous studies have shown that uneven-aged stands tend to exhibit highly right-skewed distribution curves, dominated by small-diameter woody species. In contrast, even-aged stands typically display mound-shaped diameter distribution curves, dominated by large-diameter woody species (Wittwer et al., 2004). Disturbances often result in even-aged stands with homogeneous structures, characterized by similarly aged stems and uniform temporal development (Ujházy et al., 2017). For example, Després et al. (2014) studied an old-growth stand dominated by sugar maple and yellow birch in western Quebec, Canada, and found recruitment pulses around 1870–1880 AD in 11 stands and around 1920–1930 AD in 8 of the 11 stands. These recruitment pulses were attributed to intermediate disturbances such as windstorms. Similarly, a disturbance reconstruction study in an old-growth mixed-species mountain forest in the Slovenian Alps revealed a stand-scale disturbance in the 1850s caused by strong winds, which significantly impacted the forest's structure and composition (Firm et al., 2009, Figure 8).

Understanding the age structure of forest ecosystems is crucial for investigating the historical legacy and disturbance history of forests. Diameter distribution is often used as a proxy indicator for the age of woody species, based on the assumption that young trees are typically smaller and older trees are larger (Lorimer and Krug, 1983).

A recent study conducted in the mixed forests of Nepal, which experienced high levels of anthropogenic disturbance, showed a shift in the diameter distribution that reduced the right skewness of the distribution curves. This shift decreased diameter class heterogeneity, effectively converting disturbed sites into even-aged stands (Sapkota et al., 2019, Figure 9). Although the disturbances in this study were primarily due to human intervention and thus not directly comparable to natural disturbances, the research highlights how disturbances can significantly alter forest structure, including diameter and age distributions.

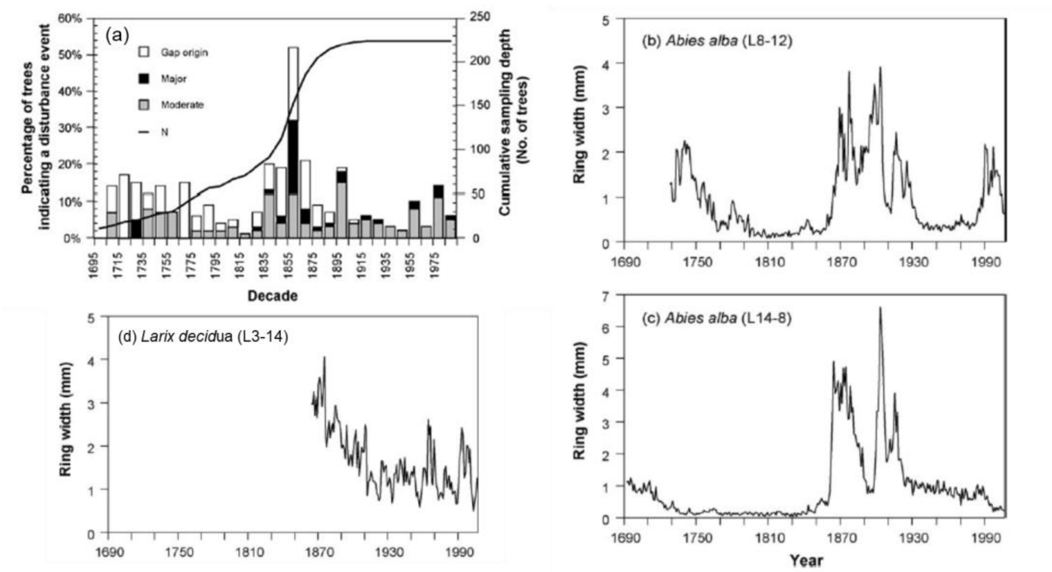

Figure 8. Disturbance chronology for the stand based on the canopy trees (a) and releases from suppression and declining growth during the 20th century for A. alba (b and c), and examples of radial growth showing a gradually declining pattern for L. decidua (d) (Firm et al., 2009).

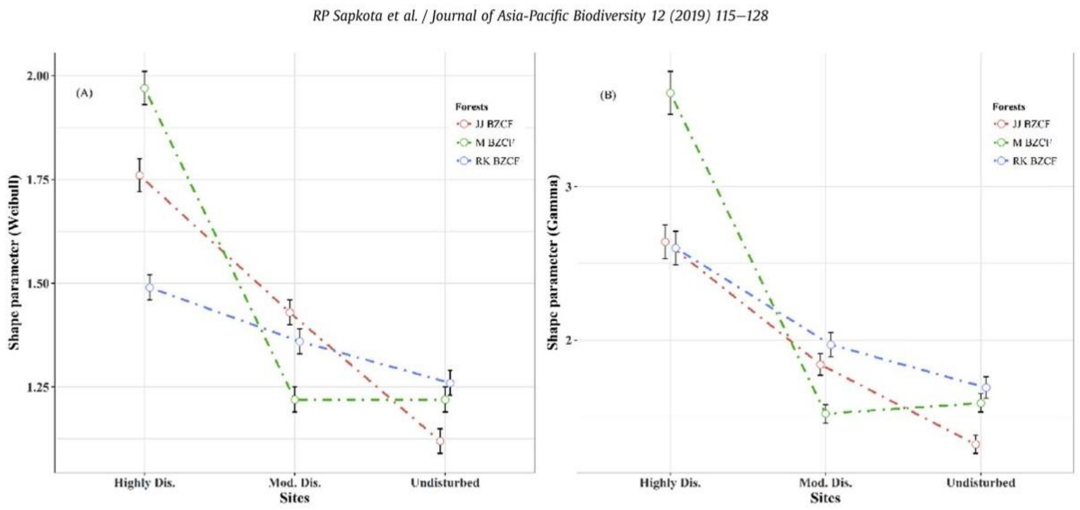

Figure 9. A study of mixed forest in Nepal showing the shape parameter for (A) Weibull and (B) gamma distributions for highly disturbed, moderately disturbed, and undisturbed sites in response to anthropogenic disturbances (Sapkota et al., 2019).

The information on diameter distribution and the age structure of forest stands is crucial for quantifying the role of disturbances in forested landscapes (Pan et al., 2011; Bradford et al., 2008). Undisturbed stands tend to develop more complex structures, which can positively influence understory diversity (Bhuyan et al., 2003; Chaudhary et al., 2016). Similarly, Ujházy et al. (2017) noted that disturbances often result in even-aged stands with homogeneous structures, characterized by similar-aged stems and uniform temporal development.

The Weibull probability density function is a valuable tool for analyzing tree density across different diameter classes (Bailey and Dell, 1973). Its flexibility allows it to fit various shapes and degrees of skewness, providing insights into mortality and recruitment patterns based on the shape parameter. The Weibull function can describe a wide range of distributions: for example, when the shape parameter (c) is less than 1, the distribution is steeply descending and monotonic; at $c = 1$, it represents a negative exponential distribution; when $c > 1$, the function becomes unimodal; for $1 < c < 3.6$, the distribution is positively skewed; at $c = 3.6$, it resembles a normal distribution; and when $c > 3.6$, the distribution is negatively skewed (Baker et al., 2005).

Baker et al. (2005) used the Weibull probability density function to examine diameter distribution in response to historical disturbances and found that the size distributions of common canopy species were often irregular, unimodal, or compound. This suggests that recruitment, growth, and mortality have not been continuous over time. The Weibull shape parameter can thus be used to infer mortality and recruitment dynamics in response to different disturbance categories. Figure 10 illustrates the effect of the shape parameter. Therefore, diameter distribution can reflect historical disturbances (e.g., low, moderate, or high disturbance) and stand age (e.g., young or old stands). Studies by Niklas et al. (2003) and Rubin et al. (2006) provided sufficient evidence to support the idea that older, relatively undisturbed communities tend to have size frequency distributions skewed to the right, whereas younger or recently disturbed communities exhibit the opposite pattern (Figure 11).

In summary, this recent research is both timely and relevant for understanding forest dynamics in response to historical disturbances. It contributes to our knowledge of how structural characteristics, such as diameter and age distribution, and forest functioning respond to variations in past disturbances.

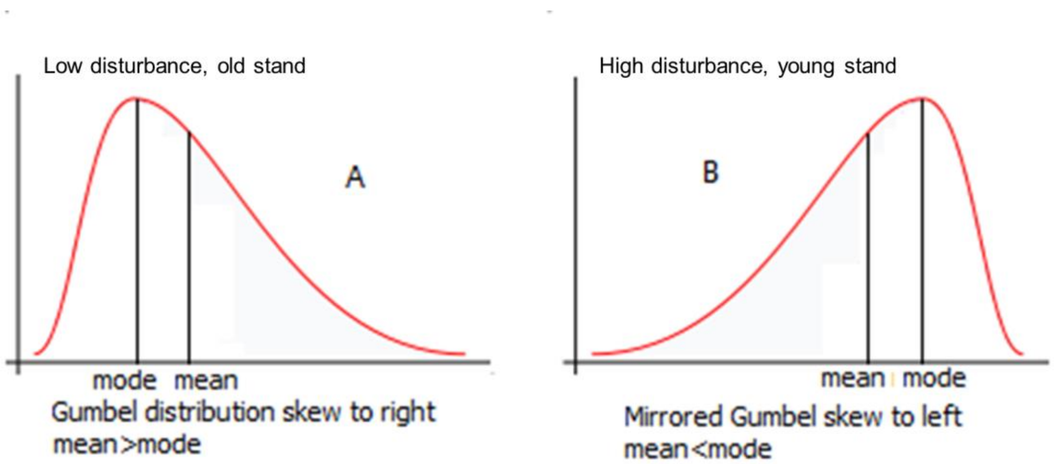

Figure 10. Hypothetical representation of the distribution based on the shape parameter as influenced by natural disturbance and stand age (Niklas et al., 2003; Rubin et al., 2006).

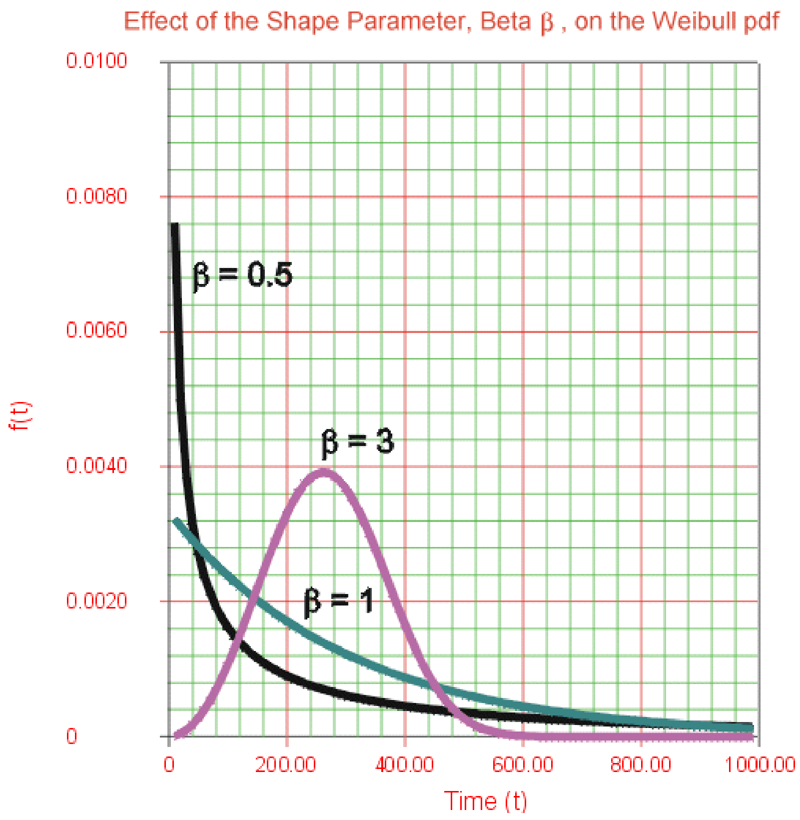

Figure 11. Effects of shape parameter for the Weibull function.

2.4 TREE DBH AND AGES AS CRUCIAL INDICATORS OF FOREST STRUCTURE

Tree size, typically measured by diameter at breast height (DBH), and tree age are essential indicators for evaluating forest structure, providing crucial insights into the composition, development, and historical changes within forest stands. In primary temperate forests, differences in DBH and age highlight important information about past disturbances and ongoing successional processes. Larger, older trees often dominate the canopy, while younger trees fill gaps created by disturbances, leading to an uneven-aged forest structure. Assessing the distribution of DBH and tree age is key to reconstructing a forest's disturbance history and predicting its future development, making these metrics indispensable for understanding forest ecology and guiding effective management strategies.

DBH is particularly important for assessing tree size inequality, which is key to understanding forest structural complexity. Indicators such as the Gini coefficient and basal area larger than the mean (BALM) are frequently used to evaluate the relative dominance of trees within a population (Valbuena et al., 2015). These metrics offer valuable insights into tree size distribution and inequality, both of which are critical for grasping the complexity of forest structures. The Gini coefficient measures the inequality in tree sizes, while BALM highlights the dominance of larger trees, helping to interpret how tree populations affect ecological dynamics and resource distribution within a forest.

Tree size inequality (TSI) significantly influences ecological processes, with research showing a positive correlation between TSI and species diversity (Zhang et al., 2023). This relationship underscores the importance of tree size variation in promoting structural complexity within forest ecosystems. A higher TSI typically indicates a wider range of habitats and more efficient resource partitioning, supporting greater species diversity. By creating diverse microenvironments, TSI fosters niche differentiation, enabling species with varying ecological requirements to coexist and thrive. These metrics not only characterize tree size distribution but also help understand forest dynamics. Larger trees often have a stronger impact on forest structure, contributing significantly to habitat complexity and resource allocation. In this way, TSI and related indicators play a vital role in explaining how forests function and in shaping management strategies aimed at preserving biodiversity and forest health.

The distribution patterns of diameter at breast height (DBH) in forest stands, such as unimodal, bimodal, and skewed distributions, are crucial for understanding tree population dynamics and overall forest structure. These distribution shapes offer valuable insights into ecological processes, management practices, and the health of forest ecosystems. Unlike traditional metrics such as the Gini coefficient, basal area larger than the mean (BALM), and Tree Size Inequality (TSI), which focus primarily on tree size inequality, DBH distribution shapes provide a more detailed view of tree population structures and their implications for forest management.

Unimodal distributions are typically associated with even-aged stands, where trees are grouped around a mean size, often forming a reverse J-shaped curve. This pattern indicates a stable growth environment where competition among trees is balanced, allowing for consistent regeneration (de-Miguel et al., 2012). On the other hand, bimodal distributions are often found in uneven-aged stands, where a mix of age classes and tree sizes exist, often reflecting disturbances or diverse management practices (de-Miguel et al., 2012; Sghaier et al., 2016). The presence of bimodal distributions may indicate ecological complexities, such as the coexistence of different species or the effects of selective logging, which can disrupt natural growth patterns (Zhang et al., 2018).

Skewed DBH distributions, particularly right-skewed ones, provide further insights into forest dynamics. Common in natural forests, right-skewed distributions indicate that while many trees are smaller in diameter, a few larger trees play significant ecological roles, such as providing habitats and influencing microclimates (Li et al., 2012). The flexibility of skewed distributions makes them useful for modeling various ecological scenarios, offering forest managers a valuable tool for predicting growth patterns and assessing forest health (Liu et al., 2022). For example, the Weibull distribution is often employed in DBH modeling, effectively capturing skewness and providing accurate predictions of tree growth and mortality (Li et al., 2012; Fu et al., 2022).

In contrast, metrics such as the Gini coefficient and basal area larger than the mean (BALM) are focused on quantifying tree size inequality rather than examining the actual distribution shapes. While these metrics are useful for indicating the level of size inequality within a stand, they do not directly reveal the ecological implications that different distribution shapes offer. For instance, a high Gini coefficient might suggest considerable size inequality, but without understanding the distribution pattern itself, it can be difficult to infer the ecological impacts or determine appropriate management strategies (Sghaier et al., 2016; Zhang et al., 2018). Similarly, BALM measures the proportion of basal area relative to the mean, which is helpful but lacks the detailed insights that DBH distribution shapes provide regarding tree interactions and forest dynamics (Zhang et al., 2018).

Thus, analyzing DBH distribution shapes—whether unimodal, bimodal, or skewed—gives a more comprehensive view of forest structure and dynamics compared to traditional metrics like the Gini coefficient, BALM, or tree size inequality (TSI). These distribution patterns not only reflect the ecological state of the forest but also offer essential information for forest management. Understanding these shapes can help guide practices aimed at sustaining biodiversity, promoting resilience, and maintaining forest health over time.

On the other hand, tree age, on the other hand, offers critical insights into the historical ecological processes that have shaped forests, particularly in old-growth stands. By analyzing tree rings, researchers can reconstruct past disturbance regimes, such as fires or windthrow events, and track changes in canopy dynamics over time. Metrics derived from tree age data are especially valuable for evaluating the natural complexity and stability of forest structures, making them essential for ecological assessments of primary and old-growth forests (Filippo et al., 2017). Age-related data not only illuminate patterns of long-term ecological stability but also contribute to understanding forest resilience, which is vital for informed forest management and conservation strategies.

Further, the relationship between DBH distribution and forest structural complexity varies depending on the type of forest stand. In even-aged stands, metrics such as basal area distribution tend to be more effective for predicting structural complexity, whereas in uneven-aged stands, tree abundance metrics play a more significant role in understanding forest structure (Peck et al., 2014). This distinction is essential for forest management, as it enables the development of tailored strategies that support biodiversity and maintain ecosystem functions across various forest types. On the other hand, remote sensing technologies, particularly lidar, have significantly improved the precision with which DBH and tree heights can be measured (Bulut et al., 2024; Xiang et al., 2024). These advancements have enhanced the accuracy of forest inventories and enabled more effective modeling of critical ecological processes, including carbon cycles, wildlife habitats, and forest growth patterns. Lidar provides a comprehensive perspective on forest structure over large areas, offering valuable insights into carbon storage and habitat provisioning potential (Huang et al., 2011).

However, despite these advancements, field inventories remain indispensable for validating remote sensing data. Remote sensing models often rely on assumptions and generalizations that may overlook the variability present in individual trees, especially in heterogeneous forest stands. Field-based measurements of DBH and tree age provide the accurate, direct data needed to ground-truth and fine-tune remote sensing outputs (Lee et al., 2024), ensuring more reliable and nuanced forest assessments.

Fieldwork offers essential insights that remote sensing cannot capture, such as tree health, species composition, and the presence of diseases or pests. These qualitative observations are critical for understanding ecological processes that shape forest structure, which are often undetectable through remote sensing alone (Huang et al., 2011). Furthermore, field inventories play a key role in refining remote sensing algorithms, as ground-truth data is necessary to ensure the accurate interpretation of metrics like DBH and biomass (Sheng et al., 2024). Without validation from field measurements, remote sensing models may yield biased or inaccurate results, particularly in complex landscapes with diverse forest structures (Peck et al., 2014).

Although remote sensing has transformed forest monitoring by providing large-scale, high-resolution data, it cannot entirely replace the detailed, precise information obtained through field inventories. The combination of remote sensing and fieldwork forms the most comprehensive approach to forest inventory, merging the broad-scale efficiency of technology with the vital, hands-on insights from on-the-ground data collection (Lamedica et al., 2011). This integrated approach is crucial for developing sustainable forest management strategies that consider both current forest conditions and potential future ecological changes.

2.5 DENDROCHRONOLOGY AND DENDROECOLOGY

Dendrochronology, the study of tree rings, is a vital tool for reconstructing disturbance histories within forest ecosystems. By examining tree growth patterns, we can better detect periods of stress and recovery linked to environmental disturbances such as fires, insect infestations, and climatic shifts. Tree rings, which form annually, serve as a chronological record of growth responses to these disturbances, offering insights into the timing and intensity of ecological events (Rozendaal & Zuidema, 2010). This historical perspective is crucial for understanding how forests have reacted to past disturbances and predicting how they might respond to future environmental changes, making dendrochronology a key approach in forest ecology.

One of the key applications of dendrochronology in reconstructing disturbance history is identifying fire events. Fire scars, visible within tree rings, provide evidence of past wildfires and their intensity. By cross-dating these scars across multiple trees, researchers can develop a comprehensive fire history for a specific region, highlighting patterns in fire frequency and severity (Copenheaver & Abrams, 2003). This knowledge is critical for forest management, as it sheds light on the role of fire in maintaining ecosystem health and resilience. For example, some forest ecosystems rely on periodic fires to promote regeneration and sustain biodiversity (Čufar et al., 2008). Consequently, dendrochronological fire histories can guide fire management strategies aimed at minimizing the risk of catastrophic wildfires while supporting natural ecosystem processes.

Dendrochronology also plays a crucial role in reconstructing the impacts of insect outbreaks on forest dynamics. Insect infestations can cause significant changes in tree growth, often leading to growth reductions or even tree mortality. By examining tree-ring patterns, researchers can detect periods of increased insect activity and link them to declines in tree growth (Druckenbrod, 2005). For instance, studies have detailed the effects of bark beetle outbreaks on coniferous forests, showing how these disturbances can influence forest composition and structure over time (Norrgård & Helama, 2021). Understanding the historical impact of insect outbreaks is essential for anticipating future disturbances and implementing strategies to manage forest health effectively.

Dendroecology, on the other hand, expands tree ring analysis by considering ecological factors that influence tree growth. This method allows researchers to evaluate how environmental stressors, such as drought or climate variability, affect tree health and growth patterns (Büntgen et al., 2014). By combining dendroecological data with climate records, scientists can reconstruct past climate conditions that shaped forest dynamics. This approach is particularly valuable in the context of climate change, as it offers insights into how trees have adapted to past climatic extremes and how they might respond to future shifts. For example, studies have revealed that trees in different regions exhibit diverse growth responses to changes in temperature and precipitation, emphasizing the need to understand these relationships for effective forest management and planning.

In addition, dendrochronology can provide valuable insights into anthropogenic disturbances, such as logging and land-use changes. By studying tree-ring records, researchers can pinpoint periods of heightened human activity and its subsequent impact on forest ecosystems (Muntán et al., 2004). This is particularly relevant in areas where historical logging practices have significantly altered forest structure and species composition. Dendrochronological studies can help uncover the timing and scale of these disturbances, offering a clearer understanding of how human actions have shaped current forest landscapes. Such insights are critical for crafting sustainable management strategies that balance ecological integrity with historical context.

Lastly, dendrochronology and dendroecology are indispensable tools for reconstructing disturbance histories in forest ecosystems. Through the analysis of tree rings, researchers can gain detailed insights into the timing and nature of disturbances such as fires, insect outbreaks, and human-induced changes. This knowledge is essential for understanding forest dynamics and informing management strategies that aim to enhance forest resilience in the face of ongoing environmental changes. As climate change continues to impact forests, integrating dendrochronological data into ecological research will become increasingly important for predicting future forest responses and ensuring sustainable management practices.

2.6 LINKING DISTURANCE HISTORY TO PRESENT FOREST STRUCTURE

Linking disturbance history to present forest structure, particularly tree ages and diameter at breast height (DBH), offers critical insights into how past events have shaped current forest ecosystems. Disturbance events such as fires, storms, and insect outbreaks influence forest dynamics by altering tree growth rates and structural composition. By reconstructing the disturbance history, we can better understand the impact of these events on the size distribution and age structure of trees. For instance, large disturbances often create gaps in the canopy, leading to regeneration events that influence DBH distribution and tree age cohorts (Fralish, 2003; Coomes and Allen, 2007).

The examination of tree ages through dendrochronology allows for the reconstruction of growth patterns and disturbance events. Tree-ring analyses provide chronological evidence of how individual trees and forest stands have responded to past disturbances. For example, growth releases identified in tree rings can indicate periods of recovery following canopy openings caused by windthrow or fire (Fraver & White, 2005). These growth patterns, when linked to specific disturbance events, help explain the current distribution of tree ages in the forest, showing which periods experienced intense regeneration versus more stable conditions.

DBH distribution is also tightly linked to historical disturbances. Forests that experience frequent low-intensity disturbances tend to have a more varied DBH structure, with a mix of small, medium, and large trees, as compared to forests that experience fewer but more severe disturbances. Large-scale disturbances, such as wildfires, often result in the dominance of younger, smaller trees due to mass regeneration events, while less severe disturbances, like selective windthrow, might maintain a broader range of tree sizes (Hart et al., 2017). By examining DBH in relation to tree ages, researchers can infer the severity and frequency of past disturbances that shaped the forest.

Understanding how past disturbances influence tree age and size distributions is crucial for forest management and conservation. Forests with diverse age structures and DBH distributions often exhibit greater resilience to future disturbances, as the variation in tree size and age provides a buffer against catastrophic events. For example, older, larger trees can survive certain disturbances, maintaining ecosystem stability, while younger trees regenerate in the gaps, ensuring long-term forest health and biodiversity (Ford et al., 2017).

Moreover, linking disturbance history to forest structure helps explain species composition in current stands. Different species respond uniquely to disturbances, with some thriving in post-disturbance environments and others being more dominant in stable, undisturbed conditions. By linking tree age and DBH to species-specific responses, forest ecologists can better understand the processes that drive current species composition and predict how future disturbances may further alter these dynamics (Franklin et al., 2007).

In summary, reconstructing disturbance history through tree ages and DBH analysis provides an essential framework for understanding the present structure of forests. This linkage highlights the importance of past events in shaping forest resilience, structural complexity, and biodiversity, thereby informing forest management practices aimed at maintaining ecological balance and preparing for future environmental changes (Fraver & White, 2005; Hart & Cox, 2017).

2.7 AIMS AND OBJECTIVES

The focus of this research is to examine the dynamics of primary montane forests in eastern and southeastern Europe in response to natural disturbances. Specifically, this study aims to determine the impact of historical disturbance agents on forest structure across the Carpathian Mountains. By analyzing the influence of these natural disturbances on forest stand characteristics, this research explores the patterns of age distribution and diameter at breast height (DBH) distribution within these forests.

Age and diameter at breast height (DBH) distributions are critical indicators of forest structure and serve as some of the most visible markers of ecological change. Understanding the patterns and dynamics of these distributions in response to past disturbances is essential for assessing forest health and resilience. By employing a dendrochronological approach, which involves the study of tree rings to date past events and analyze growth patterns, we can gain valuable insights into how historical disturbances, such as windstorms and insect outbreaks, have shaped these forests over time. This approach not only helps in reconstructing the history of forest disturbances but also in predicting how current and future disturbances may impact forest structure and function

The primary objective of this research is to assess the impact of past disturbances on the current forest structure in the primary forests of the Carpathian Mountains. The study is divided into three major publishable papers, each addressing specific research questions:

1. Analyze and compare the diameter distribution of Norway spruce at the plot and stand scales in relation to historical disturbances.
    a. Are there discernible patterns in DBH distribution across different forest stands?
    b. How does disturbance history influence current diameter distribution?
2. Investigate the impact of past disturbances on the present tree size distribution in beech-dominated forests in Europe.
    a. To what extent do past disturbances influence present tree size distributions?

    b. Which specific disturbance parameters and their timing are most influential in shaping current tree size distributions?
3. Examine the impact of past disturbances on stand age distributions in European temperate mountain forests.
    a. What is the extent of age variability in European temperate primary mountain forests?
    b. How do historical disturbance parameters influence stand age distributions in these forests?

3. METHODOLOGY

3.1 GENERAL APPROACHES USED ACROSS STUDIES

3.1.1 Study area

The study was conducted in the primary forests of the Carpathian Mountains, which are predominantly composed of European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies L. Karst*). As the second-largest mountain range in Europe, the Carpathians cover approximately 210,000 km² and extend across eight countries: Romania, Ukraine, Slovakia, Austria, the Czech Republic, Poland, Hungary, and Serbia. This region is home to some of the most significant remnants of temperate primary forests in Europe, with the majority located in Slovakia, Poland, Ukraine, and Romania (Kameniar et al., 2023; Mikoláš et al., 2019).

Historically, the forests of the Carpathians were largely protected from human activities due to their remote locations and difficult access (Sabatini et al., 2018). In contrast, lowland forests and those at lower elevations were often cleared to make way for human settlements and agricultural practices. This deforestation occurred at various points in history, particularly during the Middle Ages (ca. 500 to 1500 AD). While the mountain forests situated in steep valleys and on ridges remained largely untouched during this period, they have faced increasing pressures in recent decades. Until recently, a relatively continuous cover of mountain forests was maintained in the Romanian and Ukrainian regions, as well as parts of Slovakia, primarily due to the economic impracticality of logging in these areas.

However, the introduction of modern harvesting technologies has led to significant degradation of many previously undisturbed sites across the Carpathians. As a result, primeval forests have become increasingly rare, now representing only a small fraction of the total forest area. Despite their limited presence, the extent of these ancient forests continues to decline, primarily due to inadequate mapping of their locations and insufficient protective measures. Our research focuses on the beech and spruce forests within the Carpathians, aiming to enhance our understanding of their ecological dynamics and conservation needs.

Spanning a broad range of elevations, from about 600 to 1,700 meters above sea level, these forests thrive on diverse geological formations, including sedimentary and metamorphic bedrock (Begović et al., 2023). The region experiences varying precipitation levels, from around 600 mm in lower areas to 2,400 mm in the highest peaks of the High Tatra Mountains in Slovakia. Most sites receive annual rainfall ranging between 900 and 1,200 mm. Average temperatures also fluctuate with elevation, ranging from 13°C at lower elevations to around 0.5°C in the higher regions (Saulnier et al., 2020; Schurman et al., 2024).

Norway spruce, an important coniferous species both ecologically and economically, plays a key role in these ecosystems and has a long history of cultivation across Europe. Similarly, European beech is a dominant broadleaf species in the Carpathian forests, known for its ecological significance in maintaining forest biodiversity and resilience. Beech forests support a wide range of plant and animal species and contribute to the stability of the soil and hydrological cycles. Its natural regeneration ability and adaptability to different environmental conditions make it a crucial component of these temperate forest ecosystems.

For this research, the selection of countries and forest stands was based on the presence of mature old-growth or primary forests dominated by spruce and beech. These forests in the Carpathians have been largely protected from human influence due to their remote locations and poor accessibility. The elevation of the study areas ranged from 1,235 to 1,713 meters above sea level (masl), with a mean elevation of 1,435 masl.

In addition, the mean annual temperature in the study area ranges between 1.4°C and 5.0°C (Svoboda et al., 2014; Janda et al., 2017). The Carpathian Mountains are recognized as a biodiversity hotspot within the European temperate zone, hosting a large number of endemic species as well as significant populations of brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), grey wolf (*Canis lupus*), and capercaillie (*Tetrao urogallus*) (Oszlányi et al., 2004; Mikoláš et al., 2015; Janda et al., 2017).

Primary forests, as defined by Svoboda et al. (2014), are those "showing little to no evidence of human activity and persisting under a natural mixed-severity disturbance regime, but not necessarily in late-successional stages of development." The selection of study sites for this research was based on the presence of disturbance histories, such as windstorms and bark beetle outbreaks, ensuring that the forests analyzed have experienced significant natural events that contribute to their current structure and composition.

Further, most of the sites included in the study are under formal protection, such as national parks, natural parks, and forest reserves. Many of the beech forests are also recognized as UNESCO World Heritage sites under the designation "Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe." While there are several definitions for primary forests, and various terms used to describe forests with high natural integrity, in this context, primary forests are understood as ecosystems that show no direct human influence, where natural disturbances primarily shape the forest structure and composition. Importantly, these forests are not necessarily required to be in the old-growth stage (Kozák et al., 2018; Mikoláš et al., 2019).

Furthermore, the sites selected for data collection were identified and confirmed through a multi-step process. This involved using existing primary forest inventories (Veen et al., 2010), historical maps, archival data, and guidance from local experts to locate potential study areas. These locations were then examined in the field for characteristics indicative of forest naturalness, such as native species composition, pit and mound microtopography, large trees, and diverse age structures, along with horizontal and vertical complexity and the presence of coarse woody debris at various stages of decay. Forests showing signs of past logging, those previously used for grazing, or those located near grazing areas (within approximately 500 meters) were excluded from the study (Kozák et al., 2018; Mikoláš et al., 2019).

3.1.2 Plot establishment and data collection

For this study, plot locations were established and re-measured using a systematic approach. A fishnet grid was designed for each selected stand, with cell sizes varying depending on forest type. For spruce forests, cells were approximately 2 hectares, while for mixed forests, they were around 10 hectares. Within each cell, three random points were generated in an inner area of 0.5 hectares. When establishing new plots, the first randomly generated point was used unless the site was unsuitable due to obstacles such as steep terrain or water. In such cases, the second or, rarely, the third point was selected. For single spruce plots, the plot center was directly established at the selected point, whereas for mixed forests, nested plots were established by setting two plots 40 meters apart along the contour line from the center point (Figure 12). Before setting up two plots, the area was examined for any unforeseen issues. Within each permanent sample plot, we measured environmental attributes, including elevation and slope, along with the composition of live standing trees. For all live trees, we recorded the diameter at breast height (DBH) (measured at 1.30 m) and identified the species. In spruce forests, trees with a DBH of $\geq$ 10 cm were included, while in mixed forests, the threshold for inclusion was $\geq$ 6 cm DBH.

Re-measuring of previous plots was guided by precise GPS coordinates stored in ArcPad, with additional aids such as stone markers, pins, or tree core holes used to locate the plot center. A metal detector was employed to confirm the exact plot center. Once identified, a 'Glonas' device was positioned at a height of 1-2 meters to record the location three times, with each recording continuing until 50 data points were collected. Pins were placed on 3-5 trees closest to the plot center, at a height of 1.3 meters, and a stone grave was created to aid future re-measurements.

For spruce forest data collection, plots were sampled annually between 2010 and 2014, with plot sizes ranging from 500 m^2 in disturbed areas with high tree regeneration to 1000 m^2 in less disturbed areas. In mixed forests, starting in 2014, data collection was based on a three-level sampling system with concentric circular plots. These consisted of an inner plot (200 m^2), a middle plot (1000 m^2), and an outer plot (1500 m^2). In 2014, an additional outer ring with a radius of 25.2 meters (2000 m^2) was used, selecting up to 12 trees for coring. In the re-measuring of spruce forests conducted in 2016 and beyond, all plots were expanded to a uniform size of 1000 m^2 for consistency.

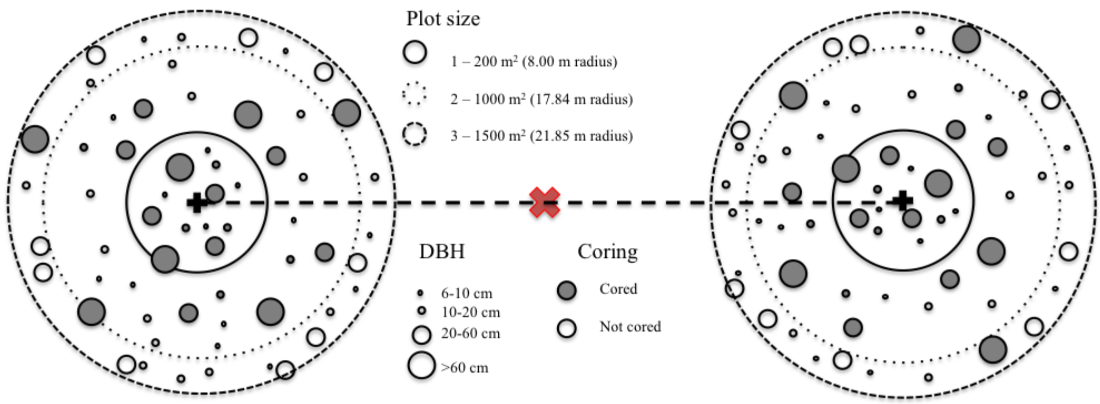

Figure 12. Example of the plot structure in the studied forests. The red flipped cross indicates the location of the single plot for spruce forests, while the black cross sign marks the location of the paired circular sample plots for mixed forests. The plot center is situated 40 meters away from the navigation point.

Each increment core, representing an individual tree, was air-dried, mounted on wooden boards, and carefully sanded using progressively finer sandpaper or prepared with steel microtome blades until the tree rings became clearly visible. The ring-width series were then measured using a Lintab sliding-stage measuring system in combination with TSAP-Win software (Rinntech, Heidelberg, Germany). Cross-dating of the tree rings was performed using marker years (Yamaguchi, 1991) and verified with CDendro (Larsson, 2015). For samples where the pith was missing, the number of missing rings and the distance to the center were estimated by analyzing the curvature and growth rates of the innermost rings (Duncan, 1989).

3.1.3 Tree ring processing

All increment cores, each representing a single tree, underwent a meticulous preparation process to ensure accurate measurement and analysis of tree rings. Initially, the cores were air-dried and subsequently glued onto wooden boards to facilitate handling. The surface of the cores was then sanded with progressively finer grit sanding paper, or alternatively, they were microtome-surfaced using steel microtome blades. This careful sanding process was crucial for making the tree rings clearly discernible, allowing for precise measurements of ring widths. The ring-width series were measured using a Lintab sliding-stage measuring system, which is coupled with TSAP-Win software (Rinntech, Heidelberg, Germany; http://www.rinntech.de). This combination of equipment and software provides a robust platform for obtaining high-resolution data on tree growth, which is essential for understanding the ecological and climatic factors influencing forest dynamics.

To ensure the accuracy of the tree-ring data, cross-dating was performed using established marker years, following the methodology outlined by Yamaguchi (1991). This process involved comparing ring patterns across different trees to identify and align growth anomalies, thus enhancing the reliability of the chronological data. The cross-dating was further verified using CDendro software (Larsson, 2015), which are widely recognized tools in dendrochronology for detecting errors in dating and ensuring consistency across measurements. For tree-ring series that exhibited missing pith, the number of missing rings and the distance to the center were estimated based on the curvature and growth rates of the innermost rings, as described by Duncan (1989). This estimation is critical for reconstructing accurate growth histories, particularly in studies focused on understanding the impacts of environmental changes on tree growth and forest structure.

3.1.4 Disturbance history reconstruction

High-quality increment core samples (properly cross-dated, undamaged, and unrotten) obtained from live trees with DBH >= 10 cm were analysed to detect two types of tree canopy accession events: (1) release – abrupt, sustained increase in tree growth, indicating mortality of a former canopy tree, and (2) open canopy recruitment – rapid juvenile growth rates indicating recruitment in a former canopy gap (Lorimer & Frelich, 1989). Release events were identified using the absolute increase method (Fraver & White, 2005) as pulses where the difference between average growth rates of adjacent 10-year running intervals (absolute increase) was greater than or equal to 1.25 standard deviations of all absolute increase values calculated for a given species group (Abies, Acer, Fagus, Picea, and Others). Releases where increased growth was not sustained for at least 7 years were excluded from further analysis as they were more likely to indicate a short-term improvement in growth conditions rather than a disturbance event (Fraver et al., 2009).

To reduce overestimation of disturbance severity caused by lateral releases of mature trees already present in the canopy (Lorimer & Frelich, 1989), an optimal cutpoint

(DBH = 25.1 cm) separating subcanopy and canopy trees was estimated based on the DBH distribution of suppressed and released trees, minimising the absolute difference of sensitivity and specificity (sensitivity = 0.92, specificity = 0.92, AUC = 0.98). Release events detected when the tree DBH was above or equal to this threshold were excluded from further analysis. For the detection of open canopy recruitment, early growth rates of released and suppressed trees were calculated as 10-year averages from age 5 to 14 years (Lorimer & Frelich, 1989; Splechtna et al., 2005) and used to estimate optimal cutpoints (OC) separating trees originating in the open canopy from those found under closed canopy conditions, minimising the absolute difference of sensitivity and specificity: *Abies* (OC = 1.509 mm, sensitivity = 0.67, specificity = 0.66, AUC = 0.71), *Acer* (OC = 2.244 mm, sensitivity = 0.72, specificity = 0.71, AUC = 0.79), *Fagus* (OC = 1.097 mm, sensitivity = 0.62, specificity = 0.62, AUC = 0.67), *Picea* (OC = 1.748 mm, sensitivity = 0.60, specificity = 0.60, AUC = 0.64), and Others (OC = 1.855 mm, sensitivity = 0.73, specificity = 0.75, AUC = 0.81).

Trees with an early growth rate greater than or equal to the established threshold were considered recruited under open canopy conditions. Because shade-tolerant tree species may need more than one disturbance to reach the canopy (Lorimer & Frelich, 1989), multiple canopy accession events were allowed for individual trees. Trees exhibiting no signs of open canopy recruitment or release event were considered to have originated under open canopy conditions for the purposes of further analysis.

The percentage of disturbed canopy area on a plot was calculated for each year as a sum of the current crown areas of reacting trees (showing release or open canopy recruitment) divided by the total crown area of all the sampled trees (including trees with low-quality increment core samples to avoid overestimation of disturbance severity – Frelich, 2002). Current crown areas were predicted based on current DBH of trees using two linear mixed-effects models for coniferous (R^2 (cond.) = 0.718, R^2 (marg.) = 0.516, RMSE = 0.888 m) and broadleaved (R^2 (cond.) = 0.692, R^2 (marg.) = 0.544, RMSE = 1.642 m) species, which were calibrated on the sample of trees with measured crown dimensions and included random intercepts accounting for the sampling design levels (stand, pair-plot, plot).

To correct for differences in the intensity of increment core sampling, only currently released trees within a radius of 17.84 m from the plot center and replacements for missing or rotten trees collected outside this radius were used for the calculations and plots with fewer than 8 high-quality increment core samples were excluded from the analysis. Additionally, each plot was resampled by randomly taking 1,000 subsamples of size m = 8 (the maximum common number of sampled trees per plot). The calculation of disturbed canopy area percentage was performed for each subsample separately and then averaged on an annual basis to produce the final plot chronology. To improve the temporal accuracy of the disturbance history reconstruction, each annually binned chronology of disturbed canopy area percentage was smoothed using kernel density estimation (Trotsiuk et al., 2018). Kernel density was smoothed using bandwidth equal to 5 with the 30 years moving window. Disturbance events were defined as peaks of kernel density function increasing at least 5 years and the minimal distance between two peaks was 10 years.

The severity of the disturbance events was determined by summing the relative current crown areas of trees dated within the 11-year window around the peak of kernel density function. Individual plot-level disturbance events were detected as peaks with severity of more than 10% of disturbed canopy area to minimize false positive cases. Our disturbance chronologies are rather conservative, even though they should be carefully interpreted due to methodological approaches that might cause more than 10% variation in disturbance severity (Trotsiuk et al. 2018, Šamonil et al. 2015).

3.1.5 R Package Libraries

A range of R packages were employed applicable to all studies to conduct statistical analyses and generate visualizations crucial for understanding the effects of disturbance regimes on forest structure. “WeibullR” was applied to fit the two-parameter Weibull function, facilitating the modeling of diameter at breast height (DBH) and age distributions. This package provided the necessary flexibility to capture diverse distribution shapes, which are key to assessing forest structural responses to varying disturbance regimes.

To analyze the influence of disturbance severity and timing on forest structure at both plot and stand levels, “lme4” was used to fit linear mixed-effects models (LMMs). The package allowed for the inclusion of both fixed and random effects, making it suitable for the hierarchical design of the study, which incorporated multiple spatial scales. For simpler analyses where random effects were not required, the base R lm function was used to model the relationships between disturbance regimes and DBH or age distributions.

To visualize the outcomes of the regression models, “visreg” was employed, providing clear graphical representations of model predictions and aiding in the interpretation of the effects of disturbance regimes on forest structure. Additionally, “sjPlot” was used to generate detailed model summaries and extract key statistical parameters, such as fixed and random effect estimates, which were essential for the interpretation of the results. Data manipulation and transformation were facilitated by “dplyr”, which streamlined the preparation of datasets for analysis. The visual representation of forest structure patterns, disturbance effects, and model outputs was accomplished using “ggplot2”, a versatile package for creating high-quality visualizations.

Model diagnostics and validation were performed using “car”, ensuring the robustness and reliability of the regression models. Furthermore, “MuMIn” was utilized to compute model selection criteria, including R^2 values, which helped assess the explanatory power of the fitted models. Finally, the “stats” package was employed for basic statistical functions, including hypothesis testing and the computation of p-values.

3.2 HISTORICAL MIXED-SEVERITY DISTURBANCES SHAPE CURRENT DIAMETER DISTRIBUTIONS OF PRIMARY TEMPERATE NORWAY SPRUCE MOUNTAIN FORESTS IN EUROPE

3.2.1 Study plots

For this study, we used dataset from three countries—Romania, Slovakia, and Ukraine—to analyze the patterns of diameter at breast height (DBH) across the Carpathians. The dataset includes 123 plots from Slovakia, 105 plots from Ukraine, and 83 plots from Romania. This research specifically focuses on the spruce (*Picea abies L.* (Karst.) forests in the Carpathian region (Figure 13; Appendix Figure A1). The Carpathians contain the most extensive tracts of primary forests in Central, Eastern, and Southeastern Europe (Sabatini et al., 2020, Mikoláš et al., 2019), and the largest remnants of primary Norway spruce forests in temperate Europe, which makes ideal for investigating natural disturbance processes over large spatial scales. The study locations were based on an existing international network of permanent inventory plots (REMOTE; https://www.remoteforests.org) that span primary forests in Central, Eastern, and Southeastern Europe and that are randomly distributed across various environmental and climatic gradients. These forests in the Carpathians were largely protected from human influence due to their remote location and limited accessibility.

The elevation ranges from 1286 to 1596 m above sea level (masl) with a mean of 1431 m asl and slope ranges from 12.35 to 42.89 with a mean of 30 (Table A1). Annual mean temperature ranges between 1.4° and 5.0°C (Svoboda et al., 2014; Janda et al., 2017). Windstorms, which are often followed by outbreaks of the native European spruce bark beetle (*Ips typographus*), are the most prevalent natural disturbance agents in the region, causing tree mortality and regeneration responses at different temporal and spatial scales (Trotsiuk et al., 2014; Janda et al., 2017).

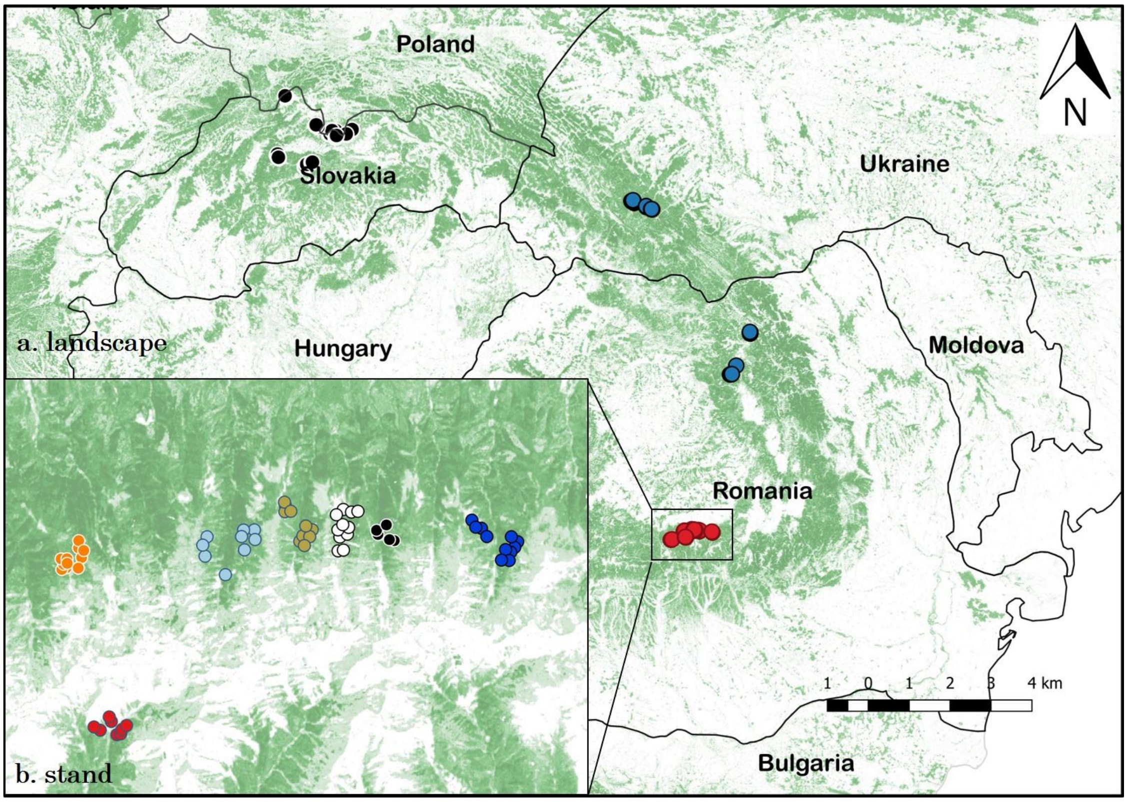

Figure 13. (a) Study region map showing plot locations across the Carpathians Mountains; Western Carpathians (black circle, n = 123), Eastern Carpathians (blue circle, n = 105); Southern Carpathians (red circle, n = 83). (b) Inset map shows the location of study plots in every stand. Each stand is represented with same color.

3.2.2 Data management prior to analyses

We divided the mountain range into three categorical landscapes: Western, Eastern and Southern Carpathians, and these correspond to the countries (regions) Slovakia, Ukraine, and Romania, respectively. Sampling was conducted in a total of seven stands in the Eastern Carpathians, nine stands in the Southern Carpathians, and twelve stands in the Western Carpathians. A total of 311 plots (0.1 ha; 7,545 tree cores) were sampled across the study area. Within each PSP, we measured environmental attributes (elevation and slope) and the composition of live standing trees. Diameter at breast height (DBH) (measured at 1.30 m height) and species were tallied and recorded for all live trees with the threshold ≥ 10 cm DBH. Structural attributes of the study area are presented in supplementary materials (Table A1).

3.2.3 Plot-level DBH distributions for spruce forests modeled using the 2-parameter Weibull function.

In this study, we employed a two-parameter Weibull function to numerically describe the diameter distributions of forest plots, which is a widely recognized approach in forest ecology for modeling tree size distributions (Figure 14). The two-parameter Weibull distribution, as highlighted by Baker et al. (2005) and Zhang et al. (2001), consists of a shape parameter and a scale parameter. The scale parameter effectively captures the abundance spread of the distribution, while the shape parameter provides insights into the skewness of the probability density function. This flexibility allows the Weibull function to model a variety of distribution shapes, ranging from reverse J-shaped distributions, which indicate balanced growth within a forest, to negatively skewed distributions that suggest the presence of several age classes within even-aged stands. By utilizing this robust statistical framework, we can gain a deeper understanding of the structural dynamics within forest ecosystems.

Prior to fitting the Weibull function to the diameter data, we implemented a selection criterion to ensure the reliability of our analysis. Specifically, we included only those plots that contained at least 30 live trees per plot, as recommended by Murphy and Farrar (1981). This threshold is critical because it helps to mitigate the effects of small sample sizes, which can lead to unreliable estimates of diameter distributions. By focusing on plots with sufficient tree density, we enhance the robustness of our findings and ensure that the resulting diameter distributions are representative of the underlying forest structure. This methodological rigor is essential for accurately assessing the influence of disturbance regimes on tree size distributions and for drawing meaningful conclusions about forest dynamics.

To analyze the influence of disturbance on diameter distributions, we adopted a two-pronged approach. First, we pooled data from all plots categorized by varying levels of disturbance severity—low to moderate, high, or very high—before fitting the Weibull function to these pooled datasets (Appendix Figure A2). This approach allows us to discern patterns in diameter distributions that are associated with different disturbance regimes, providing valuable insights into how disturbances shape forest structure. Second, we fitted the two-parameter Weibull function to the observed diameter distributions using the 'WeibullR' package in R language (R Development Core Team, 2024). This statistical analysis enables us to quantitatively evaluate the impact of disturbances on the shape of forest plot diameter distributions, thereby enhancing our understanding of the ecological implications of disturbance dynamics in temperate mountain forests. The findings from this analysis are expected to contribute significantly to the field of forest ecology by elucidating the relationships between disturbance regimes and tree size distributions. Understanding these relationships is crucial for effective forest management and conservation strategies, particularly in the context of ongoing environmental changes and climate variability. By employing the two-parameter Weibull function as a modeling tool, we can provide a comprehensive assessment of how disturbances influence forest structure, which is vital for predicting future changes in forest dynamics and ensuring the resilience of these ecosystems.

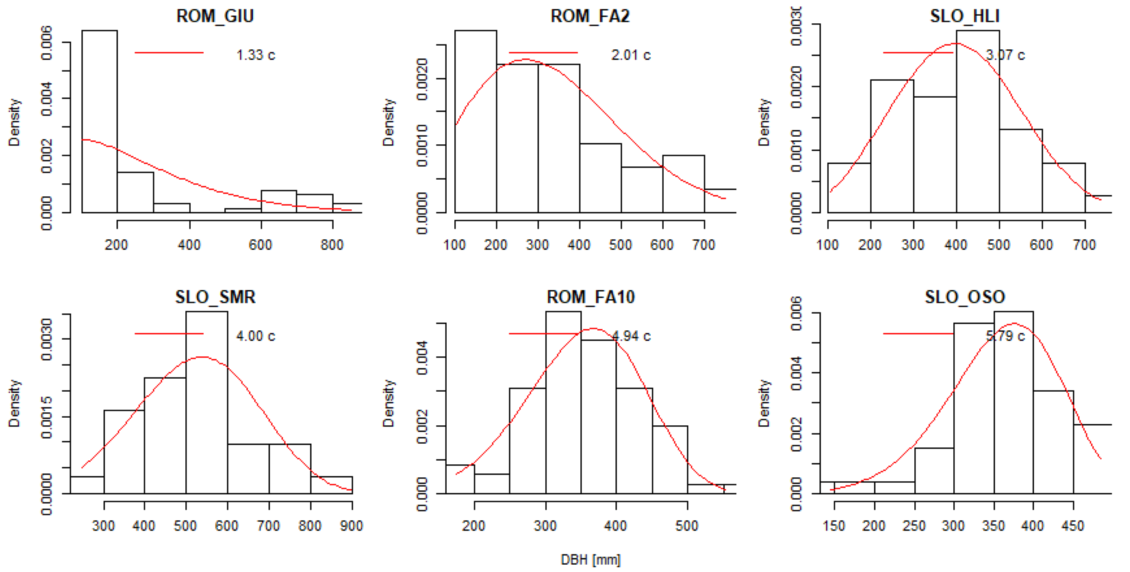

Figure 14. Weibull shape (*c*) parameter fit pooled from the original plot diameter data. When *c* < 1, steeply descending, monotonic function; *c* = 1, negative exponential; *c* > 1, the function is unimodal; 1 < *c* < 3.6, distribution has a positive skew; c = 3.6, normal distribution; and when c > 3.6, distribution has a negative skew (Bailey and Dell, 1973).

3.2.4 Data analysis: The impact of historical disturbances on current DBH distributions in spruce forests

To assess the relationship between the current diameter distribution shapes and parameters describing various aspects of plot disturbance histories we used linear mixed-effect models (LMMs). The Weibull shape parameter (of positive or negative skewness) was our dependent variable describing the diameter distribution shape, and disturbance parameters were used as explanatory variables (Appendix Table A2). In previous studies, disturbance history and the time since the last stand-replacing disturbance were strongly related to diameter distributions of live trees in unmanaged coniferous forest (Spies, 1998). Thus, in this study we tested which disturbance parameters would have a strong and positive effect on the current diameter distributions. The tested parameters included two variables describing the severity of previous disturbances, e.g., severity of the last disturbance and severity of the most severe disturbance of the last 300 years. Both of these were measured as the percentage of canopy area removed. Other parameters tested included time since the last disturbance, time since the maximum disturbance, and finally, a measure of the disturbance regime evenness. We fit a model set of disturbance parameters based on the hypothesis of how a disturbance might influence current diameter distributions using the "lme4" package in R. One or two parameters were included in models and, where appropriate, interactions between the parameters were included. Forest stands were treated as random effects in all models to account for the hierarchical nature of sampling. Highly correlated explanatory variables based on the correlation matrix were not run in the same model to avoid multicollinearity problems (Table 1). All explanatory variables were standardized and scaled. We evaluated the variance inflation factors (VIFs, Queen et al., 2002) of each model, and there was no serious multicollinearity observed in the models (all VIFs < 2.0). Residuals of all models were checked for normality and homoscedasticity. For model selection, we used the Akaike Information Criterion (AIC) for selecting the best model.

Table 1. Correlation matrix of the selected explanatory variables. Pearson correlation coefficients (above diagonal) and associated probabilities (below diagonal) are displayed. Significant correlations and p-values (α = 0.05) between response and explanatory variables are highlighted in bold.

	Dbh Shape parameter (skewness)	Max. disturbance severity (%)	Time since max. disturbance (years)	Last disturbance severity (%)	Time since last disturbance (years)	Disturbance index
Shape parameter (skewness)	-	0.446	0.139	0.405	0.382	-0.381
Max. disturbance severity (%)	**0.000**	-	-0.110	0.869	0.169	-0.736
Time since max. disturbance (years)	**0.014**	0.053	-	-0.191	0.614	0.055
Last disturbance severity (%)	**0.000**	0.000	0.001	-	0.233	-0.703
Time since last disturbance (years)	**0.000**	0.003	0.000	0.000	-	-0.204
Disturbance index	**0.000**	0.000	0.335	0.000	0.000	-

In addition, marginalized (R^2_m) and conditional (R^2_c) determination coefficients and Intraclass Correlation Coefficient (ICC) were calculated for the final model to quantify the proportion of the total variance explained by fixed effects, by both fixed and random effects, and by random effects, respectively (Nakagawa et al., 2017). We used the “visreg” R package for the output visualization of the model. All related statistical analyses were performed in the R language and environment for statistical computing (R Development Core Team, 2024).

3.3. PAST DISTURBANCES SHAPE PRESENT TREE SIZE DISTRIBUTION IN EUROPEAN TEMPERATE PRIMARY BEECH – DOMINATED FORESTS

3.3.1 Study plots

In this second study, plots from two countries, Slovakia and Romania, were utilized due to the presence of beech-dominated forests. The dataset included 238 plots, with 139 plots from Slovakia and 99 from Romania (Figure 15), covering 23 stands—fourteen in Slovakia and nine in Romania. A hierarchical structure was applied, consisting of three spatial scales: the landscape level (Slovakia and Romania), the stand level (stands within each landscape), and the plot level (plots within the stands). Topographic attributes such as slope, aspect, and altitude were recorded at each plot (Appendices Tables B1 and B2).

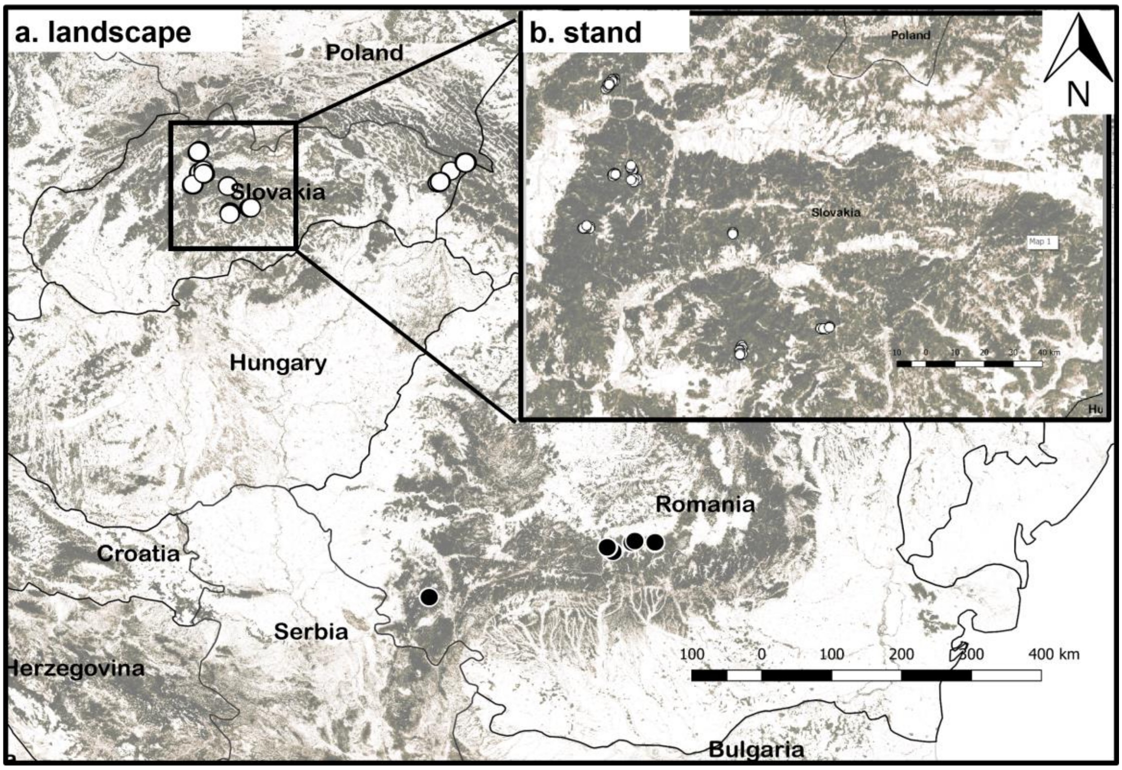

Figure 15. (a) Study region map showing plot locations across the Carpathian Mountains; Slovakia (white circle, n = 139); Romania (black circle, n = 99). (b) Inset map shows the sample plot locations within the stand within Slovakia.

3.3.2 Plot-level DBH distributions for beech-dominated forests modelled using the 2-parameter Weibull function

To model the tree size distributions of forest plots, we utilized a two-parameter Weibull function, recognized for its adaptability in representing tree size distributions across various forest types (Baker et al., 2005; Zhang et al., 2001). The Weibull function, defined by shape and scale parameters, offers insights into the distribution's spread and skewness, respectively. The shape parameter's adjustment allows the curve to depict different forest growth scenarios, ranging from reverse J-shaped distributions, which generally signal stable forest growth, to negatively skewed distributions, indicating a dominance of specific age classes in even-aged stands (Rodrigo et al., 2022; Coomes and Allen, 2007). The Weibull distribution exhibits a wide variety of shapes depending on the value of its shape parameter, c. When $c < 1$, the distribution is a steeply descending, monotonic function. For $c = 1$, it becomes a negative exponential distribution. When $c > 1$, the distribution is unimodal: if $1 < c < 3.61$, it approximates a normal distribution, while for $c > 3.6$, it exhibits negative skewness (Figure 16, Rodrigo et al., 2022); Baker et al., 2005). Rodrigo et al. (2022) illustrated the detailed distribution scenario with the shape parameter in their study in a spruce forest across the Carpathians.

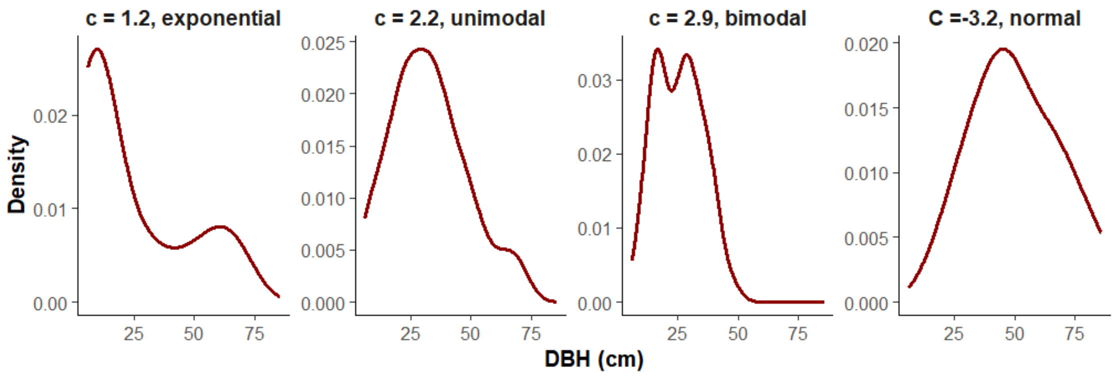

Figure 16. Actual data at the plot level fit with the Weibull shape parameter (denoted as *c*) to original plot tree size data. the interpretation of the *c* parameter is as follows: When $c < 1$, steeply descending (reverse J-shaped), monotonic function; $c = 1$, negative exponential; $c > 1$, the function is unimodal; $1 < c < 3.6$, distribution has a positive skew; $c = 3.6$, normal distribution; and when c greater than 3.6, distribution has a negative skew (Bailey and Dell, 1973).

Further, we applied a two-parameter Weibull function to evaluate how disturbances influenced the distribution shapes in forest plots, following the guidance of Baker et al. (2005) and Coomes and Allen (2007). The analyses were performed using the 'WeibullR' package within the R programming environment (R Development Core Team, 2024).

3.3.3 Data analysis: Impact of past disturbances on current tree size distributions in beech-dominated forests

Plot-level analysis: Initially, we visualized the tree size distribution using a violin plot, with the Weibull shape parameter serving as a proxy at the stand level (Appendix Figure B1). We also employed a boxplot to display the actual DBH at the stand level for further comparison (Appendix Figure B2). To investigate the impact of historical disturbances on current tree size distributions at the plot-level, we employed linear mixed-effect models (LMMs) (Zuur et al., 2009), using the Weibull shape parameter as the response variable to characterize distribution shapes (Pinheiro and Bates, 2000). Explanatory variables included metrics of disturbance history such as the severity of the last disturbance (%), maximum disturbance severity (%), time since the last disturbance (years) and time since the maximum disturbance (years). This analysis aimed to pinpoint significant disturbance drivers affecting tree size distributions, focusing on the severity and timing of past events, disturbance frequency, and recent disturbances. Modeling was conducted using the "lme4" package in R programming (Bates, 2015), with forest stands as random effects to accommodate the hierarchical structure of our data. To prevent multicollinearity, variables with high correlations were not included in the same model (Figure 17). Model selection was based on the Akaike Information Criterion (Akaike, 1987), with low variance inflation factors (VIFs, Queen et al., 2002), of each model, and there was no serious multicollinearity observed in the models (all VIFs = 1.0). Residuals of all models were checked for normality and homoscedasticity.

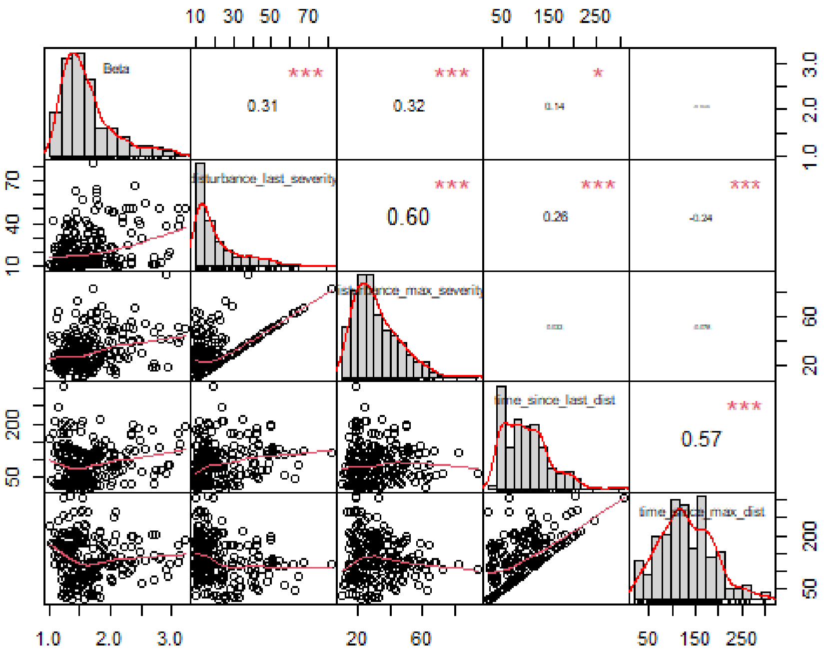

Figure 17. Correlation diagram between response and explanatory variables. Variables with high correlation were not included in the same model: Last Disturbance Severity and Maximum Disturbance Severity (r = 0.60), and Time Since Last Disturbance and Time Since Maximum Disturbance (r = 0.57).

The difference in the Akaike Information Criterion (ΔAIC) was determined by subtracting the lowest AIC in a set of models from the AIC of each model under consideration, expressed as ΔAIC = AIC_n - AIC_min. Here, AIC_n represents the Akaike Information Criterion of a given model, and AIC_min denotes the smallest AIC value observed among all models in the set (Anderson et al., 1994; Burnham et al., 2011). In addition, the model's performance was evaluated using both marginalized and conditional R^2 and the Intraclass Correlation Coefficient (ICC) (Nakagawa et al., 2017), and visualizations were generated with the "visreg" package (Breheny and Burchett, 2017).

Stand-level analysis: To further explore the effects of disturbances at the stand level, we conducted a separate analysis using linear models (LMs) due to our limited sample size of 23 stands. LMs were chosen as they are suitable for simple data structures and avoid issues related to the minimum number of categories required for random effects. In contrast, linear mixed models (LMMs) are necessary for data with multiple levels of variability but require a sufficient number of groups to estimate random effects reliably. With only 23 stands, using LMMs could lead to model convergence issues and inaccurate estimates.

For this analysis, we averaged explanatory variables across stands to assess the broader impact of disturbances, using the Weibull shape parameter as the dependent variable and past disturbance metrics as predictors. This approach ensured robust and reliable analysis, effectively exploring the stand-level effects of disturbances and providing clearer insights into the ecological dynamics at this spatial scale. This dual-scale analysis offered a view of how historical disturbances influence tree size distributions, elucidating the varied effects of past disturbances on forest structure across different spatial scales. Similarly, we extracted past disturbance parameter estimates, confidence interval (CI), and p-value (p), Coefficient of Determination (R^2), adjusted R^2 of each fitted linear model. We used the “visreg” R package for the output visualization of the model. Detailed model summaries and parameter extractions were facilitated by the "sjPlot" package in R (Lüdecke, 2024). All related statistical analyses were performed in the R language and environment for statistical computing (R Development Core Team, 2024).

3.4 THE IMPACT OF PAST DISTURBANCES ON AGE DISTRIBUTION IN EUROPEAN TEMPERATE MOUNTAIN FORESTS

3.4.1 Study plots

For this third study, the focus is on age distributions across the Carpathians, utilizing 55 forest stands spread across Slovakia (27 stands), Romania (23 stands), and Ukraine (5 stands). These stands include 590 permanent sample plots of varying sizes (500 m², 1000 m², and 1500 m²) located within the Carpathian Mountains (Figure 18). A hierarchical design was applied, incorporating three spatial scales: the landscape level (encompassing Slovakia, Ukraine, and Romania), the stand level (specific stands within the landscapes), and the plot level (individual plots within the stands). Additional details and data are provided in the supplementary materials (Appendix Tables C1 and C2).

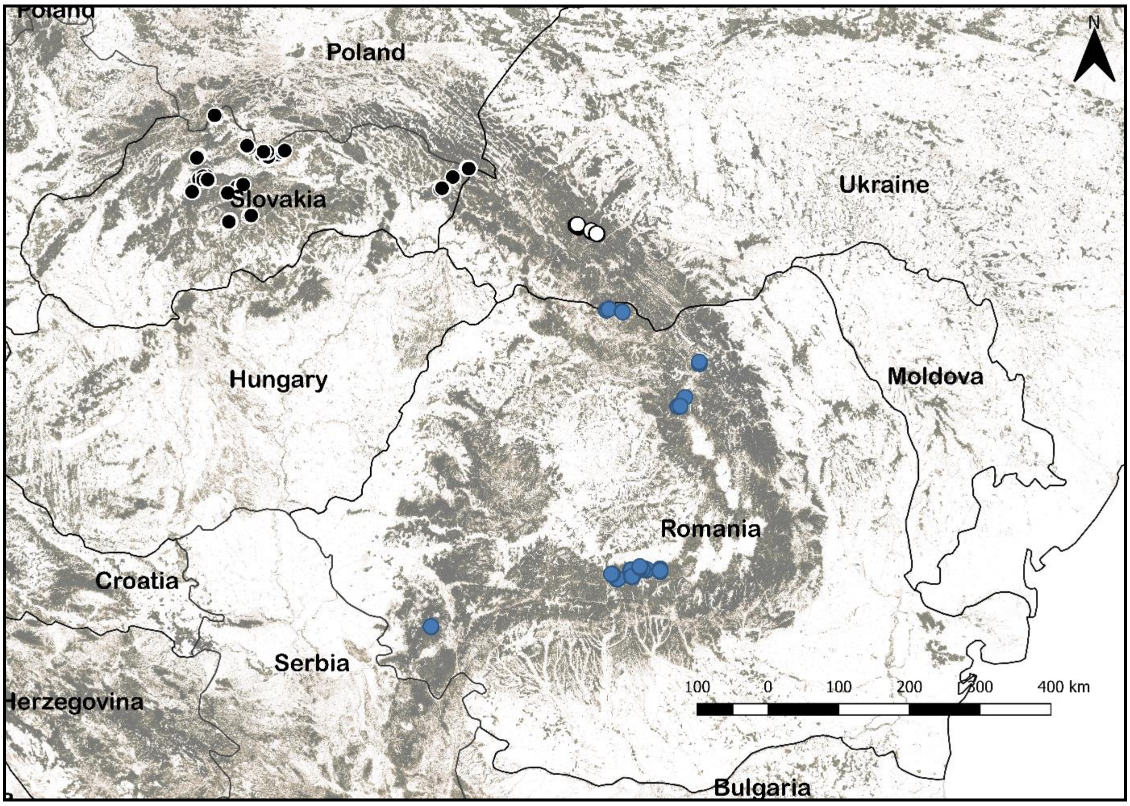

Figure 18. Map of the study region displaying plot locations across the Carpathian Mountains: Slovakia (red circles, n = 278), Romania (blue circles, n = 237), and Ukraine (white circles, n = 75).

3.4.2 Plot-level age parameter calculations

Tree age distribution within the 1000 m² plots was quantified using several statistical parameters designed to provide a detailed assessment of both central tendencies and variability, while excluding trees with more than 20 years missing to the pith or with a diameter at breast height (DBH) of less than 10 cm. The "age_90quantile" represents the 90th percentile of tree ages, capturing the upper end of the age distribution and providing insight into the older age classes within the stand. The "age_mean" reflects the arithmetic mean of tree ages, offering an average estimate of the overall age distribution across the stand. The "age_5oldest" metric focuses on the oldest cohort by calculating the mean age of the five oldest trees, serving as a proxy for assessing stand longevity and resilience. In addition to the mean-based metrics, the "age_median" was calculated to provide a robust central estimate of tree age, which is less sensitive to extreme values compared to the mean. Finally, the "age_iqr" (interquartile range) measures the spread of tree ages between the 25th and 75th percentiles, capturing the variability in tree ages while minimizing the influence of outliers.

3.4.3 Fitting 2-parameter Weibull function at stand-level age distributions

To model the distribution of tree sizes within forest stands, we employed a two-parameter Weibull function, which is highly adaptable and effective for representing tree size distributions across different forest types (Baker et al., 2005; Zhang et al., 2001). This function, characterized by its shape and scale parameters, provides valuable insights into the distribution's overall spread and skewness. By adjusting the shape parameter, the Weibull function can model a variety of forest growth scenarios, ranging from reverse J-shaped distributions, typically indicative of stable forest growth, to negatively skewed distributions that suggest a dominance of particular age classes in even-aged stands (Rodrigo et al., 2022; Coomes and Allen, 2007). The Weibull distribution can assume various forms depending on the value of the shape parameter (c). Specifically, when c is less than 1, the distribution takes on a steep, monotonically decreasing shape. At $c = 1$, it resembles a negative exponential distribution. For values of c greater than 1, the distribution becomes unimodal: if c falls between 1 and 3.61, it approximates a normal distribution, whereas for c values exceeding 3.6, the distribution becomes negatively skewed (Figure 19; Rodrigo et al., 2022; Baker et al., 2005). Rodrigo et al. (2022) provided a detailed analysis of these distribution patterns in their study of spruce forests across the Carpathians, highlighting the influence of the shape parameter on forest structure. All analyses were conducted using the 'WeibullR' package in the R programming environment (R Development Core Team, 2024).

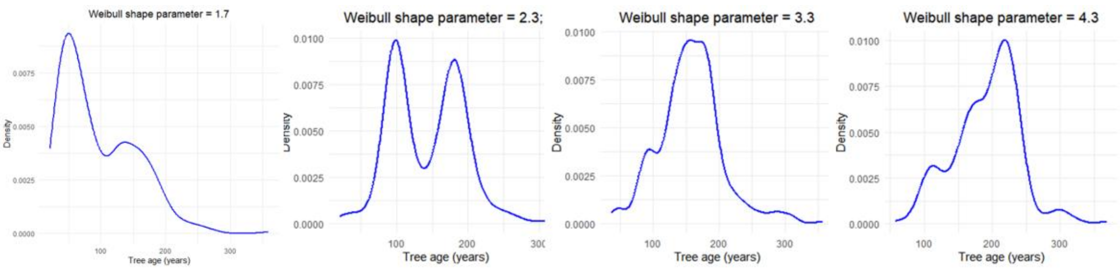

Figure 19. Actual data on tree age at the stand level fit with the Weibull shape parameter (denoted as c). The interpretation of the *c* parameter is as follows: When $c < 1$, steeply descending (reverse J-shaped), monotonic function; $c = 1$, negative exponential; $c > 1$, the function is unimodal; $1 < c < 3.6$, distribution has a positive skew; c = 3.6, normal distribution; and when c greater than 3.6, distribution has a negative skew (Bailey and Dell, 1973).

3.4.4 Data analysis: Impact of past disturbance on stand-age distributions

Plot-level analysis: Initially, prior to the analysis, we visualized the disturbance regime using age parameters to observe patterns and differences (Appendix Figure C1). We also utilized histograms to compare the age distribution among the three countries (Appendix Figure C2). To explore the patterns of age distribution at the plot level, we employed a combination of violin plots and boxplots to visualize the distribution shapes and disturbance parameters across different regions and forest types. We utilized the "ggplot2" library in R, along with additional support from the "reshape2" and "dplyr" packages, to create these visualizations. These tools provided a detailed view of how stand age distributions and disturbance histories vary by country (Romania, Slovakia, and Ukraine) and between forest types (beech and spruce).

First, we used violin plots to depict the distribution of the plot-level age parameter, categorized into three distinct shapes: negative exponential, bimodal, and unimodal, positively and negatively skewed distributions. These plots were created using the geom_violin() function in the "ggplot2" package, allowing us to compare the spread and density of age distributions across the three countries and between the two forest types. This approach highlighted any regional and ecological differences in forest structure.

Additionally, boxplots were generated to visualize the distribution of key disturbance parameters—maximum disturbance severity, last disturbance severity, time since the last disturbance, and time since the maximum disturbance. These boxplots were stratified by country and forest type, enabling a clear comparison of how disturbance histories vary across different regions and forest ecosystems. The geom_boxplot() function in "ggplot2" was used for this purpose, ensuring that the central tendencies, variability, and outliers in the data were clearly depicted.

Stand-level analysis: The analysis was conducted to investigate the influence of disturbance parameters on the age distribution of forest stands, as represented by the Weibull shape parameter. This parameter was selected as the response variable due to its ability to capture the distribution characteristics of tree ages within a stand, ranging from exponential to unimodal, bimodal, and negatively skewed distributions. Prior to model fitting, exploratory data analysis (EDA) was performed to understand the distribution of the Weibull shape parameter and the explanatory variables. Descriptive statistics were computed, and visualizations, including histograms, boxplots, and scatter plots, were generated to examine the distributions of the disturbance parameters: last disturbance severity, maximum disturbance severity, time since last disturbance, and time since maximum disturbance. In addition, to assess potential multicollinearity among the disturbance parameters, Pearson correlation coefficients were calculated. High correlations were identified between last disturbance severity and maximum disturbance severity (r = 0.85) and between time since last disturbance and time since maximum disturbance (r = 0.78). Given these high correlations, each disturbance parameter was modeled separately to avoid multicollinearity, which can lead to inflated standard errors and unreliable estimates (Figure 20).

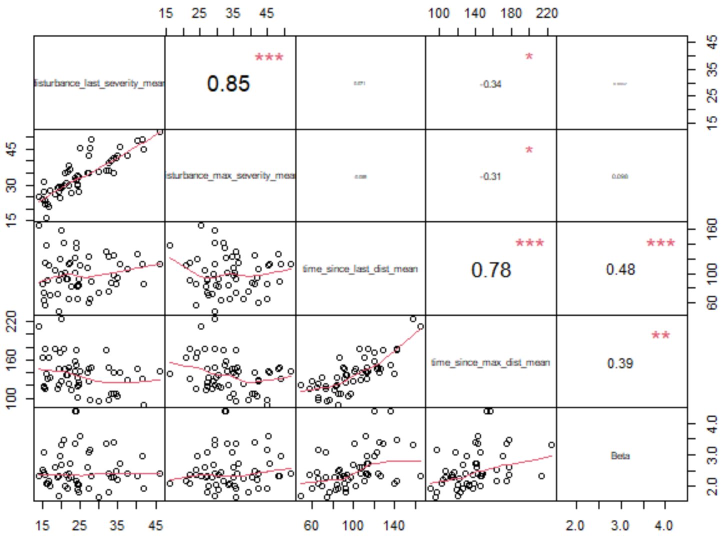

Figure 20. Multicollinearity analysis showing high correlation between last disturbance severity and maximum disturbance severity (r=0.85), as well as between time since last disturbance and time since maximum disturbance (r=0.78)

Here, four linear mixed-effects models (LMMs) were specified, each incorporating a different disturbance parameter as the primary fixed effect. The models were defined as follows:

Model 1: Weibull parameter ~ mean last disturbance severity + (1 | country) + (1 | forest type)
Model 2: Weibull parameter ~ mean disturbance maximum severity + (1 | country) + (1 | forest type)
Model 3: Weibull parameter ~ mean time since last disturbance + (1 | country) + (1 | forest type)
Model 4: Weibull parameter ~ mean time since maximum disturbance + (1 | country) + (1 | forest type)

Each model was constructed to assess the effect of its respective disturbance parameter on the Weibull shape parameter, while accounting for the hierarchical structure of the data. Random intercepts for country and forest type were included to capture variability in the Weibull shape parameter across different geographic regions and forest types.

With this, mixed-effects models were fitted using the lmer() function from the "lme4" package in R. For each model, the fixed effects, random effects, and overall model fit were assessed. Model comparison was conducted using the Akaike Information Criterion (AIC), a widely used metric that balances model fit and complexity. The model with the lowest AIC was considered the best fit, representing the most parsimonious model that adequately explained the variability in the Weibull shape parameter.

The change in AIC (ΔAIC) was calculated for each model relative to the best-fitting model. Models with ΔAIC values less than 2 were considered to have substantial support, while those with ΔAIC values greater than 10 were considered to have little support. Lastly, the random effects for country and forest type were extracted and analyzed to understand their contributions to the variability in the Weibull shape parameter. The conditional modes (intercepts) and conditional standard deviations were reported for each level of the random effects, providing insights into how much the response variable deviated from the overall intercept due to differences between countries and forest types.

4. RESULTS

4.1 HISTORICAL MIXED-SEVERITY DISTURBANCES SHAPE CURRENT DIAMETER DISTRIBUTIONS OF PRIMARY TEMPERATE NORWAY SPRUCE MOUNTAIN FORESTS IN EUROPE

4.1.1 DBH distribution shape across the landscape

A total of 15,483 live adult trees were analyzed from 311 plots. Variability of DBH distribution shapes were visible among the stands and by region (Figure 21.). The Eastern Carpathian plots differed significantly from Western Carpathian plots (p-value < 0.05) based on the Dunn test. In addition, diameter distribution based on data pooling from all plots showed a decreasing skewness from approaching a reverse J-shaped distribution in forests experiencing low-to-moderate-severity disturbance regimes, to a unimodal distribution in forest experiencing high to very high-severity disturbance regimes (Appendix Figure A2).

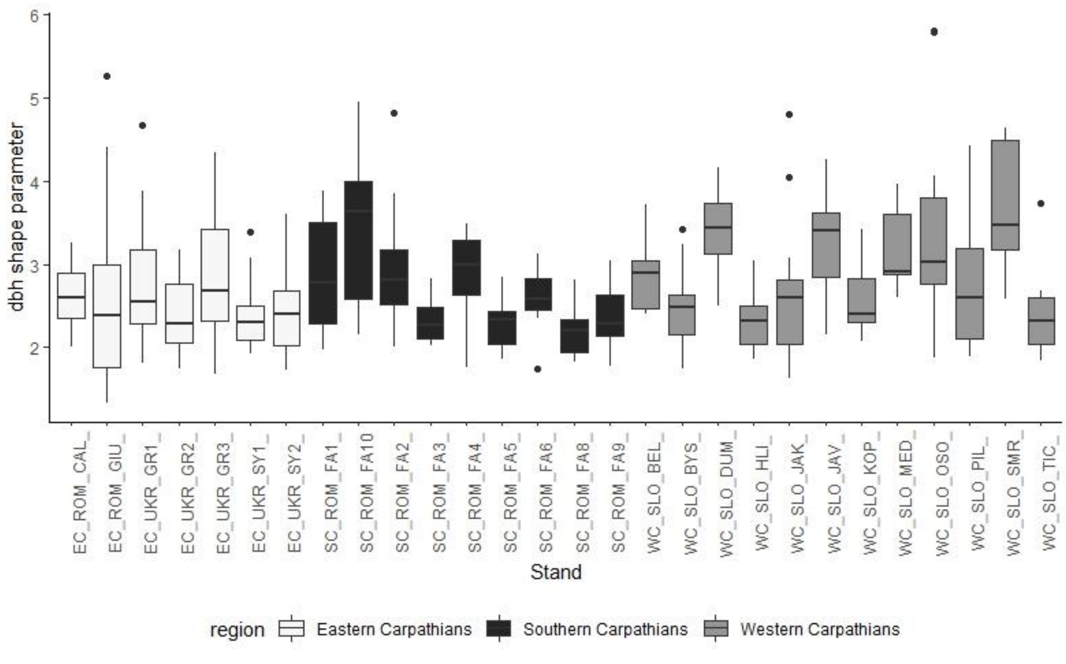

Figure 21. Boxplot of DBH shape parameter values at the plot-level across the study area (stands and landscape). Plot-Weibull shape parameter (as proxy for DBH distribution shapes). Eastern and Western Carpathians are statistically different based on a post-hoc Dunn test (p-value < 0.05).

4.1.2 Historical disturbances and current diameter distribution

Modelling analyses revealed that historical disturbances had significant and strong effects on current diameter distributions (Figure 22; Table 2). The maximum disturbance and severity of the last disturbance event showed a strong and positive relationship (β = 0.36; p-value < 0.05; β = 0.33; p-value < 0.05, respectively). Similarly, time since the maximum disturbance event showed a marginal effect on DBH distribution shape (β = 0.09; p-value < 0.05). Conversely, time since the last disturbance showed a strong and positive effect (β = 0.27; p-value < 0.05). The overall disturbance regime also showed a strong and inverse relationship with current diameter distribution (β = -0.30; p-value < 0.05).

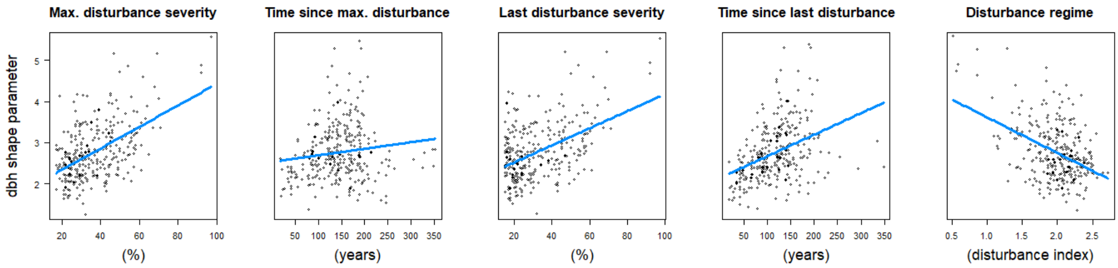

Figure 22. The effect of last historical disturbance parameters on the current diameter distribution based on the linear mixed-effects models, with skewness (Weibull shape parameter) as a proxy for current diameter distribution. Each effect plot shows expected response in each disturbance metric variable fit individually.

Table 2. Summary of historical disturbance parameter estimates, confidence interval, and p-value of each model. Each linear mixed effects model was fit using restricted maximum likelihood (REML).

	DBH shape parameter														
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	2.77	2.63 – 2.91	**<0.001**	2.77	2.62 – 2.92	**<0.001**	2.76	2.62 – 2.91	**<0.001**	2.75	2.62 – 2.88	**<0.001**	2.76	2.62 – 2.90	**<0.001**
Max. disturbance severity	0.36	0.28 – 0.43	**<0.001**												
Last disturbance severity				0.33	0.25 – 0.40	**<0.001**									
Time since max. disturbance							0.09	0.01 – 0.17	**0.026**						
Times since last disturbance										0.27	0.20 – 0.35	**<0.001**			
Disturbance regime													-0.30	-0.38 – -0.22	**<0.001**
Random Effects															
σ^2	0.37			0.38			0.47			0.41			0.40		
ICC	0.23			0.24			0.18			0.18			0.20		
Marginal R^2 / Conditional R^2	0.211 / 0.396			0.175 / 0.372			0.014 / 0.195			0.128 / 0.283			0.153 / 0.324		

Our model comparison using an information theoretic approach revealed that the severity of the last disturbance and time since the last disturbance were important components influencing current diameter distribution shapes (Table 3). The model including these components and the interaction between them was the best model based on AIC. As the last observed disturbance of a plot increased in severity, the Weibull shape parameter increased, skewing the diameter distribution negatively. As the time since the last observed disturbance increased, this shifted the distribution closer to a reverse J-shaped. These two parameters interacted so that the most marked changes in distribution shape were observed in plots experiencing very recent high-severity disturbances (Table 4, Figure 23).

Table 3. Model selection summary comparing drivers of diameter distribution shape. Each model was fit as a linear mixed effect model using restricted maximum likelihood (REML) with stand as a random effect.

	model_parameters	Df	AIC	Chisq	Pr(>Chisq)
model_new8	last severity * time since last	6	587.06	6.56	0.00
model_new6	max severity * time since max	6	593.62	15.15	0.00
model_new13	dist index * time since last	6	594.52	30.41	0.00
model_new7	last severity + time since last	5	600.58	4.41	0.00
model_new5	max severity + time since max	5	604.99	36.37	0.00
model_new12	dist index + time since last	5	606.77	25.25	0.00
model_new1	max severity	4	615.50	76.88	0.00
model_new11	dist index * time since max	6	624.93	0.00	
model_new2	last severity	4	628.20	0.00	
model_new10	dist index + time since max	5	632.01	0.00	
model_new9	dist index	4	639.36	7.99	0.00
model_new4	time since last	4	647.35	40.06	0.00
model_new3	time since max	4	687.41	0.00	
model_new0	null model	3	690.38	NA	

Table 4. Summary of the final model explaining variation in DBH distribution shape. The model was fit as a linear mixed effect model using REML, with stands as a random effect. The table displays the intercept, estimates, confidence interval (CI), *p*-value, marginal (R^2m) and conditional (R^2c), and intraclass correlation coefficient (ICC).

	DBH shape parameter		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	2.73	2.59 – 2.86	**<0.001**
Last disturbance severity (%)	0.23	0.15 – 0.30	**<0.001**
Time since last disturbance (years)	0.24	0.16 – 0.31	**<0.001**
Last disturbance severity (%) * Time since last disturbance (years)	0.15	0.08 – 0.22	**<0.001**
Random effects			
σ^2	0.33		
$\tau_{00\ stand}$	0.10		
ICC	0.23		
N_{stand}	28		
Observations	311		
Marginal R^2 / Conditional R^2	0.278 / 0.442		

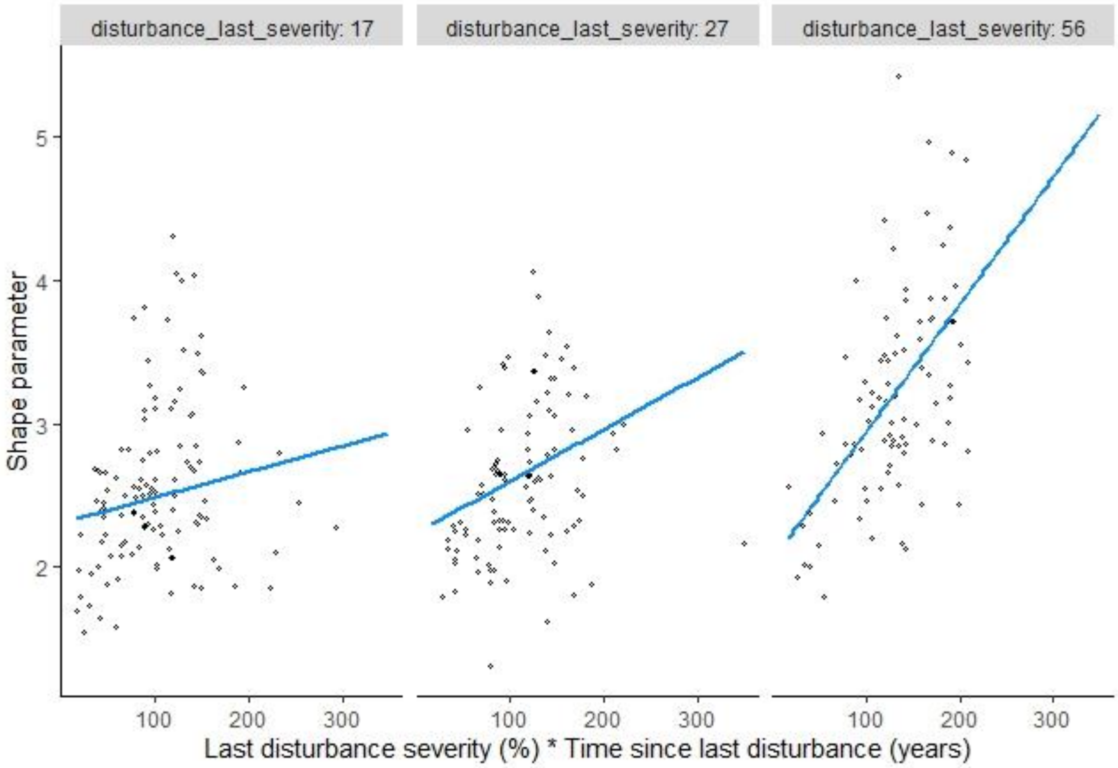

Figure 23. Magnitude of effect on current diameter distribution shape, based on the interaction of the last disturbance severity and time since the last disturbance, fit in a linear mixed-effects model.

4.2 PAST DISTURBANCES SHAPE PRESENT TREE SIZE DISTRIBUTIONS IN EUROPEAN TEMPERATE PRIMARY BEECH-DOMINATED FORESTS

4.2.1 Tree size distribution across the landscape

Analyzing 11,755 live trees across 238 plots revealed notable variability in tree size distribution shapes (Figure 24). The tree size distribution, represented by the Weibull shape parameter, showed values ranging from $c = 1$ to $c = 3$. In the Slovakian part of the Carpathians, stands such as Kundracka, Padva, and Polana displayed higher *c* parameters, whereas the lowest c values were observed in the Havesova and Vihorlat stands. Similarly, in the Romanian Carpathians, the Sebesu and Paulic stands exhibited higher c parameters, while seven other stands had *c* parameters ranging from 1 to 2.

On the other hand, Kruskal-Wallis test identified statistically significant differences among the stands ($p < 0.05$), whereas significant differences were found between the regions of the Slovakia and Romania (Mann-Whitney test, $p > 0.05$). Significant variability was observed in the violin plot, which was grouped by stand within each region. In the Romanian Carpathians, Arpasul, Boia Mica, Criva, and Ucea Mare stands exhibited distributions close to reverse-J, indicative of a predominance of smaller-sized trees. The remaining stands displayed monotonic, flat, symmetrical and unimodal distributions, suggesting an even distribution across tree size classes. Similarly, in the Slovakian Carpathians, six stands out of 14 stands exhibit reverse-J distributions such as Sramkova, Polana, Kornietiva, Stuzica, and Sutovska, and Vihorlat while eight stands depicted a flat and symmetrical distributions, reflecting a uniform tree size distribution.

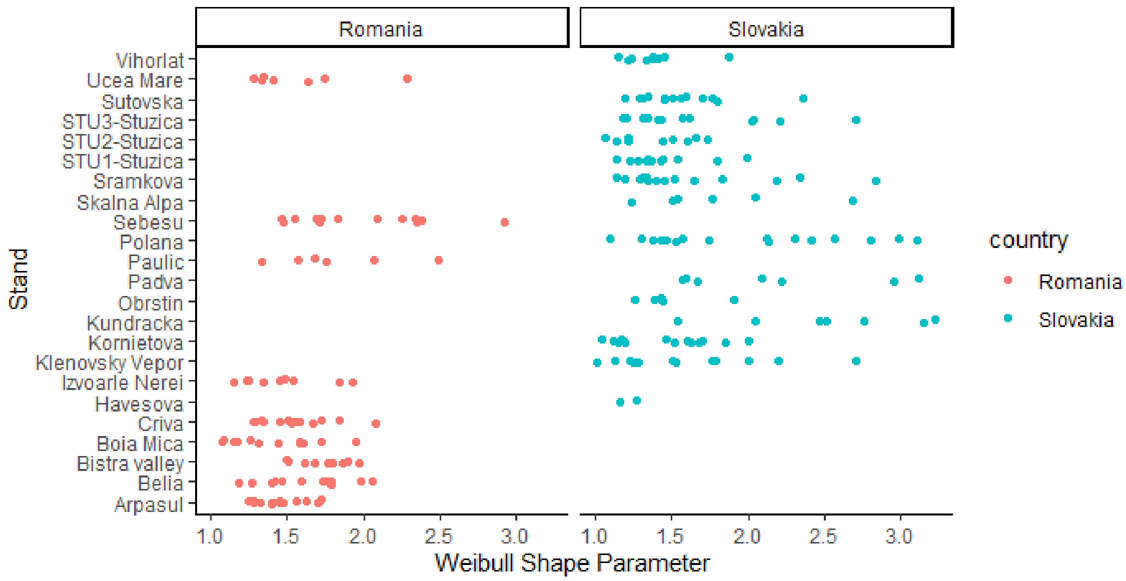

Figure 24. Dot plot of plot-level tree size distribution, represented by the Weibull shape parameter, across the Carpathian regions of Slovakia and Romania. Each point represents the Weibull shape parameter for an individual plot

Using histograms for each country, the tree size distribution across forest stands in Slovakia reveals that most stands are dominated by smaller trees, typically within the 0-30 cm diameter at breast height (DBH). Forests such as Havesova, Klenovsky Vepor, and Kornietova display this trend, suggesting a high frequency of younger or smaller trees, likely due to recent disturbances or regeneration events (Figure 25). In contrast, stands like Sramkova and Vihorlat show a broader range of tree sizes, including a significant number of larger trees (up to 120 cm DBH). This indicates a more mature forest structure in these areas, where older trees have grown to larger sizes, likely due to lower disturbance frequencies or a longer recovery period after past disturbances. Overall, while smaller trees dominate most stands, the variation in tree size distribution across Slovakia points to different stages of forest development and disturbance histories.

The Romanian forest stands, as depicted in the histograms, also predominantly feature smaller trees (0-30 cm DBH) in most sites, such as Arpasul, Boia Mica, and Criva, indicating younger or regenerating forests (Figure 26). However, a few stands, including Paulic and Sebesu, exhibit a wider distribution of tree sizes, with more trees in the 30-60 cm DBH range. These stands may represent older, less disturbed forests with a more heterogeneous structure. The absence of very large trees (over 120 cm DBH) in most Romanian stands suggests that such trees are either rare, have been removed by past disturbances, or the forests are still in a recovery phase. The variation in tree size across Romanian stands reflects different disturbance regimes or forest management practices, with some stands showing active regeneration while others are in more advanced stages of development.

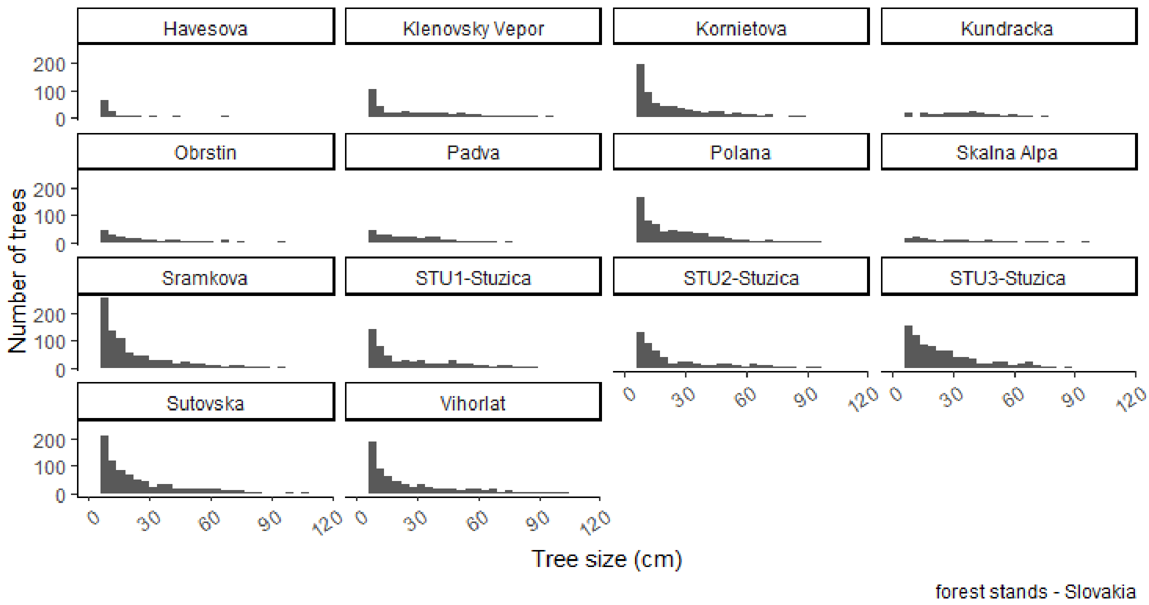

Figure 25. Histograms showing the distribution of tree sizes (measured in cm) across fourteen different forest stands in Slovakia. Each panel represents a different stand, with the x-axis displaying tree size (DBH - diameter at breast height) and the y-axis representing the number of trees.

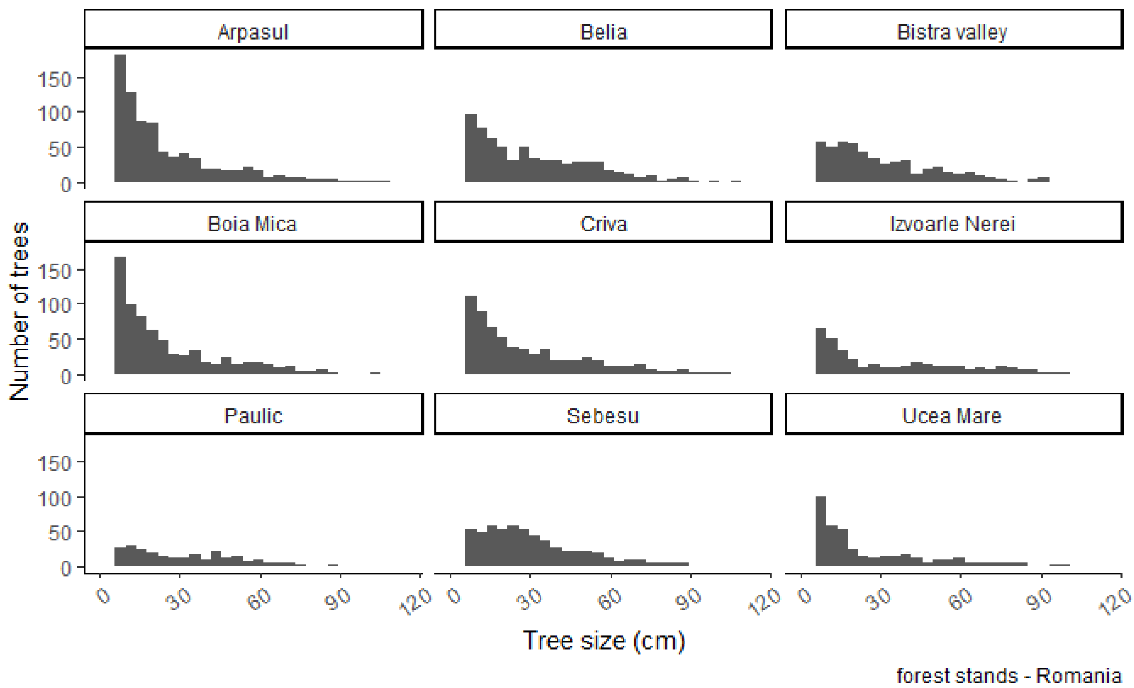

Figure 26. Histograms showing the distribution of tree sizes (measured in cm) across nine different forest stands in Romania. Each panel represents a different stand, with the x-axis displaying tree size (DBH - diameter at breast height) and the y-axis representing the number of trees.

4.2.2 Past disturbances and present tree size distributions

At the plot level, our analysis evaluates the impact of various factors on tree size shape. Specifically, we observe that the severity of the last disturbance (β = 0.26, p = 0.001) and the maximum disturbance severity (β = 0.30, p = 0.001) both significantly positively influence tree size shape (Table 5; Figure 27). This suggests that higher severities of past disturbance are associated with positively skewed tree size distributions. In contrast, the time since the last disturbance (β = 0.12, p = 0.050) did not significantly influence tree size distribution. Meanwhile, time since maximum disturbance depicted a negative relationship with tree size shape (β = -0.07, p = 0.287).

Table 5. Plot-level summary of past disturbance parameter estimates, confidence interval (*CI*), and p-value, residual variance (σ^2), Intraclass Correlation Coefficient (*ICC*), Marginal R^2 ($R^2 m$), Conditional R^2 (R^2c) values of each fitted model. Each model was fitted by LMMs restricted maximum likelihood (REML).

Predictors	***Weibull Shape parameter***			***Random Effects***			
	Estimates	*CI*	*p*	σ^2	ICC	R^2 m	R^2c
Last disturbance severity (%)	0.26	0.14 – 0.38	**<0.001**	0.28	0.5	0.066	0.324
Max. disturbance severity (%)	0.30	0.19 – 0.42	**<0.001**	0.30	0.52	0.088	0.366
Time since last disturbance (years)	0.12	-0.00 – 0.25	0.050	0.29	0.51	0.014	0.298
Time since max. disturbance (years)	-0.07	-0.19 – 0.05s	0.287	0.30	0.53	0.004	0.302

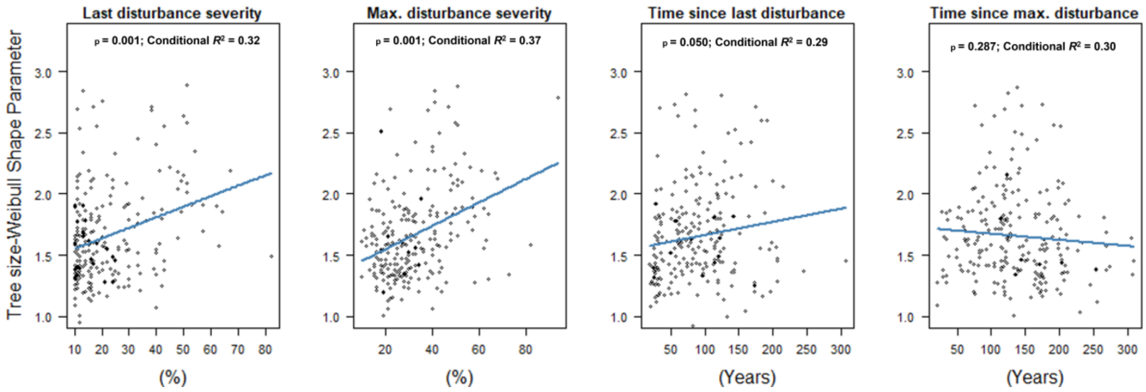

Figure 27. The effect of past disturbance parameters on the current tree size distribution (as weibull shape parameter) based on the linear mixed-effects model, with skewness (Weibull shape parameter). Each effect plot shows expected response in each disturbance metric variable fitted individually.

Using an information-theoretic approach for model comparison, we found that the severity of the maximum disturbances and the time since the last disturbance are crucial factors affecting the current tree size distribution (Table 6). The interaction model between the time since the last disturbance and the maximum severity emerged as the most effective, based on Akaike Information Criterion (AIC) values, indicating the best model ranked first. Following closely, the model combining the time since the last disturbance and maximum disturbance severity ranked second, with an AIC value of 241.18 and an AIC change of only 2.35. The third-best model, focused on maximum disturbance severity, had an AIC value of 242.47, with an AIC change of 3.67. The close AIC values of the second and third models (241.18 and 242.47, respectively) suggest that both the time since the last disturbance and the maximum disturbance severity strongly influence the current tree size distribution.

Table 6. Model ranking, based on linear mixed effects models fitted with REML and incorporating 'stand' as a random effect, discerns key drivers influences on present tree size distribution. Akaike Information criterion (*AIC*), change in AIC, and Ranking.

Models	***Parameters***	***AIC***	***Change AIC***	***Rank***
1	Time since last disturbance (years) * Max disturbance severity (%)	238.81	0.00	1
2	Time since last disturbance (years) + Max disturbance severity (%)	241.18	2.38	2
3	Max disturbance severity (%)	242.47	3.67	3
4	Time since max disturbance (years) + Max disturbance severity (%)	243.77	4.97	4
5	Time since max disturbance (years) * Max disturbance severity (%)	245.77	6.96	5
6	Time since max disturbance (years) * Last disturbance severity (%)	246.40	7.59	6
7	Last disturbance severity (%)	249.14	10.33	7
8	Time since last disturbance (years) * Last disturbance severity (%)	249.34	10.53	8
9	Time since last disturbance (years) + Last disturbance severity (%)	250.34	11.53	9
10	Time since max disturbance (years) + Last disturbance severity (%)	251.13	12.33	10
11	Time since last disturbance (years)	263.97	25.16	11
12	NULL MODEL	265.81	27.00	12
13	Time since max disturbance (years)	266.69	27.89	13

At the stand level, the results closely align with those at the plot level, with one notable exception: the time since the maximum disturbance shows a positive relationship (β = 0.20, p = 0.350), unlike at the plot level. Positive correlations were also found with the severity of the last disturbance (β = 0.42, p = 0.044), maximum disturbance severity (β = 0.30, p = 0.163), and the time since the last disturbance (β = 0.28, p = 0.189) (Figure 28; Table 7).

On the other hand, the interaction plot reveals how the relationship between time since the last disturbance and tree size distribution (represented by the shape parameter) varies at different levels of disturbance severity (16%, 29%, and 51%) (Figure 29). In the panel for the lowest disturbance severity (16%), the relationship is relatively flat, indicating little change in the tree size distribution over time, regardless of how long it has been since the last disturbance. This suggests that in stands with lower disturbance severity, time since the last disturbance does not have a significant impact on tree size distribution, likely because the effects of mild disturbances are less likely to dramatically alter the forest structure.

As disturbance severity increases to 29% and 51%, the relationship between time since the last disturbance and tree size distribution becomes stronger, with steeper positive slopes in the corresponding panels. In stands where disturbances were more severe, the tree size shape parameter increases more significantly over time, indicating that the distribution of tree sizes becomes more uneven or skewed as time progresses. This pattern suggests that more intense disturbances lead to structural changes that persist and amplify over time, with larger trees dominating the stand as smaller trees are removed or unable to regenerate. The increasing steepness of the slope at higher disturbance severities highlights the stronger influence of severe disturbances on long-term forest dynamics.

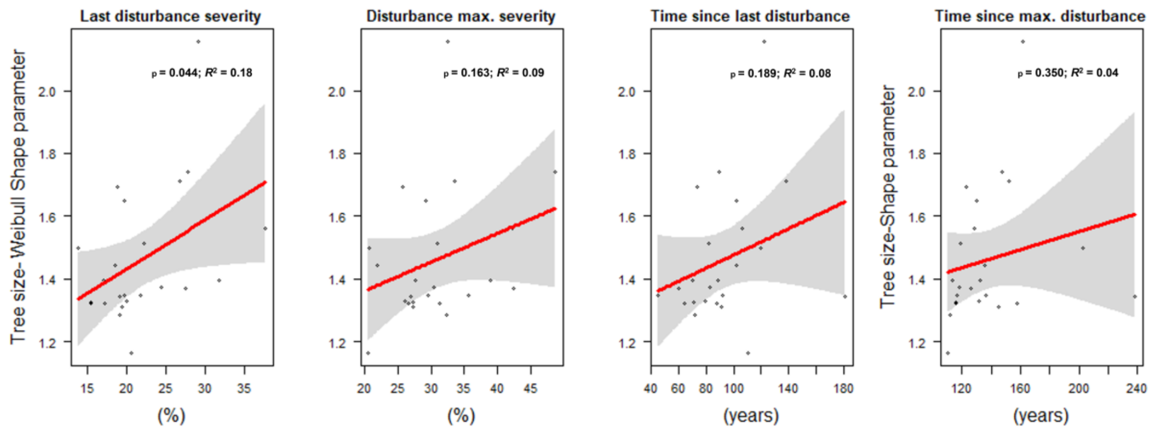

Figure 28. Stand-level effect of past disturbance on tree size distribution, represented by Weibull shape parameter. Each parameter was fit using linear model.

Table 7. Stand-level summary of past disturbance parameter estimates, confidence interval (*CI*), and p-value (*p*), Coefficient of Determination (R^2), adjusted R^2 of each fit linear model.

Response	*Weibull shape parameter*				
	Estimates	*CI*	*p*	R^2	R^2 *adjusted*
Last disturbance severity (%)	0.42	0.01 – 0.83	**0.044**	0.179	0.140
Max. disturbance severity (%)	0.30	-0.13 – 0.73	0.163	0.090	0.047
Time since last disturbance (years)	0.28	-0.15 – 0.72	0.189	0.081	0.037
Time since max. disturbance (years)	0.20	-0.24 – 0.65	0.350	0.042	0.004

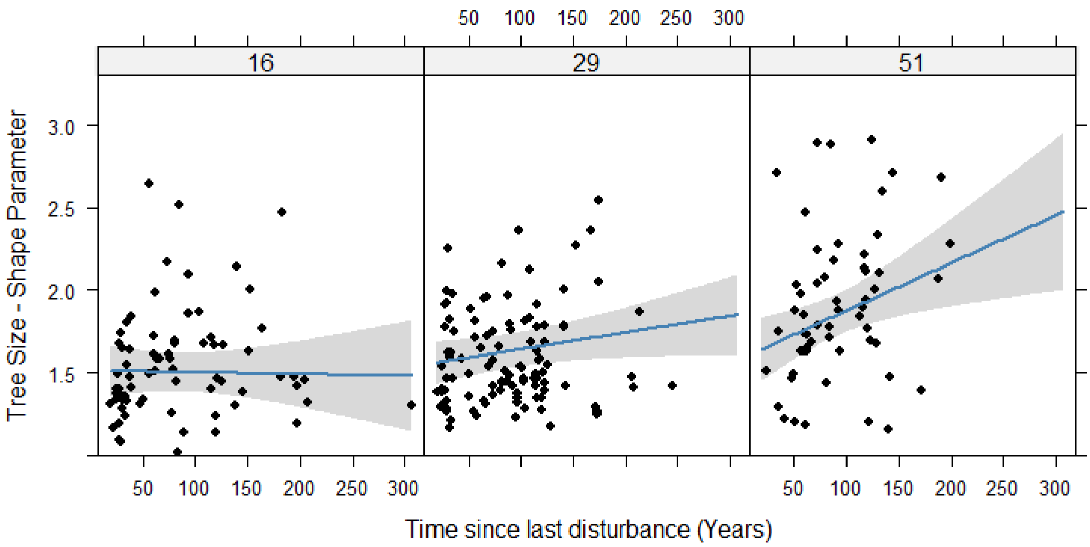

Figure 29. Interaction plot showing the relationship between time since the last disturbance (years) and tree size shape parameter at different levels of disturbance severity (16%, 29%, and 51% canopy remove). Each panel represents a different disturbance severity level, with the x-axis representing the time since the last disturbance and the y-axis representing the tree size shape parameter. The blue lines indicate the predicted relationship between time since the last disturbance and the shape parameter, with shaded areas representing the 95% confidence intervals.

4.3 THE IMPACT OF PAST DISTURBANCES ON AGE DISTRIBUTION IN EUROPEAN TEMPERATE MOUNTAIN FORESTS

4.3.1 Variability in age distribution across the Carpathian Mountains

Our results provide a clear visual comparison of age distributions within different forest types (beech and spruce) across the countries in the dataset. The median age, marked with a white point, offers a quick reference for the central tendency of the data in each group (Figure 30). The distributions reveal that spruce forests generally exhibit a wider range of ages compared to beech forests, particularly in certain countries. In contrast, beech forests often display a more concentrated age distribution, indicating greater uniformity in tree age. The presence of distinct peaks or a more uniform spread in the violin plots suggests underlying differences in the age structure of forests between the countries. Lastly, the violin plots suggest that spruce forests generally exhibit greater variability in tree age compared to beech forests, which tend to have more uniform age distributions.

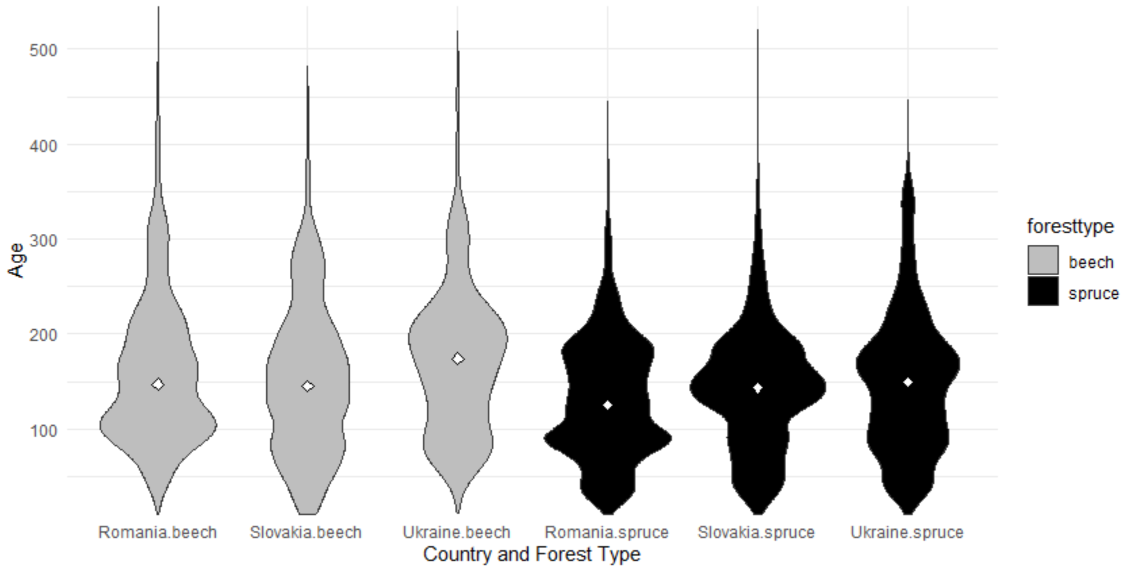

Figure 30. Violin plot depicting variability in age distribution across different regions of the Carpathian Mountains.

On the other hand, the empirical cumulative distribution function (ECDF) plot illustrates the age distribution of trees in beech and spruce forests across three countries: Romania, Slovakia, and Ukraine (Figure 31). For both forest types, the ECDF curves follow a characteristic S-shape, with tree ages on the x-axis and the cumulative proportion of trees on the y-axis. In Romania and Slovakia, there is a clear distinction between the two forest types. Spruce forests in these regions show steeper ECDF curves, indicating that spruce stands are dominated by younger trees, with the majority of trees being younger than 200 years. In contrast, beech forests exhibit a more gradual increase in the ECDF, suggesting a wider range of ages and a higher proportion of older trees. This difference implies that beech forests have a more diverse age structure and may experience fewer disturbances, allowing trees to grow older.

In Ukraine, however, the ECDFs for both forest types are more similar, with both beech and spruce forests showing a large proportion of trees within the 100-300 year range.

The slight difference between the forest types in Ukraine indicates that spruce forests are still somewhat younger than beech, but the gap is much narrower compared to Romania and Slovakia. Across all countries, the ECDF curves flatten at around 400-500 years, indicating the maximum observed tree ages in these temperate primary mountain forests, with both beech and spruce trees capable of reaching similar ages under favorable conditions.

Overall, the ECDF plot highlights notable differences in the age structure of beech and spruce forests between the countries. The steeper ECDF for spruce in Romania and Slovakia indicates that these forests are subject to more frequent or intense disturbances that favor the growth of younger trees, while beech forests, with their more gradual ECDF, may experience less frequent disturbances, allowing for the persistence of older trees. In Ukraine, where the age distributions between the two forest types are more similar, forest dynamics might be influenced by different environmental or anthropogenic factors compared to Romania and Slovakia.

Similarly, the violin plot, which represents the distribution of tree sizes using the Weibull shape parameter, highlights the variation among stands across Romania and Slovakia (Appendix Figure B1). In contrast, the boxplot in Appendix Figure B2 reveals the variation in mean DBH among the stands in the study area.

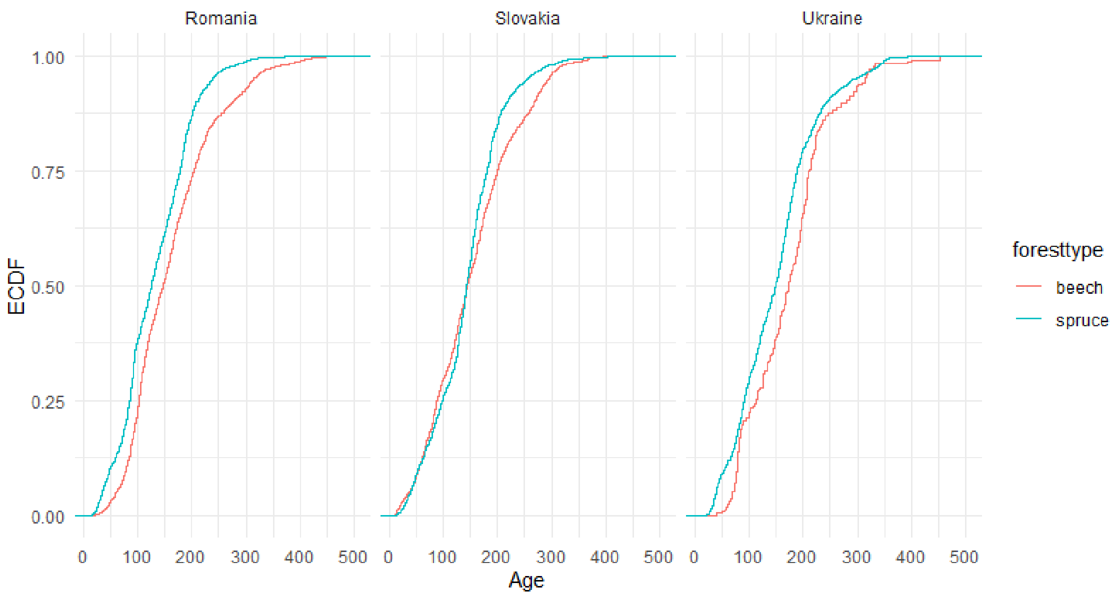

Figure 31. Empirical cumulative distribution function (ECDF) of tree age for beech and spruce forests across Romania, Slovakia, and Ukraine. The ECDF plots represent the proportion of trees below a given age (x-axis) for beech (red) and spruce (blue) forest types in each country. The y-axis shows the cumulative proportion of trees, ranging from 0 to 1. Each panel represents a different country, allowing for comparison of tree age distributions between forest types within and across countries. The curves indicate differences in the age structure of beech and spruce forests within each region. (*n = 21,727*)

On the other hand, the histogram illustrates the variation in age distribution of beech and spruce forests across three regions: Romania, Slovakia, and Ukraine (Figure 32). Each subplot depicts the density distribution of tree ages for both species within each country, offering a comparative view of the age structure in these temperate primary mountain forests. In Romania, beech forests show a relatively even distribution of tree ages, with most trees concentrated between 50 and 200 years old. The spruce forests, however, exhibit a slightly different pattern, with a sharp peak between 100 and 150 years, suggesting that spruce stands have a more uniform age structure. This could imply that spruce forests in Romania have experienced more frequent or recent disturbances, resulting in younger stands compared to the more diverse age range observed in beech forests.

In Slovakia, the beech forests display a broader age distribution, with a notable concentration of trees between 100 and 200 years, but with older trees extending beyond 300 years. The spruce forests, on the other hand, have a prominent peak around 100-150 years, similar to Romania, but the distribution is less spread out, indicating that spruce forests in Slovakia are relatively younger and more homogenous in age compared to the beech forests. This suggests that spruce forests in Slovakia may have also experienced recent disturbances or that the forest management practices favor the regeneration of younger spruce trees.

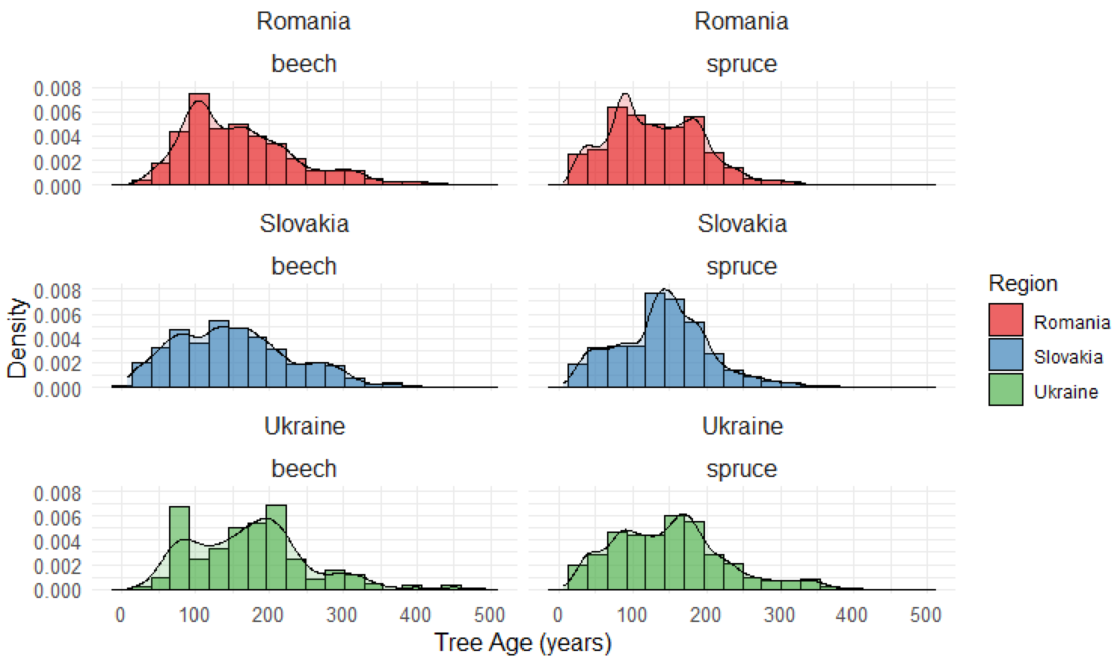

Figure 32. Age distribution of beech and spruce forests across Romania, Slovakia, and Ukraine. The histograms show tree age density for each forest type and region, highlighting differences in age structure.

In Ukraine, the age distribution patterns for both beech and spruce forests are somewhat distinct from the other two countries. Beech forests in Ukraine show a bimodal distribution with peaks around 50 and 150 years, reflecting a mixed stand structure with both younger and older trees. The spruce forests, similarly, have a bimodal distribution, with trees concentrated around 100-150 years and another smaller group around 200-250 years, suggesting more complex age dynamics compared to Romania and Slovakia. This could be indicative of varying disturbance regimes or management practices in Ukraine that lead to a more diverse age structure in both forest types. The detailed variations in age distribution for each stand in Slovakia (Figure C3), Romania (Figure C4), and Ukraine (Figure C5) are shown in the appendices.

Overall, the density distributions across the three regions show that beech forests tend to have broader and more diverse age structures compared to spruce forests, which are generally younger and more uniform in age. These patterns highlight the influence of different disturbance regimes and forest management practices in shaping the age dynamics of beech and spruce forests across Romania, Slovakia, and Ukraine.

4.3.2 Patterns of disturbance severity timing across Carpathians and forest types

Our results showed distinct differences of disturbance regime between beech and spruce forests (Figure 33). Notably, spruce forests exhibit greater variability in disturbance parameters, as evidenced by wider interquartile ranges and a higher frequency of outliers. This suggests that disturbances in spruce forests are less uniform and more heterogeneous. In contrast, beech forests display more consistent disturbance patterns, characterized by narrower interquartile ranges and fewer outliers, indicating more stable and homogeneous disturbance regimes.

While no clear country-specific patterns emerge across all disturbance parameters, some trends are evident (Figure 33). For instance, in Slovakia, both in terms of time since the last and maximum disturbance, beech forests generally recently disturbed compared to spruce forests, based on the mean values. While, on Romania region, spruce forest showed recent disturbance. Furthermore, the patterns observed for last disturbance severity and maximum disturbance severity are relatively similar across forest types, whereas the relationships involving time since the last disturbance and time since the maximum disturbance show more variation.

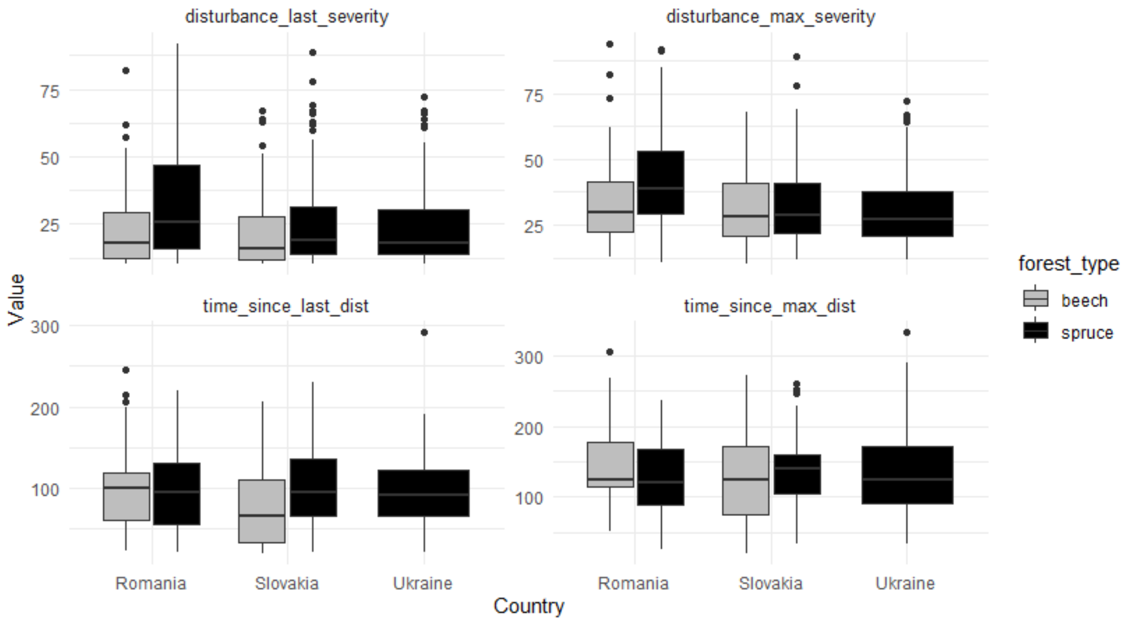

Figure 33. Boxplots illustrating the distribution of disturbance severity parameters (maximum disturbance severity and last disturbance severity) and disturbance timing (time since last disturbance and time since maximum disturbance) across different regions within the Carpathian Mountains and forest types (beech and spruce).

4.3.3 Influence of historical disturbances on stand age distributions

At the stand level, modeling analyses revealed that the timing of disturbances had significant and strong effects on stand age distributions (Figure 34). Specifically, both the time since the last disturbance and the time since the maximum disturbance showed significant effects, with p-values less than 0.05. This suggests that the timing of disturbances is crucial in shaping the forest's age structure, with more recent and historically significant disturbances having a lasting impact on tree ages. In contrast, the severity of disturbances, whether considering the last disturbance or the maximum disturbance, did not have a significant effect on diameter distributions. The p-value for the severity of the last disturbance was greater than 0.976, and for the maximum disturbance severity, it was greater than 0.478, indicating that neither had a meaningful impact on age structure.

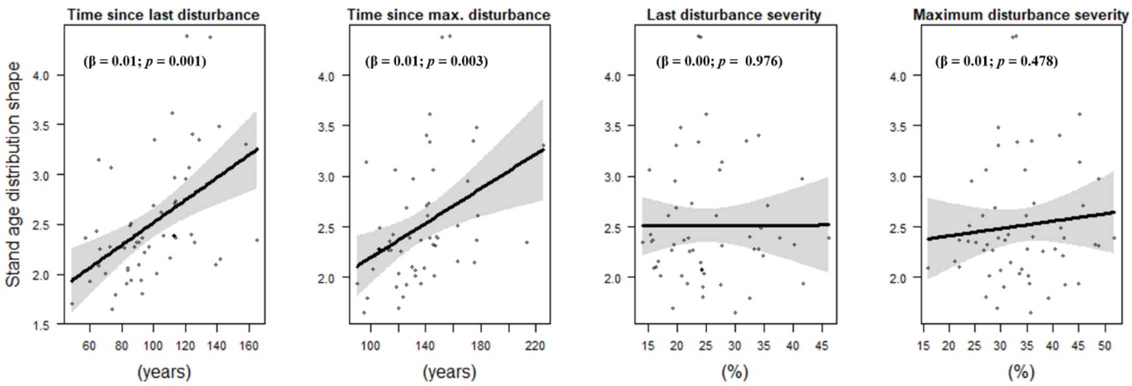

Figure 34. The effect of past disturbance parameters on the present tree size distribution. Each plot displays the expected response for each disturbance metric, with variables fit individually.

Based on the Akaike Information Criterion, our results confirmed that the time since the last disturbance was the strongest predictor of the Weibull shape parameter (Beta), which reflects the tree age distribution in the stands, with an AIC value of 108.29 (Table 8). This indicates that the length of time since the last disturbance occurred is a crucial factor. In contrast, the model for time since the maximum disturbance had a higher AIC value than the model for time since the last disturbance but was lower than those for the severity models. Specifically, the AIC values for disturbance severity (119.63 and 120.08) suggest that the intensity of disturbances, whether recent or maximum, is less important in shaping current tree age distributions compared to the timing of these disturbances. The AIC differences from the best model were 11.34 for maximum severity and 11.79 for last disturbance severity, highlighting the relatively minor role of disturbance severity.

Table 8. Summary of the mixed-effects models fit to explain the Weibull parameter, comparing the effects of various disturbance metrics. The models include random intercepts for country and forest type. The table shows the degrees of freedom (df), AIC values, change in AIC (ΔAIC) relative to the best model, and the rank of each model based on AIC.

parameters	AIC	ΔAIC	rank
Weibull parameter ~ mean time since last disturbance + (1 | country) + (1 | forest type)	108.29	0.00	1
Weibull parameter ~ mean time since max disturbance + (1 | country) + (1 | forest type)	113.63	5.34	2
Weibull parameter ~ mean disturbance maximum severity + (1 | country) + (1 | forest type)	119.63	11.34	3
Weibull parameter ~ mean last disturbance severity + (1 | country) + (1 | forest type)	120.08	11.79	4

Regarding country effects, the random effects showed slight deviations from the overall intercept, with Romania and Ukraine exhibiting slight negative deviations and Slovakia showing a slight positive deviation (Table 9). However, these deviations were minimal, indicating that country-specific effects are relatively insignificant. For forest effects, the random effects for forest type were effectively zero, suggesting no significant deviation from the overall intercept. This implies that forest type (beech vs. spruce) does not significantly contribute to the variability in the intercept across groups.

Table 9. Random effects from the best-fitting mixed-effects model (Weibull shape parameter ~ time_since_last_dist_mean + (1 | country) + (1 | forest type)), selected based on AIC. The table presents the conditional modes (intercepts) and standard deviations for each country and forest type, reflecting the variability attributed to these grouping factors in the model.

	Random effects	conditional mode	conditional standard deviation
Country	Romania	-0.00603	0.03346
	Slovakia	0.00982	0.03320
	Ukraine	-0.00379	0.03472
Forest type	beech	0.00000	0.00000
	spruce	0.00000	0.00000

5. DISCUSSION

5.1 HISTORICAL MIXED-SEVERITY DISTURBANCES SHAPE CURRENT DIAMETER DISTRIBUTIONS OF PRIMARY TEMPERATE NORWAY SPRUCE MOUNTAIN FORESTS IN EUROPE

Tree diameter distributions have become an important forest stand structural attribute for management decisions (McElhinny et al., 2005), biomass estimation, and can help evaluate potential forest resilience based on recruitment and mortality (Rubin et al., 2006). Though several structural attributes of forests exist that can be used to evaluate the effect of disturbances, we used diameter distributions due to their history of use, availability, and flexibility for modelling. Our study provides a new perspective on the effect of past disturbances on the current diameter distributions, using an extensive dataset at a large spatial scale, covering the entire range of the Carpathian Mountains.

Modelling analyses demonstrate that historical disturbances significantly influence the shape of current diameter distributions. Our analyses further indicate that increasing disturbance severity shifts the diameter distribution shape from negative exponential to unimodal and eventually to negatively skewed. This was clearly visible when we pooled all individual trees and plotted groups based on maximum disturbance severity (Appendix Figure A2). Also, we showed that diameter distribution shape is very much a function of past disturbance dynamics. Regardless of whether data were pooled by disturbance or whether plots were analyzed separately, we saw a dramatic shift in the skewness of the distribution when past disturbance severity is accounted for. Furthermore, when we accounted for the timing of disturbance, the impact of disturbance severity on distribution shape was significantly more evident. Thus, in looking at how the diameter distribution of a forest with natural disturbance dynamics differs from the reverse J-shaped distribution, we can surmise much about the disturbance regime, especially the severity and time since the last disturbance.

Previously, diameter distribution shapes have been used to describe the structure of uneven-aged forests. For over a century, the reverse J-shaped curve or the negative exponential relationship of tree density to diameter has been associated with old-growth forests and recruitment of all age classes (Niklas et al., 2003; Meyer, 1952). Several diameter distribution shapes have been reported in forests across Central, Eastern, and Southeastern Europe, where the majority of the European virgin forest remnants are located and the reverse J-shaped distribution has been traditionally considered an essential characteristic old-growth forests when it is observed (Westphal et al., 2006). This is because in forests with a reverse J-shaped distribution, small diameter tree density is sufficient to replace the current but ephemeral population of large diameter trees (Rubin et al., 2006). However, current diameter distribution shapes can be altered through a disturbance event. For example, Coomes and Allen (2007) and Canham et al. (2001) showed that simulated disturbance events killed large trees in greater numbers than small trees reducing size diversity in stands. Similarly, our results agree with the recent study by Sapkota et al. (2019), which found a reduction of positively skewed distribution curves with increasing disturbance.

From our study plots dominated by shallow rooted Norway spruce (Tjoelker et al., 2007), we can speculate that the occurrence of disturbance will decrease the prevalence of large diameter trees disproportionately. This will result in skewness of the diameter distribution shape increasing the positive skew by eliminating the larger diameter trees. For example, the common European bark beetle (*Ips typographus*) preferentially attacks older and weakened trees, which are found in abundance after wind disturbance (Wermelinger, 2004). Moreover, these beetles are specifically attracted to large diameter trees and thick bark (Schroeder, 2010). Though disturbance was found to be the main driver of DBH distribution shapes in this study, we realize that diameter distribution shapes are not entirely influenced by disturbance alone. For instance, a negative shift in skewness of distribution shape may be attained through non-disturbance processes. Small diameter trees are susceptible to death not only because of disturbance but also in the event of failed light interception during canopy closure, which eventually slows their growth rate and increases their likelihood of death (Reynolds and David Ford, 2005).

Our modelling showed that the last disturbance severity, time since last disturbance, and the interaction between them were the best predictors of current distribution shape. These disturbance parameters were better than the models which included maximal disturbance, time since maximal disturbance, and the interaction between them, indicating that last disturbances are overwriting the influence of disturbances happening further in the past. This simple result makes sense, but in a mixed-severity disturbance regime, we expected the influence of high-severity disturbances to be greater than a recent low-severity disturbance. Interestingly, the timing of disturbance parameters (e.g., time since last disturbance and time since maximum disturbance), were the two least significant variables in univariate models. This indicates that disturbance severity is the driving force shaping diameter distributions and the timing of that disturbance is mostly a conditional moderating influence. Further evidence of the importance of disturbance severity is that maximum disturbance severity and severity of the last disturbance were the best predictors of DBH distribution shape in univariate models. Panayotov et al., (2015) also found unimodal DBH distributions associated with medium-to-large-scale disturbances in their studie of Norway spruce-dominated forest reserve in Bulgaria. However, low-to-moderate severity disturbances can also create unimodal distributions (Holeksa et al., 2017) if mortality is greater among less vigorous small and large trees (Sproull et al., 2015). This situation might arise if the largest trees were killed by wind and bark beetle infestation and the smallest trees died because of light competition among neighboring taller trees (Holeksa et al., 2017). In our forest plots, however, disturbance severity had a strong impact in shaping the current diameter distribution as we predicted and as other previous studies have suggested.

The disturbance index, though describing the disturbance regime as a series of multiple events, did not sufficiently describe the diameter distribution shape. It is interesting that looking at diversity and evenness of disturbance was not as good at determining the DBH distribution shape as variables describing one parameter of disturbance, namely severity. From this, we can conclude that severe disturbances are some of the most impactful events with long legacies in forests (Schurman et al., 2018). Severity of natural disturbances poses long lasting legacies that can alter the structure of forest such as spruce-dominated or mixed forest thereby affecting the DBH structure through regeneration patterns, seedling recruitment and mortality (Kašpar et al., 2020).

In this study, I observed a driving force pushing the DBH distribution toward a reverse J-shaped in the absence of severe disturbances. Even though severe disturbances may create even-aged stands, small-scale and low-severity disturbances will increase forest complexity and a more diverse stand age structure. Forests that exhibit reverse J-shaped distributions are more ecologically stable simply by having a diversity of structure and age classes (Niklas et al., 2003). Thus, in order to maintain resilient forests in a time when disturbance severity is increasing, some resistance to disturbance is needed, otherwise more time for small-scale forest dynamics to occur will be the only way to push distributions back to the sustainable reverse J-shaped. Time, however, may not be a luxury that even-aged forests susceptible to high-severity windthrow and beetle outbreaks have (Seidl et al. 2014).

5.2 PAST DISTURBANCES SHAPE PRESENT TREE SIZE DISTRIBUTION IN EUROPEAN TEMPERATE PRIMARY BEECH – DOMINATED FORESTS

Our study investigates into the complex dynamics of primary forest ecosystems in Central Europe, focusing on how past disturbances shape the present tree size distribution in European beech-dominated forests within the Carpathian Mountains. Utilizing the Weibull shape parameter as a modeling tool, we were able to explore the patterns of tree size distributions across different disturbance regimes (e.g., timing and severity). The Weibull shape parameter has proven to be a robust and practical tool for such analyses, as it allows for the characterization of tree size distributions in a way that reflects both the history and severity and timing of disturbances (Rodrigo et al., 2022; Baker et al., 2005; Coomes & Allen, 2007). Our modeling analysis revealed that the severity of past disturbances is a critical determinant of present tree size distribution. Specifically, we observed that higher disturbance severity tends to shift the distribution from a reverse-J shape, which is indicative of a balanced size structure, towards a unimodal or positively skewed distribution. This transition is characterized by a reduction in the number of large trees and an increase in medium-sized trees, suggesting that high-severity disturbances disproportionately affect larger trees (Aszalós, 2022; Coomes and Allen, 20207). This finding is consistent with the density-dependent thinning theory, which posits that disturbances of greater intensity lead to the removal of larger trees, resulting in a more uniform size distribution (Frelich and Reich, 1999). These results are also consistent with the work of Rodrigo et al. (2022), who similarly identified a shift towards unimodal distributions in Norway spruce forests subjected to high-severity disturbances in the Carpathians.

At the plot-level, the study highlights the significant role that the time since the last disturbance plays in shaping tree size distributions. As time passes, the distribution gradually shifts towards a reverse-J shape, indicating ongoing recruitment and the establishment of younger cohorts. This finding aligns with the results of Coomes and Allen (2007), who demonstrated that the recovery process following disturbances is heavily influenced by the time elapsed since the event. The observed interaction between disturbance severity and timing emphasizes the complexity of forest dynamics, where recent high-severity disturbances have the most pronounced impact on skewing tree size distributions. The patterns we observed in tree size distribution are not isolated findings but rather part of a broader understanding of forest dynamics in response to disturbance regimes. Our results align with those of Panayotov et al. (2015) and Holeksa et al. (2017), who documented similar shifts towards unimodal diameter distributions in forests affected by medium-to-large-scale disturbances. In their study of Norway spruce-dominated forests in Bulgaria, Panayotov et al. (2015) found that medium-scale disturbances led to the prevalence of unimodal distributions, aligning with our observations in beech forests. Similarly, Holeksa et al. (2017) highlighted the role of low to moderate severity disturbances in creating unimodal distributions, further reinforcing our findings.

In contrast, Westphal et al. (2006) reported that reverse-J distributions are common in beech forests subjected to small-scale disturbances in Central Europe. This suggests that the scale and intensity of disturbances are key factors in determining the shape of tree size distributions. Our findings extend this understanding by showing that the interaction between disturbance severity and the time since the last disturbance can lead to complex distribution shapes that are reflective of both recent and historical disturbance regimes. Moreover, the work of Lorimer and Frelich (1984) supports the idea that fine-scale disturbances can cause substantial deviations in tree size distribution, contributing to structural heterogeneity within forests. The implications of our findings for forest management are substantial, particularly in the context of maintaining or enhancing forest structural heterogeneity. The observed shift towards a reverse-J distribution in the absence of high-severity disturbances suggests that such distributions may indicate a stable-cohort, structurally diverse forest. This is critical for forest managers aiming to promote structural heterogeneity against future disturbances and climate change (Seidl et al., 2018). Maintaining a mix of disturbance severities, as our study suggests, could foster structural heterogeneity, which is essential for ecosystem function and biodiversity.

At the stand level, our findings largely reflect those from the plot-level analysis, with one notable deviation: the time since the maximum disturbance exhibited a negative relationship with tree size distribution. All other predictors remained consistent. This suggests that, whether analyzing data at the plot or stand level, the primary factors influencing tree size distribution are disturbance severity, followed by disturbance timing. These results clearly indicate that disturbance severity, along with the timing of these events, are the key drivers shaping tree size distribution across different scales. Based on these findings, we can assume that past disturbances had a strong and significant effect on present tree size distribution shapes at both the plot and stand levels. Specifically, low and moderate severity disturbances are associated with reverse J-shaped distributions, while high-severity disturbances are linked to unimodal or positively skewed distributions.

However, it is important to recognize that reverse-J distributions, while can be indicative of a structurally diverse forest ecosystem, are not the only desirable outcome. The presence of large-diameter trees, as highlighted by Lutz et al. (2013) and Yuan et al. (2020), plays a crucial role in forest structural heterogeneity and carbon dynamics. Similarly, a recent study by Keith et al. (2024) highlights the importance of large-diameter trees in the forests for biomass and carbon carrying capacity. These findings suggest that primary forests' potential for carbon storage can significantly contribute to achieving the European Green Deal 2030 target (Keith et al., 2024). Therefore, forest management strategies should also focus on preserving large trees, which contribute significantly to forest structure and function. The study by Ali et al. (2021) further emphasizes that irregular distributions, including those with large trees, enhance forest complexity and ecological function. While our study provides valuable insights, it is essential to acknowledge the limitations in our study approach. The use of the Weibull shape parameter, although effective in modeling tree size distributions, may not fully capture the multi-dimensional aspects of forest structure, particularly in forests with complex disturbance histories (Kariuki, 2004). Future research could benefit from integrating additional variables such as climatic conditions, soil characteristics, and species-specific responses to disturbances. Additionally, exploring the long-term effects of varying disturbance frequencies and intensities across different forest ecosystems could provide a more comprehensive understanding of forest ecosystem dynamics.

Moreover, our study primarily focused on beech-dominated forests in the Carpathians, which limits the generalizability of our findings to other forest types or regions. Expanding this research to include a broader range of forest types and geographic areas would help to validate and extend the applicability of our results. The strong influence of disturbance severity on tree size distribution highlights the lasting legacy that disturbances leave on forest structure. Here, our findings suggest that severe disturbances have long-term impacts that can shape forest structure for decades, if not centuries. This insight is particularly relevant in the context of climate change, where the frequency and intensity of disturbances are expected to increase (Seidl, 2017). Understanding how different disturbance regimes shape forest structure will be crucial for forest management that enhance forest heterogeneity and adaptability in the face of climate change.

Lastly, our findings suggest that neither disturbance severity nor timing alone has a substantial impact on present tree size distribution. Instead, it is the interaction between these two parameters that exerts a strong influence on forest structural heterogeneity. Forests that have experienced mixed-severity disturbances tend to exhibit a form of resilience, as their structure has already adapted to these recurring events (Johnstone et al., 2016). This adaptability is likely due to the cumulative effect of both the frequency and severity of disturbances over time, rather than the influence of either single factor. This underscores the importance of considering the combined effects of disturbance timing and severity when evaluating their impact on forest dynamics and structural diversity. By understanding these combined effects, forest managers can better predict and manage the long-term consequences of disturbances on forest ecosystems.

5.3 THE IMPACT OF PAST DISTURBANCES ON AGE DISTRIBUTION IN EUROPEAN TEMPERATE MOUNTAIN FORESTS

Our findings indicate that stand age distributions in these forests vary significantly depending on the disturbance regime and regional context. The variability in age distribution across the Carpathian regions, highlights the heterogeneity in forest structure particularly age (Appendix Figure C2). These differences likely reflect the diverse historical disturbance regimes that have shaped these forests. For instance, areas with frequent low-severity disturbances tend to exhibit a more uniform age distribution, while regions that have experienced more severe or infrequent disturbances show greater variability in age structure (Frelich, 2002). This variation in age distribution is consistent with the idea that disturbance regimes play a crucial role in shaping forest dynamics and resilience. Further, this results align with Frelich's (2002) theory, which categorizes stand age distributions into stable and unstable types. In our study, regions showing flat or monotonically decreasing age distributions suggest a stable disturbance regime, where forests have maintained their structure over time despite disturbances. This stability is particularly evident in certain regions where the time since the last disturbance and disturbance severity did not drastically alter the age distribution, suggesting that these forests have developed resilience to the typical disturbance patterns in their environment.

Conversely, stands exhibiting unimodal or multimodal age distributions with significant changes in shape relative to disturbance parameters are indicative of unstable forest dynamics (Appendix Figures C4, C5, C6). These unstable distributions may signal that the disturbance regime in these regions is changing or becoming more irregular, potentially due to factors like climate change, increased human intervention, or natural variability (Frelich, 2002). Such patterns were particularly noticeable in areas where maximum disturbance severity or the time elapsed since the last major disturbance showed strong relationships with shifts in age distribution. This suggests that in these regions, forests are less able to maintain a consistent age structure over time, reflecting a dynamic and possibly shifting disturbance regime.

Additionally, the distinct peaks and uniform spread observed in the age distributions of these forest types may reflect underlying ecological dynamics and the natural disturbance regimes specific to each forest type. Beech forests, particularly in Central Europe, often develop with consistent age structures due to their resilience to disturbances and the tendency for synchronized regeneration following smaller-scale events (Kameniar et al., 2023). This results in less variability in tree age within these forests. On the other hand, spruce forests, which are more susceptible to large-scale natural disturbances, such as windstorms or insect outbreaks, often exhibit a more varied age structure (Angelstam and Kuuluvainen, 2004; Romeiro et al., 2022). These differences highlight how natural disturbance regimes, rather than human management, shape the demographic characteristics of forest stands, contributing to the distinct age distributions observed across different countries in our study.

On the other hand, our analysis revealed notable differences in disturbance patterns between beech and spruce forests across the Carpathian region. These findings are consistent with research indicating that spruce forests often experience more variable and heterogeneous disturbance regimes compared to beech forests (Kameniar et al., 2023). For instance, studies have shown that spruce-dominated forests in the Carpathians are subject to a wider range of disturbance intensities and frequencies, likely due to their higher susceptibility to factors such as windthrow, bark beetle infestations, and varying management practices (Kenderes et al., 2009; Kenderes et al., 2007; Zeibig et al., 2017). This greater variability in disturbance parameters, as indicated by wider interquartile ranges and more frequent outliers in our results, underscores the less uniform nature of disturbances in spruce forests, which contrasts with the more stable and homogeneous disturbance patterns observed in beech forests.

Additionally, the lack of clear country-specific patterns across all disturbance parameters, with some regional trends evident, further supports the complex interplay between disturbance dynamics and forest types in the Carpathians. For example, our observation that beech forests in Slovakia tend to be more recently disturbed compared to spruce forests aligns with the notion that beech forests, despite their general stability, may experience periodic disturbances that reset their age structures (Kameniar et al., 2023; Zeibig et al., 2005). Conversely, the recent disturbances observed in Romanian spruce forests may reflect ongoing ecological factors specific to that region, such as responses to climate change or pest outbreaks (Sousa-Silva et al., 2018). These regional variations highlight the importance of considering both forest type and local environmental conditions when assessing disturbance impacts across the Carpathians (Feurdean et al., 2017).

The influence of historical disturbances on stand age distributions in Carpathian forests is a critical factor in understanding the current forest structure. Our findings that the timing of disturbances significantly affects age distributions align with previous research indicating that past disturbances play a pivotal role in shaping forest dynamics (McDowell et al., 2020; Seidl and Turner, 2022) . For instance, studies in the Western Carpathians have shown that historical disturbances, particularly those of moderate to high severity, have had lasting impacts on forest structure by altering the age distribution and composition of tree species (Holeksa et al., 2017; Janda et al., 2017). These disturbances often create a mosaic of age classes within a forest, promoting diversity in tree ages and sizes, which can enhance the resilience of forests to future disturbances (Frelich et al., 2018; Bengtsson et al., 2000). Our observation that the time since the last disturbance is a stronger predictor of age distribution than disturbance severity emphasizes the importance of disturbance timing in determining forest structure.

Furthermore, the minimal impact of disturbance severity on tree age distribution, as revealed by our results, supports findings from other studies that suggest the intensity of a disturbance may not always be the primary driver of forest structural changes (Bradford et al., 2008). Previous research indicates that while severe disturbances can drastically alter the landscape in the short term, it is the frequency and timing of these events that more profoundly influence long-term forest dynamics (Turner, 2010; McDowell et al., 2020). This is particularly relevant in the Carpathian context, where the timing of disturbances, often linked to climatic events or human activities, has been shown to shape the forest's recovery trajectory and age structure over time (Kholiavchuk et al., 2023; Griffiths et al., 2014). Our study's findings that country-specific effects are minimal further suggest that these disturbance patterns and their impacts on age distribution are relatively consistent across the region, despite the varying management practices and ecological conditions.

The relatively minor role of forest type (beech vs. spruce) in influencing the variability in the intercept of age distributions across groups, as indicated by our analysis, also finds support in the literature. Research has shown that both beech and spruce forests in the Carpathians respond similarly to historical disturbances, with the primary difference being the scale and intensity of disturbance events that each forest type typically experiences (Kameniar et al., 2023; Janda et al., 2017). Beech forests, which are generally more resilient to disturbances, tend to recover with a more uniform age distribution, while spruce forests, which are more susceptible to large-scale disturbances like windthrow or pest outbreaks, often exhibit a more heterogeneous age structure (Janda et al., 2017; Rodrigo et al., 2022).

However, our disturbance parameters were averaged from the plot-level information, the limitation of the use of the mean value to represent the stand level information might be limited due to the variability of the data across the plots in each stand. Although, we are fully aware the limitations of using mean values and we only have 55 stands could limit the result of our modelling. Despite, this limitation, we can confidently assume that our results are valid and align with the results from published recent studies. Hence, our findings can contribute to the growing body of evidence that highlights the importance of disturbance timing over severity in shaping forest age distributions. The consistency of these effects across different countries and forest types in the Carpathians suggests that regional disturbance regimes, driven by both natural and anthropogenic factors, play a crucial role in determining the long-term structural characteristics of these forests. Understanding these dynamics is essential for developing effective forest management strategies that can enhance the resilience of Carpathian forests to future disturbances.

5.4 FUTURE RESEARCH PERSPECTIVES ON FOREST STRUCTURE AND DISTURBANCE DYNAMICS

Future research on forest structure and dynamics in primary temperate mountain forests, particularly in the Carpathians, should focus on the long-term effects of various disturbance regimes on tree size and age distributions. Given the findings of this dissertation, it is essential to explore how different types of disturbances—such as windthrow, insect outbreaks, and anthropogenic influences—interact with natural processes to shape forest structure over time. Longitudinal studies that combine historical data with contemporary observations can provide valuable insights into how these disturbances influence tree growth patterns and age distributions. Such research could utilize dendroecological techniques to reconstruct past disturbance events and correlate them with current forest conditions, thereby enhancing our understanding of resilience mechanisms in these ecosystems (Svoboda et al., 2013; Bertogliati, 2010).

Another critical area for future investigation is the role of climate change in modifying disturbance regimes and their subsequent impact on forest structure. As climate change intensifies, the frequency and severity of disturbances are expected to increase, potentially leading to shifts in tree size distributions and forest structure. Research should focus on modeling these changes under various climate scenarios to predict how primary temperate forests might respond. This could involve using statistical models to assess the implications of changing disturbance patterns on tree growth and survival. Understanding these dynamics will be crucial for developing adaptive forest management strategies that aim to maintain biodiversity and ecosystem services in the face of ongoing environmental changes (Ramírez-Barahona et al., 2021; Turner, 2010).

Furthermore, integrating ecological and socio-economic perspectives into forest management practices is vital for ensuring the sustainability of primary mountain forests. Future research should examine how local communities interact with these forests and the implications of their management practices on forest structure and resilience. By incorporating traditional ecological knowledge alongside scientific research, forest management strategies can be tailored to reflect both ecological realities and community needs. This holistic approach can help mitigate the impacts of disturbances while promoting the conservation of biodiversity and ecosystem functions (Taylor & Lindenmayer, 2020; Bowd et al., 2021). Engaging stakeholders in the research process can also foster a sense of stewardship and responsibility towards forest conservation.

Lastly, the exploration of restoration techniques aimed at enhancing forest resilience is an important avenue for future research. Given the findings that highlight the significance of disturbance timing and severity on forest structure, studies should investigate restoration practices that can help re-establish structural complexity and diversity in disturbed forests. Additionally, research should assess the effectiveness of various restoration strategies in different forest types and under varying disturbance regimes, thereby contributing to a more comprehensive understanding of how to restore and maintain healthy forest ecosystems in the face of changing environmental conditions (Luo et al., 2018; Bertogliati, 2010).

Overall, future research on primary temperate mountain forests should prioritize understanding the complex interplay between disturbance regimes, climate change, and forest structure. By focusing on long-term ecological studies, integrating socio-economic factors, and exploring restoration techniques, we can better contribute to the sustainable management and conservation of these vital ecosystems. The insights gained from such studies will be essential for predicting future changes in forest dynamics and ensuring the resilience of temperate mountain forests in the face of ongoing environmental challenges.

6. CONCLUSION

Forest structure, including tree size distributions such as diameter at breast height (DBH) and age distributions, serves as a critical indicator of ecological changes and forest dynamics. In primary temperate forests, these structural attributes reflect the cumulative effects of historical disturbances and ongoing environmental changes. Understanding these dynamics is essential for assessing forest resilience and predicting future changes in forest structure and ecosystem functioning. The primary aim of this dissertation is to explore the impact of past disturbances on forest structural attributes—specifically DBH and age distributions—in primary temperate mountain forests in Europe, particularly within the Carpathian Mountains. This dissertation is comprised of three major studies, all of which highlights the significant influence of disturbance regimes on forest structure and function, with a specific focus on DBH and age distributions.

6.1 CONCLUSION OF STUDY 1: HISTORICAL MIXED-SEVERITY DISTURBANCES SHAPE CURRENT DIAMETER DISTRIBUTIONS OF PRIMARY TEMPERATE NORWAY SPRUCE FORESTS IN EUROPE

The first study of this dissertation highlights the profound impact of disturbance regimes on diameter distributions in spruce-dominated forests. The findings reveal that increased disturbance severity leads to more unimodal and negatively skewed DBH distributions, indicating a loss of structural complexity. This shift in diameter distribution suggests a decline in the sustainability and resilience that size diversity typically provides, particularly in spruce ecosystems. As climate change is expected to increase the severity and frequency of disturbances, these findings highlights the potential for further modifications to forest structures. Understanding these dynamics is crucial for developing effective forest management strategies that prioritize the conservation of larger trees, which play a critical role in carbon sequestration and habitat provision.

The implications of these findings extend beyond the immediate context of spruce-dominated forests. The suggestion is that forest management practices must adapt to the changing disturbance regimes driven by climate change. By focusing on maintaining a diverse size distribution, particularly the retention of larger trees, forest managers can enhance the resilience of these ecosystems. This approach not only supports biodiversity but also contributes to the overall carbon storage potential of the forest, aligning with broader climate mitigation goals. Future research should continue to explore the long-term effects of various disturbance types on diameter distributions, providing a more comprehensive understanding of how these dynamics influence forest status and function.

Overall, the first study emphasizes the critical need for adaptive management strategies that account for the impacts of disturbance regimes on tree size distributions in spruce-dominated forests. By recognizing the importance of maintaining structural complexity and size diversity, forest managers can better prepare for the challenges posed by climate change. This research contributes valuable insights into the crucial relationships between disturbance, tree size distribution, and forest resilience, ultimately informing practices that promote sustainable forest ecosystems.

6.2 CONCLUSION OF STUDY 2: PAST DISTURBANCES SHAPE PRESENT TREE SIZE DISTRIBUTION IN EUROPEAN TEMPERATE BEECH-DOMINATED FORESTS

The second study focuses on beech-dominated primary forests within the Carpathians, revealing how the interaction between maximum disturbance severity and the time since the last disturbance plays a key role in shaping tree size distributions. The results indicate that higher disturbance severities are associated with unimodal or bimodal size distributions, while longer periods since the last disturbance result in reverse-J shaped distributions, which may indicate of more sustainable and resilient forest structures. These insights highlight the importance of considering both disturbance severity and recovery time in forest management practices. By understanding how these factors influence tree size distribution, forest managers can implement strategies that enhance structural heterogeneity and promote biodiversity.

Our study provides insights into how past disturbances have shaped present tree size distributions in European temperate beech-dominated forests. We found that both the severity and timing of disturbances play critical roles in influencing the structure of these forests. Specifically, high-severity disturbances tend to shift tree size distributions towards unimodal shapes, while lower-severity disturbances often maintain reverse-J shaped distributions, indicative of greater structural diversity.

One of the key findings is that the interaction between disturbance severity and the time elapsed since the last disturbance creates varying levels of structural heterogeneity. This heterogeneity is a crucial factor in maintaining the ecological functions of forests, as it promotes resilience and productivity such as potential carbon storage. Contrary to the assumption that any specific distribution is optimal, we demonstrate that mixed-severity disturbances contribute to a complex mosaic of tree size distributions, enhancing overall forest structure.

Lastly, our results can be linked to the current understanding that structural heterogeneity is one of the most desired attributes of forest ecosystems, as it fosters both ecological resilience and functional diversity. Moderate disturbances, in particular, appear to create a balance between maintaining large trees and promoting regeneration, leading to a diverse range of tree sizes. However, future research should further explore how different disturbance regimes affect other forest functions beyond tree size distributions, such as habitat provision, carbon dynamics, and biodiversity, to provide a more comprehensive understanding of forest structure dynamics.

6.3 CONCLUSION OF STUDY 3: IMPACT OF PAST DISTURBANCES ON AGE DISTRIBUTIONS IN EUROPEAN TEMPERATE MOUNTAIN FORESTS

The results of this study highlight the critical role that disturbance timing plays in shaping the age distribution of forest stands in the Carpathian Mountains. We showed that beech forests consistently have higher median ages and a more balanced age distribution, with a noticeable presence of older trees, particularly in Ukraine while spruce forests display greater variability in age distribution, with a higher concentration of younger trees, especially in Romania and Slovakia. Also, our results showed that beech forests have experienced lower and more concentrated disturbance severities, with relatively uniform timing of disturbances around 100 years ago across all three countries.

In contrast, spruce forests show greater variability in both severity and timing, where disturbances have been more frequent and severe, suggesting a more dynamic disturbance history for spruce compared to beech. Overall, among the disturbance parameters analyzed, time since the last disturbance emerged as the most influential factor, significantly affecting the Weibull shape parameter, which characterizes the stand age distribution. In contrast, the severity of disturbances—both last and maximum—showed minimal impact on the age distribution, suggesting that while disturbances occur, it is their timing rather than intensity that most profoundly influences forest structure.

The implications of these findings are profound, as they indicate that forest management practices must prioritize the timing of interventions to enhance forest resilience. By recognizing that the age distribution of trees is more sensitive to the timing of disturbances than to their severity, we can implement strategies that promote a balanced age structure within forest stands. This approach not only supports biodiversity but also contributes to the overall health and stability of forest ecosystems. Future research should further explore the mechanisms by which disturbance timing influences age distributions, providing valuable insights for adaptive management practices.

Lastly, the third study emphasizes the critical importance of incorporating the temporal aspects of disturbance into forest management strategies. By understanding how disturbance timing influences age distributions, we can better support the resilience and sustainability of temperate mountain forests. This research contributes valuable knowledge to the field of forest ecology, highlighting the important relationships between disturbance dynamics, tree age distribution, and forest functioning. Ultimately, these insights will inform practices that promote the conservation and management of these vital ecosystems in the face of ongoing environmental challenges.

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APPENDIX A

Appendix A. contains the additional supporting materials for **Subsection 3.2/ 4.1/ 5.1**.

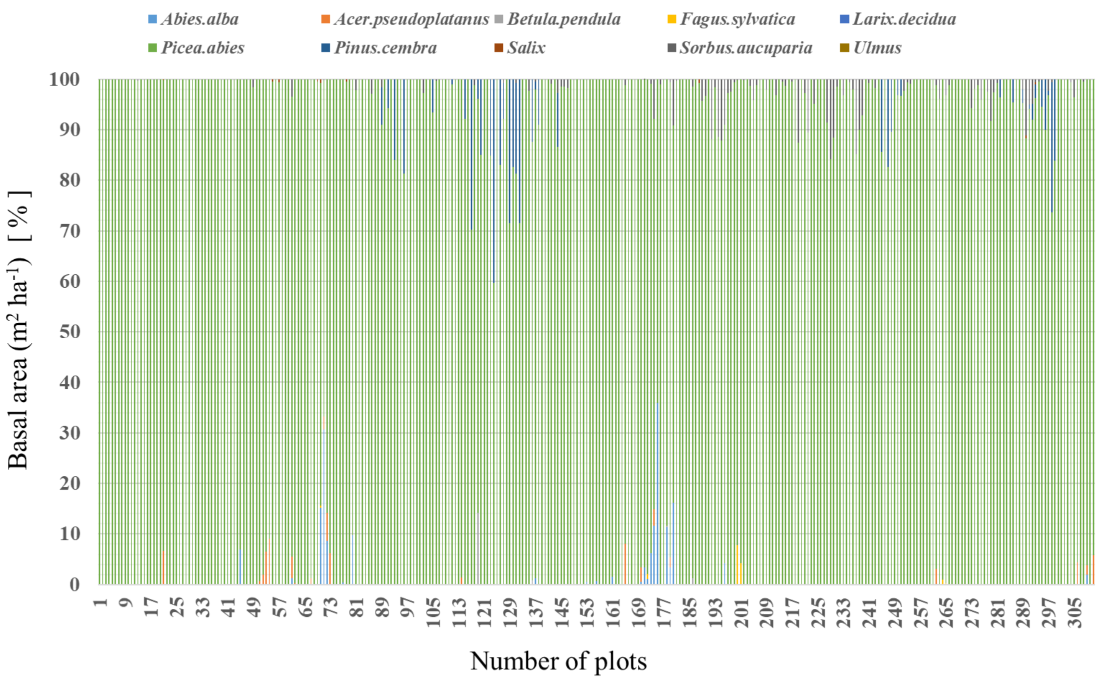

Figure A1. Percentage of basal area (m^2/ha) calculated per species per plot showing the dominance of Norway spruce trees in our study plots.

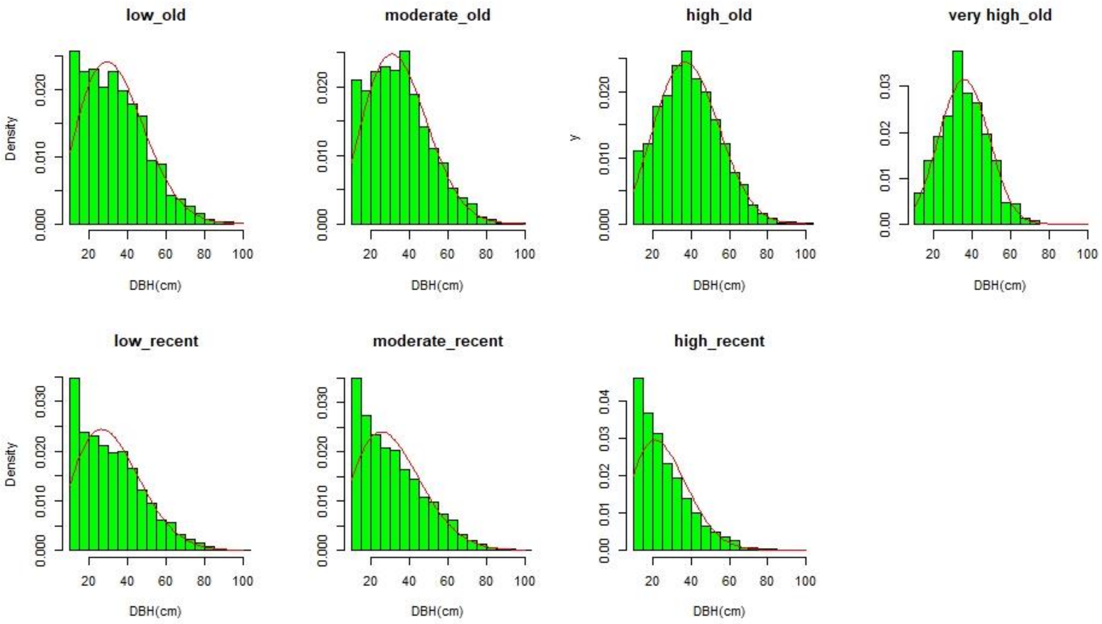

Figure A2. Diameter distributions within the study areas obtained by pooling the data from 311 plots based on the last disturbance severity category as follows: low (< 20 %, *n* = 80 plots), moderate (20-40 %; *n* = 138 plots), high (40-60 %; *n* = 78 plots), and very high (> 60 %; *n* = 15 plots). Disturbance timing such as old (>100 years since last disturbance) and recent (<100 years since last disturbance. Density is the total number of trees within a selected size bin (10 cm). A decrease in skewness is observed with increasing disturbance severity in combination with timing (old).

Table A1. Structural attributes of the study area.

	region	country	standid	nb_plots	nb_trees	minDBH	medianDBH	maxDBH	avgDBH	avgSlope	avgElevation
1	Eastern Carpathian	Northern Romania	ROM_CAL_	8	303	10	42.8	91.0	42.0	26	1597
2			ROM_GIU_	29	1349	10	29.7	105.0	33.3	26	1424
3		Ukraine	UKR_GR1_	13	598	10	30.2	86.2	31.4	26	1381
4			UKR_GR2_	12	516	10	31.3	85.1	32.3	30	1356
5			UKR_GR3_	11	620	10	28.2	79.8	29.5	32	1334
6			UKR_SY1_	19	1216	10	23.3	73.5	26.4	28	1424
7			UKR_SY2_	13	612	10	29.9	84.3	31.8	26	1366
8	Southern Carpathian	Southern Romania	ROM_FA1_	11	715	10	30.2	80.4	32.4	36	1513
9			ROM_FA10	9	480	10	34.5	81.4	36.2	35	1507
10			ROM_FA2_	11	609	10	33.2	91.3	34.4	37	1443
11			ROM_FA3_	5	265	10	32.0	83.5	33.5	39	1409
12			ROM_FA4_	10	504	10	36.5	97.5	37.9	36	1479
13			ROM_FA5_	9	508	10	32.2	100.4	34.9	37	1463
14			ROM_FA6_	11	521	10	33.0	83.1	34.6	36	1542
15			ROM_FA8_	9	527	10	30.4	111.4	33.2	43	1462
16			ROM_FA9_	8	453	10	33.6	116.6	36.1	35	1558
17	Western Carpathian	Slovakia	SLO_BEL_	8	505	10	29.1	80.9	30.1	27	1344
18			SLO_BYS_	13	549	10	30.9	92.0	33.4	31	1406
19			SLO_DUM_	17	769	11	37.3	98.0	37.7	14	1494
20			SLO_HLI_	11	470	10	33.2	92.3	35.7	29	1436
21			SLO_JAK_	14	496	10	38.3	87.5	40.2	30	1287
22			SLO_JAV_	8	381	10	32.5	79.8	32.8	12	1438
23			SLO_KOP_	11	732	10	21.7	69.8	25.1	31	1412
24			SLO_MED_	5	257	10	35.4	75.0	35.7	32	1516
25			SLO_OSO_	11	463	10	37.5	81.9	37.3	30	1353
26			SLO_PIL_	5	165	10	41.9	93.0	43.7	21	1340
27			SLO_SMR_	9	291	10	44.7	89.7	43.8	28	1383

28		SLO_TIC_	11	609	10	26.1	84.2	29.8	26	1405
			311	15483						

Note: DBH (cm); slope (degrees); elevation (masl); plot size was 1000 m^2.

Table A2. Historical disturbance metrics and of the spruce forest in Carpathian primary forests as stand-level means, with standard deviations in the brackets.

	region	stand	DHH shape parameter (skewness)	Max. disturbance severity (% canopy removed)	Time since max. disturbance (year)	Last disturbance severity (% canopy removed)	Time since last disturbance (year)	Disturbance index (Shannon diversity index)
1		ROM_CAL_	2.62 (0.42)	43.50 (8.93)	184 (30)	40.12 (12.25)	176 (33)	1.72 (0.36)
2		ROM_GIU_	2.56 (0.97)	41.34 (16.36)	157 (71)	36.28 (19.16)	102 (62)	1.79 (0.45)
3		UKR_GR1_	2.82 (0.80)	35.08 (12.82)	112 (55)	29.38 (15.42)	91 (32)	2.18 (0.19)
4	Eastern Carpathians	UKR_GR2_	2.41 (0.48)	30.42 (9.55)	157 (51)	23.50 (11.73)	111 (49)	2.23 (0.19)
5		UKR_GR3_	2.88 (0.90)	33.45 (9.08)	165 (38)	27.73 (10.83)	120 (41)	2.02 (0.18)
6		UKR_SY1_	2.38 (0.38)	26.84 (7.68)	169 (116)	22.68 (7.07)	120 (98)	2.16 (0.22)
7		UKR_SY2_	2.51 (0.62)	34.46 (9.17)	145 (45)	27.23 (13.78)	101 (51)	2.29 (0.23)
8		ROM_FA1_	2.91 (0.72)	44.73 (10.57)	147 (55)	39.36 (15.04)	129 (52)	1.71 (0.35)
9		ROM_FA10	3.47 (0.93)	51.00 (23.16)	158 (50)	48.89 (25.88)	141 (37)	1.66 (0.40)
10	Southern Carpathians	ROM_FA2_	2.97 (0.79)	46.18 (13.18)	146 (30)	45.91 (13.75)	134 (25)	1.72 (0.35)
11		ROM_FA3_	2.34 (0.33)	25.80 (5.07)	159 (64)	21.80 (7.05)	128 (72)	2.23 (0.26)
12		ROM_FA4_	2.88 (0.55)	44.30 (6.65)	156 (32)	38.30 (13.40)	144 (45)	1.84 (0.26)
13		ROM_FA5_	2.31 (0.31)	35.56 (11.35)	136 (42)	33.56 (12.60)	123 (36)	2.08 (0.26)

14		ROM_FA6_	2.59 (0.38)	34.82 (8.92)	146 (23)	33.73 (10.33)	140 (26)	1.98 (0.22)
15		ROM_FA8_	2.23 (0.35)	43.78 (13.80)	92 (24)	40.67 (16.18)	84 (24)	1.87 (0.25)
16		ROM_FA9_	2.38 (0.43)	37.50 (10.04)	104 (20)	30.38 (9.20)	83 (23)	1.99 (0.25)
17		SLO_BEL_	2.88 (0.45)	26.00 (7.01)	162 (49)	24.00 (8.21)	137 (34)	1.99 (0.31)
18		SLO_BYS_	2.48 (0.48)	29.54 (7.23)	111 (32)	23.23 (6.67)	79 (31)	2.12 (0.29)
19		SLO_DUM_	3.36 (0.51)	41.88 (13.85)	143 (17)	39.29 (16.70)	131 (20)	2.00 (0.22)
20		SLO_HLI_	2.35 (0.39)	27.00 (4.56)	133 (53)	22.55 (4.72)	94 (39)	2.17 (0.24)
21		SLO_JAK_	2.66 (0.88)	36.14 (20.02)	119 (63)	35.21 (20.67)	87 (48)	1.95 (0.47)
22	Western Carpathians	SLO_JAV_	3.29 (0.69)	29.88 (9.61)	181 (32)	23.12 (8.44)	140 (47)	2.09 (0.15)
23		SLO_KOP_	2.62 (0.46)	34.55 (15.29)	131 (77)	30.36 (17.05)	84 (47)	1.91 (0.41)
24		SLO_MED_	3.19 (0.56)	31.40 (10.06)	148 (29)	26.00 (11.96)	116 (32)	2.11 (0.34)
25		SLO_OSO_	3.47 (1.28)	32.64 (14.87)	143 (45)	29.00 (16.06)	123 (44)	1.97 (0.48)
26		SLO_PIL_	2.84 (1.02)	23.20 (4.55)	157 (90)	21.00 (4.30)	153 (91)	1.96 (0.39)
27		SLO_SMR_	3.65 (0.81)	45.67 (12.47)	145 (17)	30.67 (17.64)	122 (23)	1.89 (0.27)
28		SLO_TIC_	2.41 (0.53)	44.27 (10.87)	103 (64)	40.27 (14.55)	94 (55)	1.96 (0.22)

APPENDIX B

Appendix B. contains the additional supporting materials for **Subsection 3.3/ 4.2/ 5.2**.

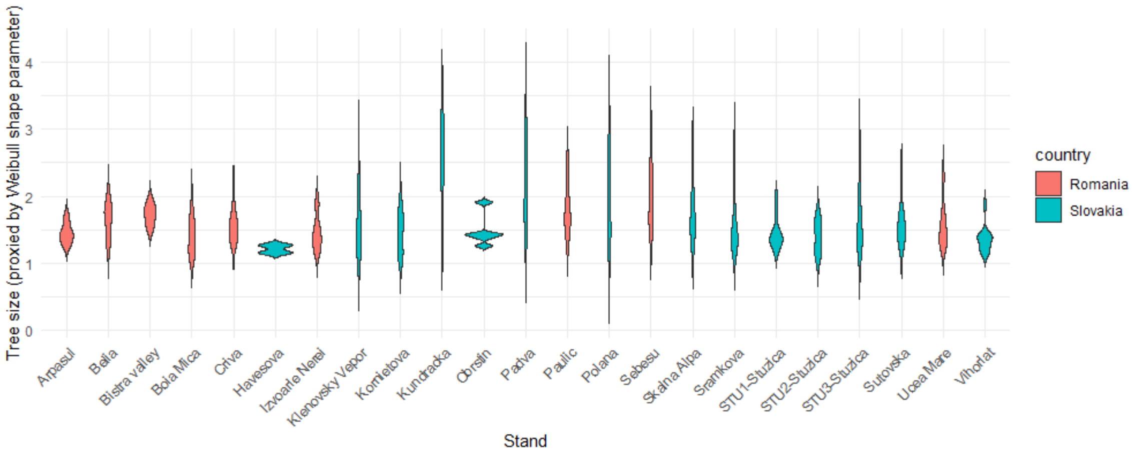

Figure B1. Violin plot showing the distribution of tree size, proxied by the Weibull shape parameter, across different forest stands in Romania and Slovakia. Each violin represents the density of tree sizes within a stand, with the width indicating the relative frequency of tree size values. Red violins represent stands in Romania, while blue violins represent stands in Slovakia. The plot illustrates variations in tree size distribution between the two countries, with some stands exhibiting a more evenly distributed range of tree sizes, while others show more concentrated or skewed distributions.

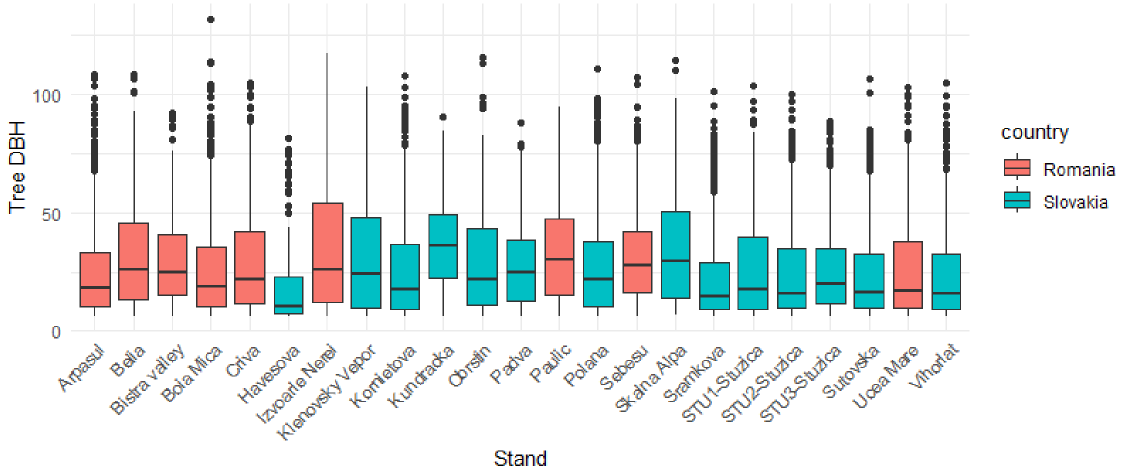

Figure B2. Boxplot of tree diameter at breast height (DBH) distributions across forest stands in Romania and Slovakia. The DBH values (in cm) are displayed for individual stands, with Romania and Slovakia represented by red and blue, respectively. Each box shows the median, interquartile range (IQR), and potential outliers for the tree DBH in each stand, highlighting the variability in tree size distribution between the two countries. The x-axis represents different forest stands, while the y-axis shows the DBH values.

Table B1. Forest structure of the study area in the Carpathians. This table presents the stand name, country, number of plots (nb_plots), number of trees (nb_trees), diameter at breast height (cm; minimum, maximum, mean, median, 25 quartile, and 75 quartile), and mean altitude (m) for each stand.

	stand	country	nb_ plot	nb_ trees	DBH_ MIN	DBH_ MAX	DBH_ MEAN	DBH_ 25Q	DBH_ MEDIAN	DBH_ 75Q	ALTITUDE_ MEAN
1	Arpasul	Romania	14	790	6.0	108.7	25.1	10.4	18.1	33.2	1127.5
2	Belia	Romania	14	654	6.0	108.4	31.2	13.5	26.0	45.6	1229.5
3	Bistra valley	Romania	11	505	6.1	92.6	30.4	15.1	24.7	41.0	1062.1
4	Boia Mica	Romania	12	706	6.0	132.0	26.3	10.1	18.5	35.5	1201.4
5	Criva	Romania	13	645	6.0	105.0	29.3	11.8	21.5	42.2	1014.0
6	Havesova	Slovakia	2	137	6.0	81.6	20.2	7.6	10.4	22.7	624.4
7	Izvoarle Nerei	Romania	9	365	6.0	117.5	34.8	12.0	25.8	54.3	1107.9
8	Klenovsky Vepor	Slovakia	12	399	6.0	103.0	31.6	9.8	24.1	48.3	1194.3
9	Kornietova	Slovakia	13	673	6.0	108.0	25.8	9.2	17.6	36.8	1133.7
10	Kundracka	Slovakia	7	229	6.1	90.7	37.8	22.5	36.2	49.3	1089.4
11	Obrstin	Slovakia	5	219	6.2	115.5	29.5	11.1	21.8	43.3	902.3
12	Padva	Slovakia	7	279	6.2	88.2	27.5	13.0	24.8	38.7	1176.4
13	Paulic	Romania	6	254	6.0	94.7	32.9	15.0	29.9	47.5	1015.2
14	Polana	Slovakia	16	699	6.0	111.1	27.5	10.2	21.5	38.1	1132.6
15	Sebesu	Romania	13	581	6.0	107.5	31.5	16.6	27.6	42.0	1162.3

16	Skalna Alpa	Slovakia	6	170	6.5	114.2	35.3	14.0	29.4	50.3	1133.8
17	Sramkova	Slovakia	14	837	6.0	101.5	22.1	9.0	14.6	28.9	1036.6
18	STU1-Stuzica	Slovakia	11	518	6.0	103.5	26.8	9.4	17.6	39.8	930.4
19	STU2-Stuzica	Slovakia	9	508	6.1	100.3	25.3	9.9	16.1	34.8	962.6
20	STU3-Stuzica	Slovakia	13	813	6.0	88.9	26.0	11.6	20.2	35.0	971.1
21	Sutovska	Slovakia	13	777	6.0	106.5	24.1	9.6	16.4	32.8	1037.7
22	Ucea Mare	Romania	7	387	6.0	103.3	26.4	9.8	16.9	38.1	999.7
23	Vihorlat	Slovakia	11	610	6.0	104.6	24.4	9.1	16.0	32.8	800.2
	TOTAL		238	11755							

Table B2. Stand-level information Ssummary: forest type, tree size distribution (Weibull shape), and disturbance parameters. Includes: last disturbance severity, maximum disturbance severity, time since last disturbance, time since maximum disturbance. Note: SD denotes standard deviation.

	stand	Forest_ type	Stand_ short	Country	Weibull_ Shape	Last Disturbance Severity	Maximum Disturbance Severity	Time since last disturbance	Time since maximum disturbance
1	Arpasul	beech	ARP	Romania	1.45 (0.15)	17.00 (12.94)	27.64 (11.55)	69.79 (43.07)	132.57 (59.93)
2	Belia	beech	BEL	Romania	1.64 (0.26)	37.64 (16.39)	42.21 (11.96)	106.43 (28.24)	128.50 (38.59)

3	Bistra valley	beech	BIS	Romania	1.72 (0.16)	19.73 (8.59)	29.18 (9.26)	102.09 (29.41)	129.64 (29.50)
4	Boia Mica	beech	BOI	Romania	1.41 (0.28)	21.67 (12.12)	35.58 (14.25)	91.75 (49.27)	136.50 (43.03)
5	Criva	beech	CRI	Romania	1.55 (0.23)	18.46 (6.46)	21.77 (7.26)	101.92 (40.86)	135.69 (59.85)
6	Havesova	beech	HAV	Slovakia	1.21 (0.08)	20.50 (6.36)	20.50 (6.36)	110.50 (40.31)	110.50 (40.31)
7	Izvoarle Nerei	beech	IZV	Romania	1.47 (0.27)	19.11 (7.72)	26.89 (6.88)	181.44 (74.49)	238.44 (55.14)
8	Klenovsky Vepor	beech	VEP	Slovakia	1.62 (0.50)	17.17 (8.83)	26.50 (8.84)	87.67 (61.96)	157.42 (40.40)
9	Kornietova	beech	KOR	Slovakia	1.47 (0.31)	15.38 (6.79)	31.31 (16.79)	63.92 (45.87)	115.92 (65.57)
10	Kundracka	beech	KUN	Slovakia	2.53 (0.60)	29.00 (16.38)	32.43 (13.65)	122.43 (53.10)	161.57 (68.03)
11	Obrstin	beech	OBR	Slovakia	1.48 (0.25)	27.40 (21.24)	42.40 (15.32)	60.00 (27.63)	125.80 (84.53)
12	Padva	beech	PAD	Slovakia	2.17 (0.64)	18.71 (8.79)	25.71 (7.57)	73.57 (50.81)	122.71 (56.76)
13	Paulic	beech	PAU	Romania	1.82 (0.41)	26.67 (8.66)	33.50 (13.22)	138.50 (23.76)	152.00 (32.04)
14	Polana	beech	POL	Slovakia	2.00 (0.64)	31.69 (18.70)	38.94 (13.80)	88.50 (45.16)	113.06 (36.94)
15	Sebesu	beech	SEB	Romania	1.98 (0.44)	27.77 (21.83)	48.77 (24.87)	89.38 (54.17)	147.31 (53.68)
16	Skalna Alpa	beech	SKA	Slovakia	1.80 (0.51)	13.83 (7.00)	20.67 (4.08)	119.83 (82.99)	202.50 (90.99)
17	Sramkova	beech	SRA	Slovakia	1.63 (0.50)	19.64 (11.20)	29.50 (8.93)	45.07 (26.95)	116.57 (54.80)
18	STU1-Stuzica	beech	STU	Slovakia	1.45 (0.25)	15.45 (5.32)	27.27 (7.25)	70.73 (36.91)	115.45 (47.44)
19	STU2-Stuzica	beech	STU	Slovakia	1.40 (0.24)	19.89 (11.95)	26.11 (11.33)	79.00 (48.51)	131.56 (71.55)
20	STU3-Stuzica	beech	STU	Slovakia	1.64 (0.46)	22.15 (12.50)	30.92 (13.76)	82.00 (43.37)	118.85 (60.31)
21	Sutovska	beech	SUT	Slovakia	1.56 (0.30)	24.38 (15.37)	30.46 (15.85)	82.62 (48.00)	118.46 (67.56)
22	Ucea Mare	beech	UCE	Romania	1.57 (0.36)	19.43 (8.75)	27.29 (8.46)	91.00 (34.89)	145.29 (56.22)
23	Vihorlat	beech	VIH	Slovakia	1.36 (0.20)	19.09 (9.36)	32.27 (18.14)	71.45 (35.60)	111.91 (48.28)

APPENDIX C

Appendix C. contains the additional supporting materials for **Subsection 3.4/ 4.3/ 5.3**.

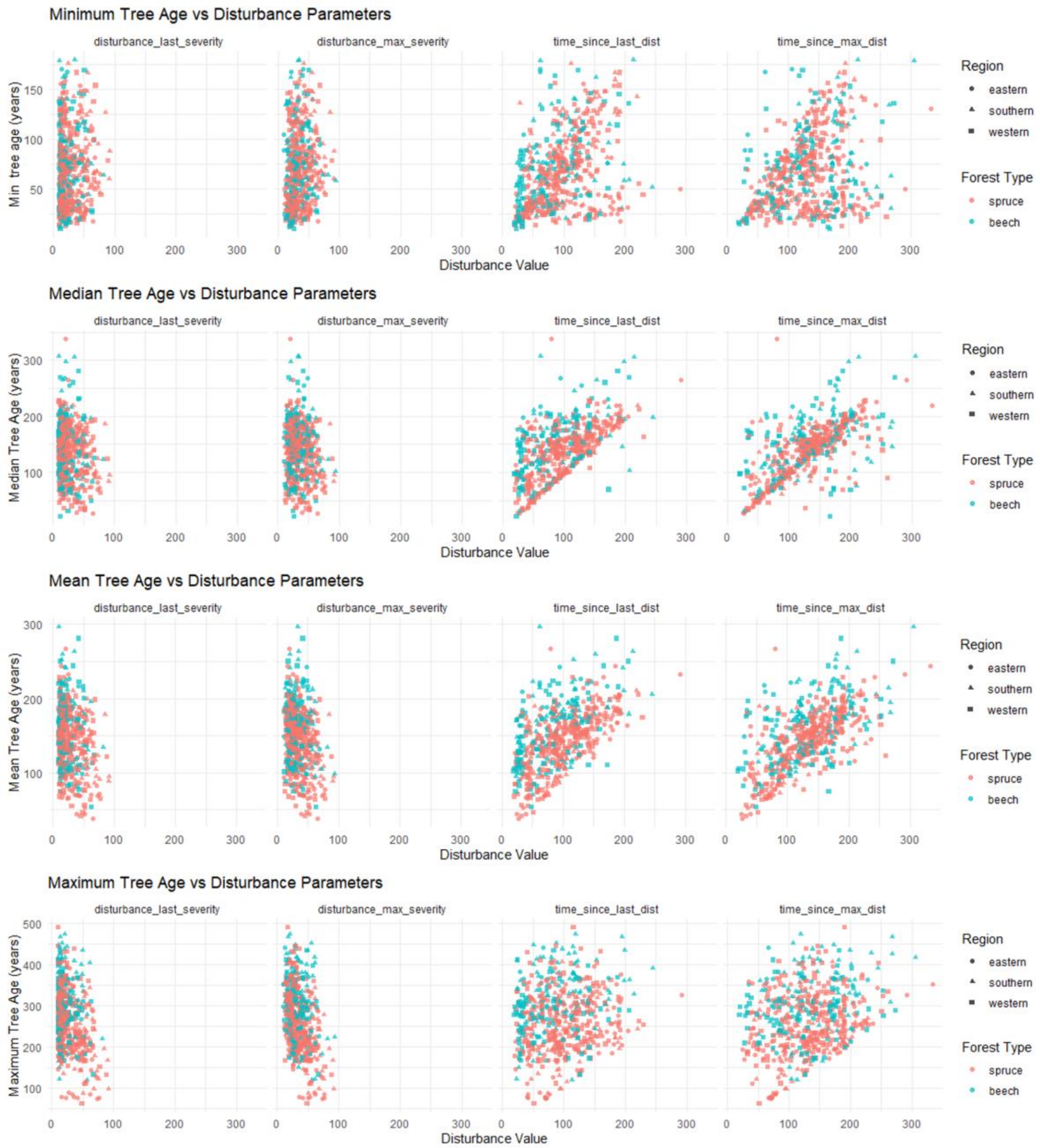

Figure C1. Relationship between age parameters and disturbance factors.

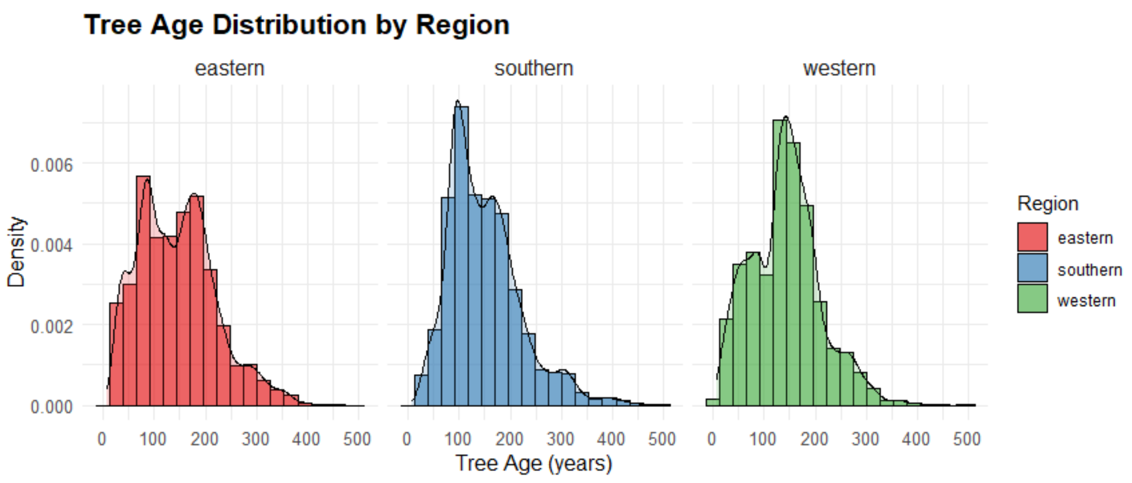

Figure C2. Tree age distribution across different regions (eastern, southern, and western) of the study area. The density plots illustrate the variation in tree age, with distinct patterns observed for each region, reflecting differences in forest structure and disturbance history.

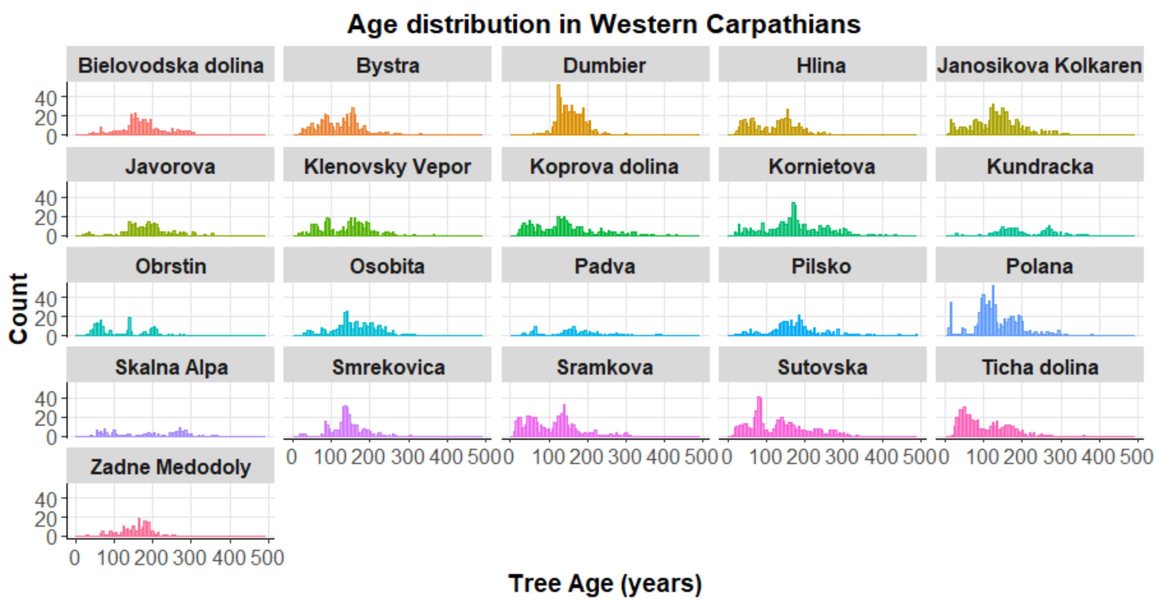

Figure C3. Stand-level age distributions across various sites in the Western Carpathians (Slovakia).

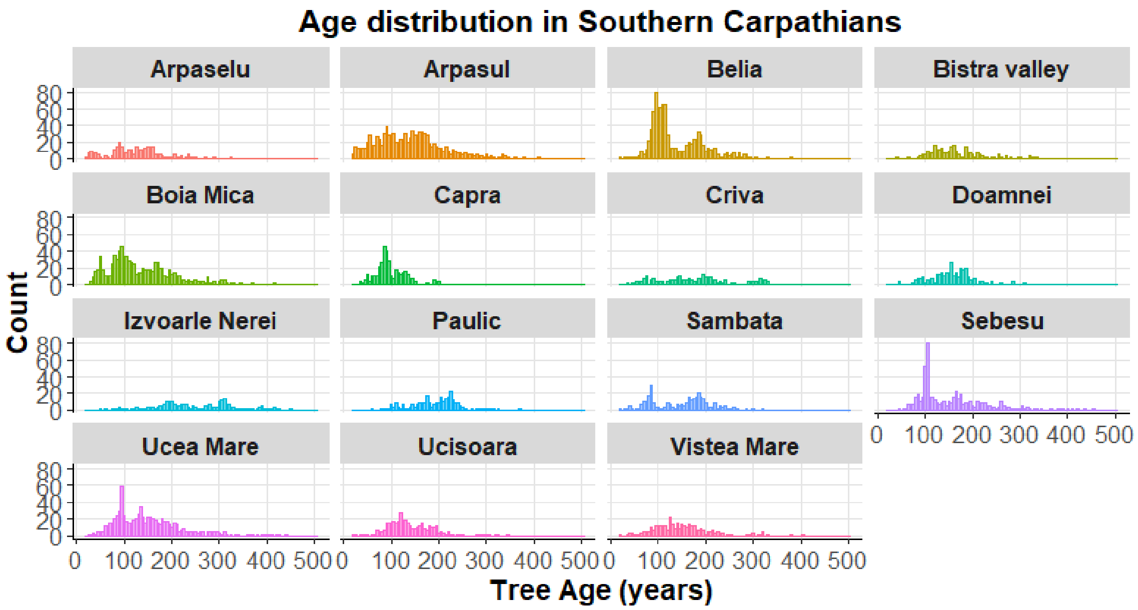

Figure C4. Stand-level age distributions across various sites in the Southern Carpathians (Romania).

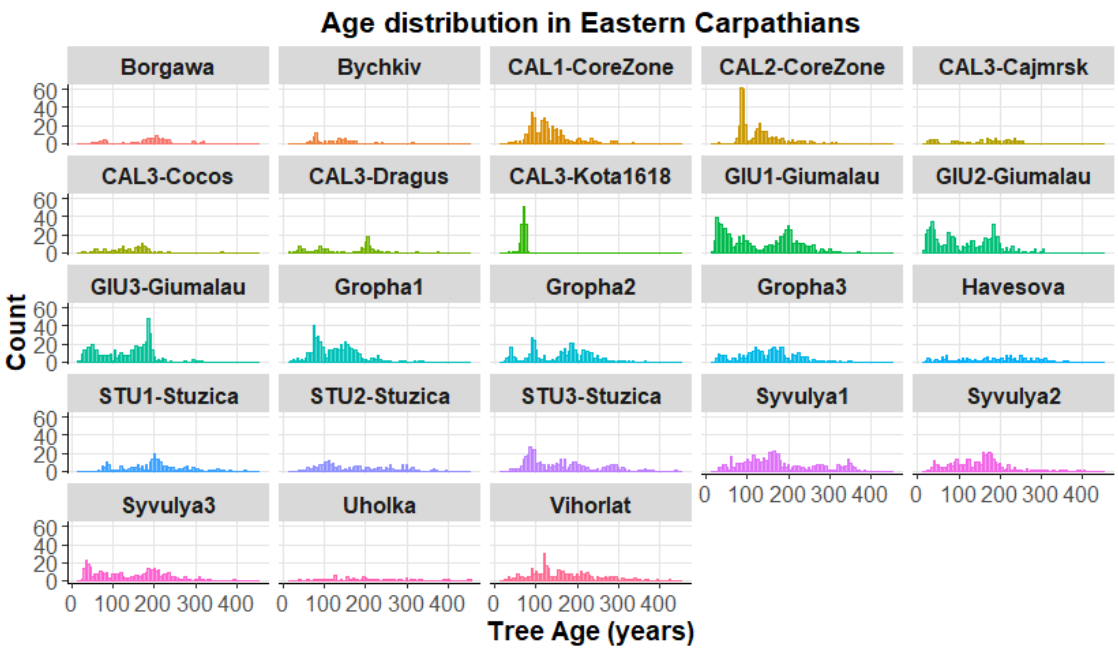

Figure C5. Stand-level age distributions across various sites in the Eastern Carpathians (Ukraine).

Table C1. Forest structure of the study area in the Carpathians. This table presents the stand name, country, number of plots, number of trees, diameter at breast height (cm; minimum, maximum, mean, median, 25 quartile, and 75 quartile), and mean altitude (m) for each stand.

	stand	country	nb_plot	nb_trees	DBHMIN	DBHMAX	DBHMEAN	DBH25Q	DBHMEDIAN	DBH75Q	ALTITUDEMEAN
1	Arpasul	Romania	14	790	6	108.7	25.06519	10.4	18.05	33.2	1127.477
2	Belia	Romania	14	654	6	108.4	31.18364	13.525	26	45.55	1229.495
3	Bistra valley	Romania	11	505	6.1	92.6	30.42495	15.1	24.7	41	1062.137
4	Boia Mica	Romania	12	706	6	132	26.34518	10.1	18.45	35.475	1201.441
5	Criva	Romania	13	645	6	105	29.33101	11.8	21.5	42.2	1013.957
6	Havesova	Slovakia	2	137	6	81.6	20.21314	7.6	10.4	22.7	624.365
7	Izvoarle Nerei	Romania	9	365	6	117.5	34.80658	12	25.8	54.3	1107.948
8	Klenovsky Vepor	Slovakia	12	399	6	103	31.63233	9.75	24.1	48.25	1194.346
9	Kornietova	Slovakia	13	673	6	108	25.78796	9.2	17.6	36.8	1133.744
10	Kundracka	Slovakia	7	229	6.1	90.7	37.82271	22.5	36.2	49.3	1089.45
11	Obrstin	Slovakia	5	219	6.2	115.5	29.4621	11.05	21.8	43.3	902.3242
12	Padva	Slovakia	7	279	6.2	88.2	27.54158	13	24.8	38.7	1176.43
13	Paulic	Romania	6	254	6	94.7	32.94606	15.025	29.9	47.45	1015.177
14	Polana	Slovakia	16	699	6	111.1	27.53805	10.2	21.5	38.1	1132.572
15	Sebesu	Romania	13	581	6	107.5	31.5062	16.6	27.6	42	1162.324
16	Skalna Alpa	Slovakia	6	170	6.5	114.2	35.29824	14.025	29.4	50.25	1133.806
17	Sramkova	Slovakia	14	837	6	101.5	22.0951	9	14.6	28.9	1036.576

18	STU1-Stuzica	Slovakia	11	518	6	103.5	26.78475	9.4	17.6	39.8	930.4402
19	STU2-Stuzica	Slovakia	9	508	6.1	100.3	25.26949	9.875	16.05	34.825	962.563
20	STU3-Stuzica	Slovakia	13	813	6	88.9	25.95314	11.6	20.2	35	971.0713
21	Sutovska	Slovakia	13	777	6	106.5	24.05817	9.6	16.4	32.8	1037.737
22	Ucea Mare	Romania	7	387	6	103.3	26.41628	9.8	16.9	38.1	999.6615
23	Vihorlat	Slovakia	11	610	6	104.6	24.44377	9.1	15.95	32.75	800.1557
			238	11,755							

Table C2. Stand-Level Information Summary: forest type, tree size distribution (weibull shape), and disturbance parameters. Includes: last disturbance severity, maximum disturbance severity, time since last disturbance, time since maximum disturbance. Note: SD denotes standard deviation.

	stand	**foresttype**	**standshort**	**country**	**Weibul_shape**	**dist_last_sev**	**dist_max_sev**	**time_since_last**	**time_since_max**	**altitude_m**	**slope**
1	Arpasul	beech	ARP	Romania	1.45 (0.15)	17.00 (12.94)	27.64 (11.55)	69.79 (43.07)	132.57 (59.93)	1,126.29 (63.99)	32.00 (4.76)
2	Belia	beech	BEL	Romania	1.64 (0.26)	37.64 (16.39)	42.21 (11.96)	106.43 (28.24)	128.50 (38.59)	1,236.93 (40.38)	10; (NA)
3	Bistra valley	beech	BIS	Romania	1.72 (0.16)	19.73 (8.59)	29.18 (9.26)	102.09 (29.41)	129.64 (29.50)	1,059.27 (70.81)	35.73 (4.15)
4	Boia Mica	beech	BOI	Romania	1.41 (0.28)	21.67 (12.12)	35.58 (14.25)	91.75 (49.27)	136.50 (43.03)	1,200.42 (46.90)	34.83 (6.19)

5	Criva	beech	CRI	Romania	1.55 (0.23)	18.46 (6.46)	21.77 (7.26)	101.92 (40.86)	135.69 (59.85)	1,006.62 (93.16)	12; (NA)
6	Havesova	beech	HAV	Slovakia	1.21 (0.08)	20.50 (6.36)	20.50 (6.36)	110.50 (40.31)	110.50 (40.31)	626.50 (9.19)	13.50 (0.71)
7	Izvoarle Nerei	beech	IZV	Romania	1.47 (0.27)	19.11 (7.72)	26.89 (6.88)	181.44 (74.49)	238.44 (55.14)	1,109.22 (74.71)	23.11 (7.36)
8	Klenovsky Vepor	beech	VEP	Slovakia	1.62 (0.50)	17.17 (8.83)	26.50 (8.84)	87.67 (61.96)	157.42 (40.40)	1,190.67 (56.51)	8; (NA)
9	Kornietova	beech	KOR	Slovakia	1.47 (0.31)	15.38 (6.79)	31.31 (16.79)	63.92 (45.87)	115.92 (65.57)	1,127.54 (79.17)	30.31 (6.64)
10	Kundracka	beech	KUN	Slovakia	2.53 (0.60)	29.00 (16.38)	32.43 (13.65)	122.43 (53.10)	161.57 (68.03)	1,091.43 (70.40)	33.14 (6.36)
11	Obrstin	beech	OBR	Slovakia	1.48 (0.25)	27.40 (21.24)	42.40 (15.32)	60.00 (27.63)	125.80 (84.53)	895.20 (52.75)	31.80 (4.09)
12	Padva	beech	PAD	Slovakia	2.17 (0.64)	18.71 (8.79)	25.71 (7.57)	73.57 (50.81)	122.71 (56.76)	1,166.43 (69.17)	28.43 (5.41)
13	Paulic	beech	PAU	Romania	1.82 (0.41)	26.67 (8.66)	33.50 (13.22)	138.50 (23.76)	152.00 (32.04)	1,019.50 (59.70)	33.67 (3.78)
14	Polana	beech	POL	Slovakia	2.00 (0.64)	31.69 (18.70)	38.94 (13.80)	88.50 (45.16)	113.06 (36.94)	1,151.56 (76.00)	15; (NA)
15	Sebesu	beech	SEB	Romania	1.98 (0.44)	27.77 (21.83)	48.77 (24.87)	89.38 (54.17)	147.31 (53.68)	1,187.62 (109.97)	33.38 (5.47)
16	Skalna Alpa	beech	SKA	Slovakia	1.80 (0.51)	13.83 (7.00)	20.67 (4.08)	119.83 (82.99)	202.50 (90.99)	1,140.83 (41.06)	26.00 (5.25)
17	Sramkova	beech	SRA	Slovakia	1.63 (0.50)	19.64 (11.20)	29.50 (8.93)	45.07 (26.95)	116.57 (54.80)	1,048.64 (62.52)	32.57 (3.67)
18	STU1-Stuzica	beech	STU	Slovakia	1.45 (0.25)	15.45 (5.32)	27.27 (7.25)	70.73 (36.91)	115.45 (47.44)	914.09 (67.14)	17.55 (5.15)
19	STU2-Stuzica	beech	STU	Slovakia	1.40 (0.24)	19.89 (11.95)	26.11 (11.33)	79.00 (48.51)	131.56 (71.55)	951.67 (83.64)	8; (NA)
20	STU3-Stuzica	beech	STU	Slovakia	1.64 (0.46)	22.15 (12.50)	30.92 (13.76)	82.00 (43.37)	118.85 (60.31)	967.08 (52.15)	27.69 (4.59)
2	Sutovska	beech	SUT	Slovak	1.56 (0.30)	24.38	30.46	82.62	118.46	1,012.00	32.92

1				ia		(15.37)	(15.85)	(48.00)	(67.56)	(128.56)	(4.61)
2				Roman		19.43	27.29	91.00	145.29		33.14
2	Ucea Mare	beech	UCE	ia	1.57 (0.36)	(8.75)	(8.46)	(34.89)	(56.22)	997.43 (62.16)	(3.08)
2				Slovak		19.09	32.27	71.45	111.91	799.27	10; (
3	Vihorlat	beech	VIH	ia	1.36 (0.20)	(9.36)	(18.14)	(35.60)	(48.28)	(103.72)	NA)