Czech University of Life Sciences in Prague

Faculty of Forestry and Wood Sciences

Reconstruction of the growth dynamics of primary beech-dominated forests in Central Europe using dendroecological methods

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CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Forestry and Wood Sciences

Ph.D. THESIS ASSIGNMENT

Ing. Michal Frankovič

Forestry Engineering
Forest Biology

Thesis title

Reconstruction of the growth dynamics of primary beech-dominated forests in Central Europe using dendroecological methods

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Objectives of thesis

Our main objectives were to reconstruct the natural disturbance regime in mixed beech-fir forests – one of the most dominant forest vegetation types in Europe – in the Carpathian Mountains, with aims to describe how historical processes influence forest dynamics and structure. Further, we evaluated disturbance synchronicity in time and disturbance synchronicity – species composition relationship.
i) Estimate the range of past disturbance activity, as well as quantitatively describe the spatial and temporal variation in disturbance frequency and severity across the study stands.
ii) Understand which type of disturbance regime – gap dynamics, intermediate-severity or high-severity disturbance regime – most affects the study plots on the spatial scale.
iii) Determine the difference in the temporal and spatial extent of the disturbance regimes in the Western and Eastern Carpathian regions.
iv) Explain the species-specific relationships between tree species composition and the temporal and spatial extent of natural disturbances.

Methodology

Natural disturbances are critical factors in forming forest ecosystem structure and dynamics. Investigation of disturbance regimes' spatial and temporal extent is critical for understanding forest structural heterogeneity, biodiversity habitats and development stages. Quantifying disturbance regimes is, therefore, imperative for the appropriate management of forests and protected areas. However, natural disturbance regimes have rarely been assessed using dendrochronological methods on a regional scale across primary mixed beech-fir forest stands. To study the natural disturbance regimes of beech-dominated mixed-forest stands, we established numerous permanent study plots with an area of 0.15 ha across primary forests in the Carpathian Mountains, which still contain large areas of primary forest. We reconstructed the plot and stand-level disturbance history using a tree-ring-based approach. The temporal synchronicity of disturbance events was then evaluated by delineating stand-level disturbance events using a kernel density function and detecting plot-level disturbances with severities greater than 10 %. The results obtained from the chronologies showed substantial variability in time and space.

The proposed extent of the thesis

100

Keywords

Natural disturbances, Dendroecology, Disturbance regime, Beech-dominated forest, Natural dynamics, Primary forest, Species composition, Synchronization

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Recommended information sources

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Expected date

2023/24 WS – FFWS – State Doctoral Examinations

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I hereby confirm that this PhD. thesis "Reconstruction of the growth dynamics of primary beech dominated forests in Central Europe using dendroecological methods" was elaborated independently with the usage of quoted literature and based on consultations and recommendations of my supervisor.

I agree with publishing this PhD. thesis according to Czech law n. 111/1998 Sb. about the universities in its current valid wording.

December 25th, 2023, Prague

Acknowledgements

I would like to say deep thank you to all members of the Department of Forest Ecology, all members of the dendrolaboratory and members of the Faculty of Forestry and Wood Sciences who contributed to the processing of data collection, analysis, research in the field, data analysis, text writing, and giving advice which contributed to the realisation of publishing and discovering the science behind unique ecosystems of temperate beech dominated primary forests. This would not be possible without supervisor prof. Ing. Miroslav Svoboda, Ph.D., thanks to whom I could be a part of such an amazing research project.

Abstract

Natural disturbances are critical factors in forming forest ecosystem structure and dynamics. Investigation of disturbance regimes' spatial and temporal extent is critical for understanding forest structural heterogeneity, biodiversity habitats and development stages. Quantifying disturbance regimes is, therefore, imperative for the appropriate management of forests and protected areas. However, natural disturbance regimes have rarely been assessed using dendrochronological methods on a regional scale across primary mixed beech-fir forest stands. To study the natural disturbance regimes of beech-dominated mixed-forest stands, we established numerous permanent study plots with an area of 0.15 ha across primary forests in the Carpathian Mountains, which still contain large areas of primary forest. We reconstructed the plot and stand-level disturbance history using a tree-ring-based approach. The temporal synchronicity of disturbance events was then evaluated by delineating stand-level disturbance events using a kernel density function and detecting plot-level disturbances with severities greater than 10 %. The results obtained from the chronologies showed substantial variability in time and space.

Our main objectives were to reconstruct the natural disturbance regime in mixed beech-fir forests - one of the most dominant forest vegetation types in Europe - in the Carpathian Mountains, with aims to describe how historical processes influence forest dynamics and structure. Further, we evaluated disturbance synchronicity in time and disturbance synchronicity – species composition relationship.

We aimed to:

i) Estimate the range of past disturbance activity, as well as quantitatively describe the spatial and temporal variation in disturbance frequency and severity across the study stands.

ii) Understand which type of disturbance regime - gap dynamics, intermediate-severity or high-severity disturbance regime - most affects the study plots on the spatial scale.

iii) Determine the difference in the temporal and spatial extent of the disturbance regimes in the Western and Eastern Carpathian regions.

iv) Explain the species-specific relationships between tree species composition and the temporal and spatial extent of natural disturbances.

Our results are:

i) A detailed description of the past 250 years long disturbance history, where a wide variation of disturbance events was found. Disturbances affected several plots simultaneously over short periods, thus creating a coarse-grained forest structure. The disturbance regime was characterised by substantial variability in time and space, with fluctuation, especially in the mid-19th century. Low and moderate-severity plot-level disturbance events were most common, but high- and extremely high-severity plot-level disturbance events also occurred. The observed spatial and temporal variability suggests that the beech-dominated forests were primarily driven by mixed-severity disturbance regimes, with windstorms as the main disturbance agent.

ii) Low- and moderate-severity disturbances prevailed, but the occurrence of plot-level high- and very-high severity disturbances were also documented. Disturbances affected several plots simultaneously over short periods, thus creating a coarse-grained forest structure.

iii) We found significantly higher synchronicity of disturbances within the forests of the Western Carpathians compared to the Eastern Carpathians, where tree species richness is higher than in the Eastern Carpathians. No significant differences in patch sizes were detected between the Western and Eastern Carpathians. The size of patches was more heterogeneous in the East than in the West.

iv) We found significantly higher synchronicity of disturbances in forests where the species composition was richer – in the Western Carpathians, with the suggestion that the mixture of spruces as a gapmaker had a significant effect on the disturbance pattern. Moreover, the GLM of the species composition – disturbance synchronicity relation showed a strong dependence of synchronicity on the number of tree species per stand. The results contradict the general assumption that mixed forests have higher resilience, because of the significant mixture of spruces.

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1. Introduction

Primary forests are key biodiversity hotspots and serve as model ecosystems for studying natural disturbance regimes and effects of climate change on forest ecosystems (Kozák et al. 2018; Mikoláš et al. 2019). Because of historical land use and civilisation expansion in Europe, primary forests have become fragmented, and rare and therefore now have high conservation value. The area of primary forests is rapidly decreasing around the world, with other forested landscapes heavily influenced by intensive forest management (Hansen et al. 2013).

As primary forests are undisturbed by direct anthropogenic influences, natural stand dynamics occur uninterrupted, including natural disturbance regimes. We may define disturbance following the general definition offered by White and Pickett (1985) which describes disturbance as "any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability or the physical environment.'' Because natural disturbances are the key processes shaping forest ecosystems, primary forests are characterized by high vertical and horizontal structural diversity and complexity (Meigs et al. 2017). The structure and natural dynamics of temperate primary forests of Central Europe are significantly influenced by natural disturbances. The traditional concept describes forest development as the different cohorts of trees passing through several development stages in a cyclical pattern from the early growth stage, followed by ageing and mortality, and then return to regeneration. Disturbances such as windstorms, insect outbreaks and others can interrupt this cyclical pattern and allow younger growth cohorts to regenerate alongside mature trees and can create a mosaic of different age and size classes. Quantifying disturbance patterns such as size, shape, severity, frequency, return interval and intensity in forest stands is a key challenge for ecological research. Morover, when the research is conducted in primary and natural forests, the data about disturbance regimes could be referencing value for appropriate forest management in natural forestry, protected areas and also in commercial harvesting processes.

Disturbance events can differ in size, frequency and severity and their variations can be high, ranging from background mortality to catastrophic high-severity disturbances. Such scenarios also occur in beech-fir forests. (Frelich, 2002; Seidl et al. 2020). The small- or fine-scale dynamics of disturbance which is creating canopy gaps in forests seem to be crucial processes shaping stand structure and trajectories of development in forests, and it seems crucial for the beech forests (Pickett and White, 1985; Hobi et al., 2015). Larger-scale disturbances also may occur in forests but to a lesser frequency and depending on local environmental factors and atmospheric conditions (Senf & Seidl 2018; Pettit et al. 2021). In temperate forests in Central Europe, higher severity disturbances with a bigger area of canopy removals are likely connected to windstorms and thunderstorms and can result in more than 40% canopy area removal on the given study plot (Nagel et al., 2014). Some forest ecosystems are shaped by disturbances that create a mixture of gap dynamics, and intermediate and high-severity disturbance effects on forests. When they are combined, it can result in a mixed-severity disturbance regime, which was mainly discussed in connection with forest fire as the main disturbance agent in forest ecosystems (Perry et al., 2011; Halofsky et al., 2011; Trotsiuk et al. 2014; Frankovič et al. 2021). A mixed-severity disturbance regime appears to be a natural phenomenon central to the formation of forest structures in temperate mountain forests in Europe and enhances structural diversity and biodiversity (Mikoláš et al. 2019; Meigs et al. 2017; Kulakowski et al.,2017; Kozák et al., 2021; Mikoláš et. al. 2021).

The description of the natural disturbance regime in primary mountain Norway spruce (*Picea abies* (L.) Karst.) forests shows that historical disturbances in the Carpathians varied from low- to high-severity, including stand-replacing disturbances of tens of hectares in size. In recent decades, there have been widespread and severe disturbances caused by wind and substantial bark beetle outbreaks in Central Europe (*Ips typographus* L.) (Lausch et al., 2013). Complex spatiotemporal disturbance patterns often affected large areas, were variable in spatial and temporal ways, and sharp borders of gaps and patcher were missing (Svoboda et al. 2012; Janda et al. 2014). Therefore, the overall discussion about the disturbance regime of mountain spruce forests showed that past disturbance patterns across larger regions documented a complex mix of low, intermediate, and rare high-severity disturbance events consisting of numerous disturbance events. They are driven by different disturbance agents and can create combinations of small and large patches affecting larger or smaller areas (Perry et al. 2011, Halofsky et al. 2011; Trotsiuk et al. 2014; Frankovič et al. 2021). When they combine, they can result in mixed-severity disturbance regimes (Perry et al., 2011). It seems it is the best description of the spatially and temporally complex processes in the mountain forests which lead to the diverse forest structure with a predominance of intermediate severity events (Svoboda et al., 2014; Trotsiuk et al., 2014). In temperate coniferous forests, complex spatiotemporal patterns of different disturbance severities have been observed, which creates high heterogeneity and complexity in forest structure (Janda et al., 2017).

A number of studies have previously investigated natural disturbances and the dynamics of beech-dominated forests in Europe (Nagel and Svoboda, 2008; Trotsiuk et al. 2012; Feldmann et al., 2018; Orman et al.,2018; Frankovič et al., 2021). Past studies described complex spatiotemporal patterns of disturbance severities, which create high heterogeneity and complexity in forest structure (Trotsiuk et al. 2014; Janda et al., 2017).

Studying complicated disturbances, mortality, and regeneration processes is indeed necessary to capture the temporal extent of the disturbances. This can be conducted by using dendrochronological analyses of tree core samples to study growth patterns in the past.

Quantitative reconstructions of historical processes can help us better understand the range of disturbance severity and frequency that might occur in different forest ecosystems. The ability to recognise the tolerance and resiliency capacity of forests is crucial in time of global climate change, which increases the severity of disturbances (Kulakowski et al., 2017; Seid et al. 2020).

Studying primary forest ecosystems can provide the reference values for understanding the effect of global climate change on forest ecosystems, forest growth, and development patterns. It can be used as a guide for forest management to mimic natural disturbance and potentially mitigate the effects of global change in the forests.

2. Literature review

2.1 Primary forests definitions and distribution

The term "primary forest" refers to naturally regenerated forests of native species where there are no signs of anthropogenic activity and where the ecological processes are not dramatically altered.

Primary forest ecosystems with high naturalness, native species, undisturbed ecological natural processes, and without visible and known anthropogenic activities can be defined as primary forest sites (FAO, 2015; Buchwald, 2005).

FAO (2015) defined unique characteristics should have primary forests:

- Natural forest dynamics, such as natural tree species composition, the occurrence of dead wood, natural age structure, and natural regeneration processes;
- sufficient geographic extent to maintain “natural characteristics”
- the absence of significant human intervention, or in the case of some, the last significant human intervention, should have been long enough ago to have allowed the natural processes and species composition to have been re-established.

Various analogous terms, such as "*primary,*" *"frontier*," "*virgin*," and *"old growth*," are used to describe forests whose composition and structure largely reflect natural processes. "Primary forest" is the preferred terminology at the intergovernmental level (Kormos et al., 2017). A frequent and important term used is “*old-growth forest,*” which has a diverse meaning and depends on geographical area. Generally, it refers to the developmental stage of the forest, which consists of old trees. However, it can also be a secondary forest, which is often a formerly managed stand which was left for spontaneous development (Vandekerkhove et al., 2022). The term old growth forests is especially related to Western European forest reserves. However, the structural and natural characteristics such as deadwood, tree species composition, diameter at breast height (DBH) diversity, and overall structural diversity remained strongly altered and differed from primary forests (Sabatini et al., 2028). However, there are no doubts about the importance and promotion of such forests in Europe and around the globe.

The terms such as "*virgin*" , "*untouched*," and intact or "*undisturbed by man*" may also appear as synonyms for primary forest in literature (Veen et al., 2010; Parviainen et al., 2005). However, the situation is more complicated, and these words may also describe the other developmental stages or some intensity of land use. Many traditionally viewed forested areas considered as primary forests, or untouched forests by man, have been shaped by the native inhabitants and local tribes for a long time. Such areas have more character as the agroforestry system with low-intensity management. Thus, the situation is more complicated in the areas where humans are an integral part of the local ecosystem. There may be a similar situation in densely populated Europe, especially in the past. It is difficult to totally exclude some human activity in some of the forest ecosystems; probably all of the forests and ecosystems were subject to some more or less intensive use. Despite that, there is a probability of the occurrence of such fragments of primary forests in Central and Southeastern Europe, especially in the mountains, which remained untouched until today. Such areas are also the subject of the study of this dissertation thesis.

Thus, it is possible to exclude direct human influence only when the extent was so intensive to identify changes in forest structure. However, due to human-induced climate change by shifting natural forest composition, indirect anthropogenic influence is unfortunately globally presented in almost every ecosystem. Together with climate change, it is also changed an integral part of natural forests - the natural disturbance regime. Thus, intact forest cover is rare in Europe, and it is essential to define and characterise the locations and establish accurate protection of such areas.

The word „*intactness*" is commonly used in connection with primary forest topics worldwide. An area of current forest that contains an uninterrupted expanse of natural ecosystems that have not been damaged and fragmented by human land use and industrial activity is described as an intact forest landscape (IFL) (Potapov et al., 2008). No size criterion can be used to distinguish between intact and fragmented forest landscapes, much like in a primary forest in general. Size thresholds can vary based on the purpose of the study or the climatic zone, local conditions and landscape, and in the context of land use history and local environmental gradients. An intact forest landscape (IFL) size threshold of 50,000 ha was used for global reconnaissance assessments (Potapov et al., 2008). However, such thresholds can be used only in the case of spatial studies in boreal and tropical forests. Only 3% of the primary forest in the temperate forest zone is found in blocks larger than 50,000 hectares, highlighting how extensively these forests have been removed (Lindenmayer et al., 2012).

With primary temperate forest fragments in Europe, structural intactness is important. It refers to the vertical structure of vegetation regarding canopy height, overstory tree layers, canopy gaps, structure diversity and composition. In horizontal structure, the old and young, big and small, are all trees, which are essential components of the intact forest cover in different spatial scales. The horizontal structure ranges from small canopy openings to consequences of high-severity disturbances in the forest, creating large canopy gaps with regenerating tree layers. The structure is mostly continuous across the landscape, creating a mosaic of successional stages depending on the local natural disturbance regime and other ecosystem types. The mosaic of intact forest cover is critical in an area of heavily disturbed landscape. Its forest matrix of intact forests improves options for the restoration of the forests and can be suitable for refuges for endangered species (Chazdon, 2003). However, in the case of temperate primary forests, there is a small possibility of the occurrence of intact forest cover in such a biome. Europe is significantly forested, but most of the forests are heavily influenced by anthropogenic activities, and the area of primary forests is much less.

Forest ecosystems naturally cover significant areas of the Earth's terrestrial surface. However, forest cover itself has been rapidly shrinking for the last 300 years, mainly due to human activities. Approximately 35% of forest cover has been lost, and actual forest cover is estimated to be approximately 4.06 billion hectares, around 31% of land surface (FAO, 2020). Some of this area was changed to some extent, affecting many developed and exploited areas - for example, Europe, where most of the forest cover is altered.

Due to the global clearing of forested land for agriculture or active management, primary forests are becoming increasingly rare and fragmented (Potapov et al., 2017). Approximately 57% of forests have been degraded by human development, such as logging, road building and agriculture sites (FAO, 2012), leading to only 1.3 billion hectares of the planet's current forest cover being primary forests (32%).

Because of notable fragmentation in the numerous regions around the globe, primary forests are also ecologically important (Sabatini et al., 2018). In such regions, primary forests may serve as refuges or shelters for propagules for rare species sensitive to anthropogenic disturbances and endangered species. (Paillet et al., 2015). Such anthropogenically undisturbed ecosystems can serve as the baseline for understanding natural disturbance and successional dynamics in the global climate change context. Understanding the baselines for providing ecosystem services under unmanaged conditions, including carbon stocks and sequestration, is especially important when losing the last defragmented areas of the primary forests.

Approximately 34% of yearly anthropogenic carbon emissions are captured by forest ecosystems, making them significant terrestrial carbon sinks. Through undamaged forest diversity and structure, which is vertically and horizontally diverse, it is an important biodiversity habitat for a species with complex habitat requirements (Mikoláš et al., 2017). However, long-term forest functionality and integrity are heavily dependent on biodiversity. Both are necessary to mitigate global climate change in the context of the effectiveness of carbon storage in the functioning ecosystem (Parrish et al. 2003).

The main drivers of a dynamic ecosystem should be natural disturbances of various scales and developmental pathways, which are heterogeneous and diverse, which can lead to competitive interactions driving spatial patterns of mortality and recruitment, and all of this is the result of local natural conditions (Donato et al., 2012).

Both, spruce- and beech-dominated primary forests in the Carpathians are typically characterised by vertically and horizontally heterogeneous structures (Commarmot et al., 2005, Rodrigo et al., 2022). The structural variability required to maintain high biodiversity is generally created by natural disturbances, which cause significant fluctuations in the mortality of trees and can subsequently release carbon because of the subsequent decomposition of the trees after disturbance. Whether forests can simultaneously sustain both high carbon and high biodiversity is still poorly studied. Thanks to high structural heterogeneity and spatial variability, the primary forest can provide an environment for high levels of biodiversity and carbon storage variables (Keeton, 2018).

Human-dominated regions in Europe faced historical deforestation and forest exploitation, which is the main reason for the shrinking of the area of primary forests and their elimination. (Potapov et al., 2017). In the last century, the area of primary forests was significantly reduced (Hansen et al. 2013). Most of the forests are now mainly composed of semi-natural forests and managed stands, and the area of forests without human intervention accounts for only 4% of the total, approximately 300 00 ha (Parviainen, 2005; FOREST EUROPE, 2015).

Primary forests in Europe account for only 4% of the total forest area (FOREST EUROPE, 2015), and primary forest sites are severely fragmented. In Europe, no intact forest landscapes with more than 500 square kilometres exist except in the European part of Russia and the boreal part of northern Europe (Potapov et al., 2017). Some Eastern and South-eastern European countries contain bigger or smaller fragments of primary forests. These remains are very often fragmented; localities are unprotected and are disappearing. Other European countries may still contain relatively large areas of primary forests, especially in extensive areas with unmanaged old-growth forests in a mountain and remote areas, especially in eastern, south-eastern, and northern Europe (Veen et al., 2010, Sabatini et al., 2018). The general trend in Europe is an increase in the number of primary forest areas from the west to the east and from the south to the north. Most of the primary forests are in the Carpathians ecoregion (0.16 Mha), Finland (0.9 Mha), and the Balkans, especially in the Dinaric Mountains ecoregion (0.08 Mha) (Sabatini et al., 2018). The Carpathian ecoregion is the second-largest mountain range in Europe (210,000 km^2) and stretches across eight European countries. Due to the remote localities and deep and steep valleys, mountain ridges remained mainly intact at that time. The Dinaric Mountains ecoregion is approximately 700 km in length and 200 km in width and crosses 9 European countries.

Nevertheless, there is a very long history of human influence, and the forest cover has almost completely changed since that time because of pasture, metal mining, and ship construction; the last of the actual primary forests are scattered in the most isolated places throughout the Dinaric Mountains. Thus, this area's largest continuous old-growth extensive areas are found in the Carpathian Mountains region with continuous forest ecosystems (Sabatini et al., 2018). A small amount of primary forest in Europe is expected, for example, in the Mediterranean, considering the historically high population density and long land use history.

The spatial distribution of beech primary forest is closely related to the history of the post-glacial spreading and following human disturbance-related effects. For the last 1 million years, European beech survived unfavourable climatic conditions during the phases of ice ages in the periods of the ice gaps in the refuge areas in the southern parts of Europe. The occurrence of the beeches in such areas was possible thanks to specific natural conditions in steep mountains hosting high environmental heterogeneity and creating good conditions for a „Stau Effect” (intercepting moisture from the sea). After the last ice age (approximately 11,000 years ago), beech forests started expanding from the refugia in Southern Europe to the surrounding areas. Subsequently, they covered much of the European continent (Magri et al., 2006). The process of expansion included temporal and spatial parameters. Spread of the

Beech entered the formerly mixed-deciduous forests created by an aerial recolonisation of Oak, Hazel, Lime, and Hornbeam. On lowlands, it created mono-dominant forests, and in higher elevations, it started to be mixed with Spruce (*Picea abies* L.*)* and Fir (*Abies alba,* Mill*)*, especially on the mountain belts with other vegetation types. In the still ongoing process of beech migration, numerous plant communities have been created in beech forests, and these ecosystems are occupying largely different environments. A high diversity of beech forest communities was formed because of the various climatic conditions in various parts of Europe, including the humid Atlantic climate in the west and the dry Continental climate in the east, as well as the summer dry, warm Mediterranean climate in the south and the cold Baltic climate in the north. Together with the different species pool available in the different floristic regions and with the different tempo of migration of other species after the ice age, it formed a high diversity of beech forest communities.

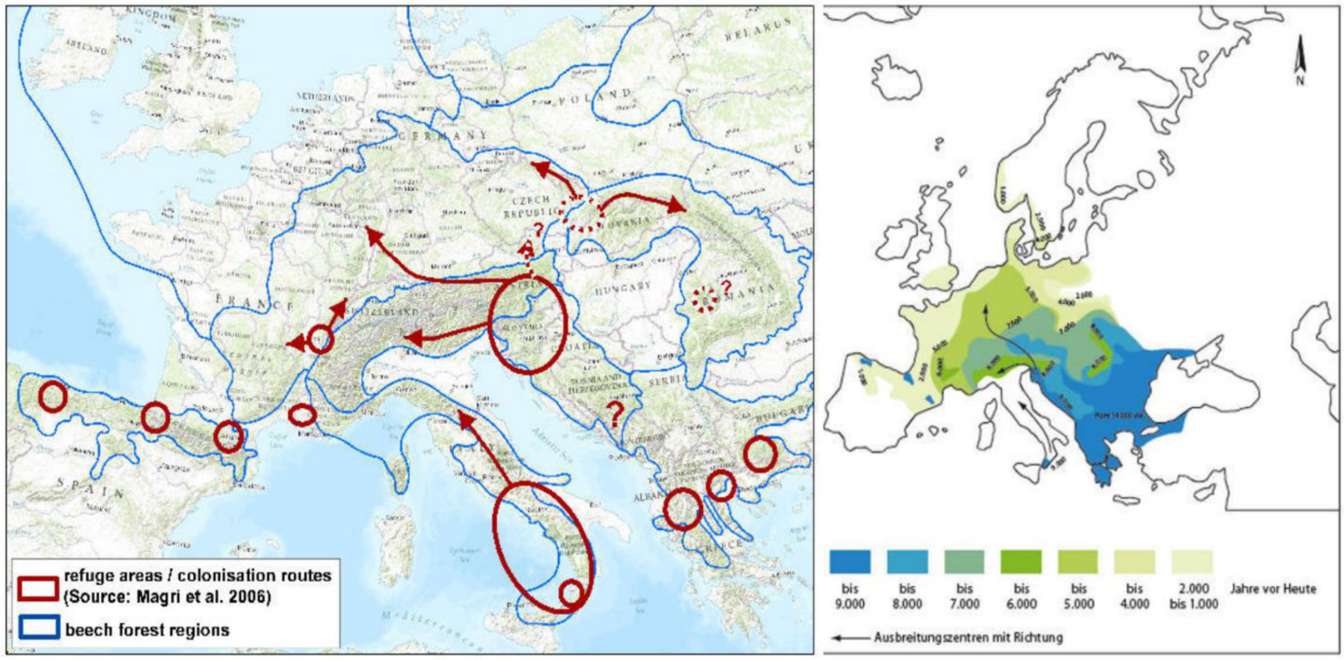

Figure 1: Refuge areas and postglacial expansion paths of European beech - left: E.C.O. Institute of Ecology, right: LEIBNITZ INSTITUT FÜR LÄNDERKUNDE, both modified according to Magri et al. 2006 (Kirchmeir et al. 2016).

After the last ice age, approximately 10,000 years ago, the postglacial expansion of forests altered the development of many ecological subtypes of beech forests, and it was mainly a natural and evolutionary process and was not significantly affected by humans.

Forestry and other human disturbances altered the European landscape significantly in the last 1000 years, primarily through the Industrial Revolution.

Globally, the distribution of primary forests depends mainly on rainfall to maintain canopy trees, and primary forests can be found in all climates, including boreal, temperate and tropical regions. Approximately 98% of the total area of primary forests occurs in 25 countries around the globe, and in the year 2015 75% of the area of the primary forests reported to occur in Brazil, Canada, the Russian Federation, Indonesia, the Democratic Republic of the Congo, Peru and United States (Morales-Hidalgo et al.,2015). Thus, the distribution of primary forests is highly asymmetric around the world, and the context of what is primary forest should also depends on the context of a given study and the spatial scale of the study (www.remoteforests.org, 2022)

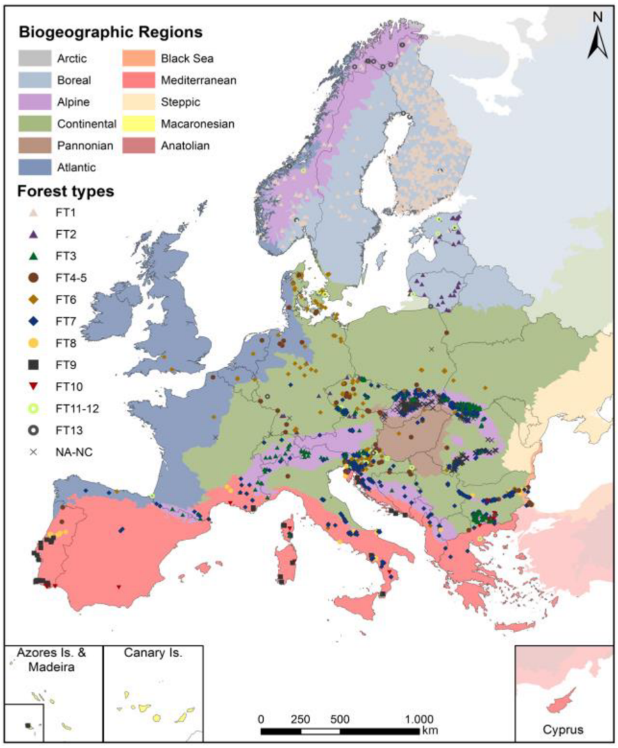

Figure 2: Spatial distribution of primary forests patches in Europe (points) and forests types (colors).The background color represents biogeographical region follows BfN (2003). Forest types follow EEA (2006): FT1—boreal forest, FT2—hemiboreal and nemoral coniferous-mixed forest, FT3—alpine coniferous, FT4-5—mesophytic deciduous and acidophilus forest, FT6—beech forest, FT7—mountainous beech forest, FT8—thermophilus deciduous forest, FT9—broadleaved evergreen forest, FT10—coniferous Mediterranean forest, FT11-12—mire and swamp forests and floodplain forest, FT13—nonriverine alder, birch or aspen, NA-NC—no data/unclassified (Published in: Sabatini et al. 2018).

2.2 Natural disturbances

Disturbances are the primary drivers of spatial and temporal heterogeneity in ecological systems (Turner et al. 2010). Disturbance is the critical element affecting all ecological systems across a wide range of scales, including all terrestrial, aquatic, and marine ecosystems (Turner et al. 2010). The definition of disturbances has various forms, and the most common useful definition fitting forest ecosystems defines disturbances as: "Disturbance is any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability or the physical environment''(White and Pickett, 1985). Disturbances alter the system state and an ecosystem's trajectory; thus, they are critical drivers of spatial and temporal heterogeneity. While site conditions and climate mainly define the environmental filter for the regional species pool, disturbances influence the structural features, successional dynamics, and, consequently, the distribution of functional groups and species interactions.

Disturbance can happen relatively in a short time interval. Periods can extend from seconds to hours (hurricanes, windstorms etc.); days and weeks (volcanos, eruptions), or they can last months and years (bark beetle outbreak in spruce forest ecosystems). Origin can be abiotic (hurricanes, windstorms or volcanic eruptions), biotic (overgrazing, the spread of an invasive insect, pest or pathogen) or a combination of both, which is for example, the forest fire (fire needs abiotic conditions but adequate fuel for fire is biotic; bark beetle outbreak - the vulnerable spruces are the result of consequences of drought and bark beetle breeding on this material is biotic). Disturbances are very often strongly affected by climate. However, the different disturbance severity can vary across the ecosystems and also can vary the different disturbance agents in the same ecosystem across the time. Disturbance events can vary within the same ecosystems, can have similarities, and can result to the *disturbance regime*. It refers to the spatial and temporal dynamics of disturbances over a longer period, while disturbance events are distinct abiotic or biotic events in which cohorts of organisms were replaced, changed, or eliminated. It includes characteristics such as spatial distribution of disturbances, disturbance frequency, return interval, rotation period, disturbance size, intensity, and severity (Turner 2010). Disturbance regime components and definitions together with others modified from White and Pickett (1985) and Turner et al (1997):

Intensity: Physical energy of the event per area per time (e.g., the heat released per area per time period for fire, or wind speed for storms); characteristic of the disturbance rather than the ecological effect.

Severity: Effect of the disturbance event on the organism, community, or ecosystem; closely related to intensity because more intense disturbances generally are more severe.

Size Area disturbed: mean area per event, area per time period, or percentage of some study area per time period.

Rotation period: Mean time needed to disturb an area equivalent to some study area, which must be explicitly defined.

Frequency Mean or median number of events occurring at an average point per time period, or decimal fraction of events per year; often used for probability of disturbance when expressed as the decimal fraction of events per year.

Return interval: Mean or median time between disturbances; the inverse of frequency; variance may also be important, as this influences predictability.

Size Area disturbed: mean area per event, area per time period, or percentage of some study area per time period.

Residuals Organisms or propagules: Survivals of a disturbance event are referred to as biotic legacies. Residuals are a measure of severity and, thus (at least within one disturbance) an intensity index.

Disturbance regimes are because of global climate change in the times of rapid change. Despite their tremendous effects on ecosystems and landscapes, disturbances receive little attention. An increase in the frequency of wildfires, floods and other drivers of disturbances can be expected during the 20th century in Europe, Asia, Africa, the America, and Oceania (Millennium Ecosystem Assessment 2005).

2.3 Natural forest disturbances

Generally, we can divide forest disturbances into anthropic–human–altered disturbances and natural disturbances – caused by natural phenomena. It means biotic or abiotic disturbances.

Because of the purpose of the whole study, which is to reconstruct and describe disturbances in primary forests, we will cover the natural disturbances and their temporal and spatial extent. Primary forests, as natural ecosystems without significant human activity, can serve as the reference boundaries for understanding the effects of global change on forest ecosystems and studying the temporal and spatial scale of natural disturbances (Schurman et al., 2018).

Natural forest disturbances are events or processes that cause significant changes in forest ecosystems (White and Pickett, 1985). These disturbances play a crucial role in shaping forest composition, structure, and dynamics. Structure plays a critical role in whole ecosystem functioning, including biodiversity maintaining functions, and they are essential for the long-term health and biodiversity of forest ecosystems (Turner 2010, Rodrigo et al., 2022; Kozák et al., 2021, Mikoláš et al., 2021, Langbehn et al., 2021).

In temperate primary forests in Central Europe, natural disturbances such as windstorms or insect outbreaks have a significant effect on the structure and dynamics. (Dale et al., 2001; Seidl et al., 2017). The disturbance regime is an important factor for shaping forest ecosystems and determining their development trajectory in the way of horizontal and vertical diversity. For example, the species composition and structure of forests are strongly influenced by the disturbance. Forest stands, which are frequently affected by severe disturbances, are often dominated by even-aged forests with shade-intolerant species. On the contrary, forests dominated by shade-tolerant species may have a main disturbance regime with less severity and can allow the forest to develop into such a stadium. Forest stand age distribution can vary between these two scenarios and depends on the context and environmental conditions of the site (Rodrigo et al., 2022).

Disturbances are key elements for forming forest structures across multiple spatial changes (Perry, 2002), from the death of individuals and groups of trees creating canopy gaps through bigger patches to large-scale, stand-replacing disturbances. Disturbance events occur abruptly over hours to years but have long-lasting impacts on forest structure and demography, i.e. creating biologically valuable early seral stages and generating a wide range of biological legacies such as deadwood, open canopy gaps and other for biodiversity-important structures such as trees-related microhabitats, pits and mounds etc. (Kozak et al. 2018; Schurman et al., 2018).

2.3.1 Disturbance regime components

To understand the forest disturbance dynamics is important to apply and modify the disturbance regime components list from White and Pickett (1985) and Turner et al (1998).

Disturbance intensity in forest ecology refers to the amount of energy released in the context of the physical amount in the disturbance process. In the case of fires, it is the intensity of the fire line per time unit or energy released per unit length. Forest fire also has a dimension of the flame length (Johnson 1992). Discussion about flame length is more important in some special environmental conditions, where low-intensity fire with the length of flames less than one meter can affect a large proportion of an area and cause high mortality of the trees. Then it is a low-intensity disturbance with high severity.

Disturbance severity refers to the mentioned amount of mortality that occurs among tree populations in a disturbed area, which is recalculated on some area unit or as a proportion. However, regarding the correlation between intensity and severity, there is very often a good correlation, especially in the case of windstorms. The higher the peak of the speed of wind and wind gusts, the higher the proportion of trees which were affected. Based on (Frelich, 2002), coniferous temperate forests were described on a disturbance severity scale in North America as:

a). Low-severity disturbances are the scenario when the small part of the understory and overstory is affected by mortality. The resulting forest structure after such disturbance has the structure of canopy gaps allocated across the forest stand. Windstorms can uproot a few larger trees, creating scattered patterns of bigger and smaller canopy gaps.

b). Moderate-severity disturbances are when most of the overstory or understory trees are killed, but a significant number of mature trees or seedlings survive as a legacy for subsequent disturbance regeneration. Windstorms can significantly affect the overstory trees, but siblings are mostly intact. The created forest structure has a high diversity of vertical and horizontal structures.

c). High-severity disturbances kill most of the understory and overstory layers of the trees.

In the case when the study is focused on a forest, the severity can be pronounced directly as the size of the area disturbed in the units of area or percentage of area. In numerous spatial and temporal studies about forest disturbances, the severity is directly recalculated as a disturbed area. Numerous studies are focusing directly on quantitative research of gap sizes or canopy opening sizes respectively (Kucbel et al., 2010; Šamonil et al., 2009; Drossler & von Lupke, 2005; Szwagrzyk & Szewczyk, 2001; Orman and Dobrowolska, 2017), or dendroecological studies where are additional robust quantitative analyses of disturbance intensity and severity across broad temporal scales, which is important for capturing not only the spatial scale but also describing the historical pattern of disturbances, thus disturbance regime and historical range of variability. (Lorimer and Frelich, 1989; Svoboda et al., 2014; Janda et al., 2017; Frankovič et al. 2021; Kameniar et al. 2023).

The rotation period is the length for which all areas of interest (landscape or forest stand) are disturbed. It applies to all types of disturbance agents, such as wind, fire, logging, etc. The natural disturbance rotation period refers to natural disturbance agents. The commercial disturbance rotation period refers to the ideal logging and timber production rate. Usually, the period of time is between 80 and 120 years and, on average, 100 years (Cardellini et al. 2018). The primary difference between the natural and commercial rotation periods is the selection of the trees, which are affected by mortality. While natural disturbance is the random selection of the trees based on the environment, logging is purposely finding appropriate individuals based on the purpose of harvest.

2.3.2 Natural disturbances in mixed-species forests

Natural disturbances in mixed-species forests, which are projected to become more common due to climate change, may threaten the delivery of ecosystem services. Mixed-species forests have often been shown to be more productive and resistant than monocultures, probably because the mixed forest stands being in part more resistant to various biotic and abiotic disturbance factors (Jactel et al. 2017; Fares et al. 2015; Seidl et al. 2016). This phenomenon discusses the insurance hypothesis theory, which is based on spreading some natural hazards between multiple species and tree diversity, mitigating the impact of the disturbance. A probable assumption for why mixed forests are likely to withstand disturbances better than monoculture forests is that they are made up of multiple tree species with varying functional traits, thus they react to different stressors differently. Thus, there is a higher probability that at least some tree species are more resilient to the various stressors. Thus, it means that there are more opportunities to preserve forest cover and sustain basic ecosystem functions, even though other species may experience damage or death.

This is why there is a need to develop forest management strategies that enhance forest resistance to the threat of multiple stressors and synergistic stress factors. Management practices leading to better resistance to forest stands may include species composition and individual forest silvicultural treatment. However, some of the forest management operations can have opposing effects because each may have different effects on multiple species. For example, thinning can favour some individual trees to not be under competition stress; however, thinned stands may experience drought and wind damage. The same situation is with natural disturbances when the multiple risks can synergise. For example, such a situation may happen when a more severe fire is caused by a drought, not only because of a dry environment but also because the increased susceptibility of drought-stressed trees provided additional fuel for the fire. Thus, in some cases, the synergising effect may act contradictorily to the general assumption that mixed-species forests are more resistant. Thus, some cases of 'lucky monocultures' and 'unlucky mixtures' (mixed forests that were heavily damaged because of their diversity) exist. These concepts suggest that the mixtures of certain tree species in certain environments may lead to bigger damage (Jactel et al. 2017; Pautasso et al. 2005). However, the natural occurrence of certain mixtures of the forests is the result of the successful genesis of the environment. Thus, such mixtures should be more resistant to the natural environmental stressors in which they developed.

2.3.3 Historical range of variability (HRV)

To improve ecosystem management by incorporating knowledge of historical spatial and temporal variability of the ecosystem, the concept of historical range and variability was introduced (HRV). The system HRV serves land use planning and ecosystem management as a critical spatial and temporal foundation to implement possible possible treatment management to improve ecosystem health and integrity (Landres et al., 1999). When it comes to resource planning and management, understanding mountain forest ecosystems' historical range of variability (HRV) might be an important way to capture sustainable ecosystem restoration. Biodiversity, resiliency, and ecosystem integrity were basic terms for the description of the ultimate goal of ecosystem management, which will lead to the restoration of a sustainable ecosystem characterised by a stable structure. Restoration in an ecological way is increasingly important in maintaining a forest ecosystem including natural processes such as natural disturbances and its regime (Keane et al., 2009). Whereas not static but dynamic processes drive the ecosystems with numerous responses to some change, the whole process is indeed the description of forest structure and disturbance regime which existed before the forest management planning and significant land-use changes. Effective implementation of ecosystem management requires a benchmark, which is the reference for the conditions that fully describe the functional environment. The theory behind HRV is that the broad historical envelope of possible ecosystem conditions, such as burned area, vegetation cover type area, or patch size distribution, provides a representative time series of reference conditions to guide land management (Keane et al. 2009). To design and carry out potential treatments to increase ecosystem integrity, HRV provides land use planning and ecosystem management with a crucial spatial and temporal foundation. Knowledge of the historical range of variability (HRV) of mountain forest ecosystems can play a key role in resource planning and management decisions Any quantification of HRV requires an explicit specification of the spatial and temporal context. The spatial context is needed to ensure that the variation of the selected ecological attribute is described across the most appropriate area relative to the spatial dynamics of the ecosystem or landscape.

The concept of historical range and variability (HRV) may be the result of dendroecological research on the temporal and spatial extent of disturbances that may be set up as a baseline for appropriate forest management in forest areas with high biological values. It can be the next step for the sustainable management of forests, which is especially important with climate change mitigation. However, it is possible that the disturbance regime will also change during global climate change. Thus, research on the existing historical range of variability in the given areas may help us better understand the potential damage to forests.

2.4 Disturbance regime of temperate beech-fir forest in Europe

Natural disturbances like windstorms or insect outbreaks have a significant impact on the structure and dynamics of temperate primary forests in Central Europe (Picket & White, 1985; Dale et al., 2001; Seidl et al., 2017).

The passing of several different forest development stages characterises the traditional concept of forest development. It highlights the importance of individual trees' mortality, which are replaced by regenerating layers of trees in a cycling pattern. Tree cohorts pass through each other. Early-growth cohorts are followed by mature ones developing old-growth forest stadiums, which pass through ageing and mortality stages and then return back to regeneration and the early growth phases (Korpeľ, 1995; Meyer, 1999). This cycle of natural forest development can be interrupted by disturbances, allowing younger growth cohorts to regenerate alongside more mature ones. This significantly impacts the horizontal and vertical forest structure, resulting in a higher diversity of structures (Trotsiuk et al., 2012; Mikoláš et al., 2017).

Forest disturbance is characterised as a distinct event that can interrupt this forest development cycle. Natural disturbances like windstorms or insect outbreaks substantially impact the structure and dynamics of temperate, primary forests in Central Europe. Tree species composition, structure, dynamics, and creation of biological legacies, such as dead wood, are significantly influenced by natural disturbances (Seidl et al., 2017; Nagel et al., 2017; Synek et al., 2020; Vítková et al., 2018; Lindenmayer et al., 2019).

It allows younger individuals to regenerate due to the changed resource conditions among mature trees,, which can significantly create diverse forest structures (Trotsiuk et al. 2012). Disturbances also increase forest heterogeneity from stand to landscape scales (Turner 2010). Combining canopy gaps with larger disturbance patches helps create a diverse spatial structure embedded within intact forest cover. Quantifying the regional differences in drivers of disturbance and the effect of post-disturbance developmental pathways on species composition and forest resilience is a key challenge in times of accelerating environmental change.

Variations in size, frequency and severity are the main factors of disturbances shaping forest ecosystem and dynamics (Dale et al., 2001; Seidl et al., 2017). Studies have indicated that the disturbance regime that is prevalent in mixed beech forests in Europe is diverse. The most common disturbances are low-severity disturbances and relatively frequent background mortality, which can lead to the death of a single or small group of trees (Zeibig et al., 2005; Šamonil et al., 2009; Wagner et al., 2010; Trotsiuk et al., 2012; Hobi et al., 2015; Feldmann et al., 2018; Orman & Dobrowolska, 2017; Frankovič et al., 2021). According to past studies, the characteristics of disturbance events vary with variations in size, frequency, and severity. The disturbance regime of European beech-dominated forests (*Fagus sylvatica* L.) is usually dominated by small-scale gap dynamics, (Trotsiuk et. al. 2012). Research studying the size, structure, and composition of canopy gaps showed that most canopy gaps are limited to areas smaller than 150 square meters (Zeibig et al., 2005; Nagel et al., 2017; Feldmann et al., 2018; Orman & Dobrowolska, 2017). Small-scale dynamics with low-severity disturbances were recognised as the crucial process mostly caused by the mortality of a single tree or a group of 2-3 trees (Drosser & von Lupke, 2005). These small- or fine-scale gap dynamics have been identified as critical mechanisms that define forest development trajectories and shape stand structure (Pickett & White, 1985). These small gaps in canopies in forests are the most frequent disturbance structure formed by the mortality of one or several individuals. It can be the result of age or stress-related mortality of an individual or group of several individuals.

Larger-scale disturbances do happen in forests, but they occur at a less frequent rate. Larger canopy gaps have been discovered, for example, in Slovakia, where 10% of canopy gaps were between 250 and 1000 m^2 (Drossler & von Lupke, 2005). Due to the atmospheric conditions concerning forest disturbances in Central Europe, the severity of these disturbances indicates that they were likely caused by thunderstorms or windthrows (Nagel & Diaci, 2006; Drössler & von Lupke, 2005). Such severities of disturbances are less frequent. However, some studies detected intermediate-severity disturbances with more than 40% canopy area removal in the Dinaric mountains or the Western Carpathians (Nagel et al., 2014; Frankovic et al., 2021). Intermediate-severity disturbance events with more than 40% canopy loss were also documented in the Dinaric Mountains and Romanian oak-beech forest (Nagel et al., 2014; Petritan et al., 2017). In beech-fir mixed forests were also documented in the Alps (Firm et al., 2009). Disturbances with a range of severities lasting from low to intermediate severity create a combination of diverse patches, resulting in a coarse-grained structure with interconnected canopy gaps, with likely strong winds and local thunderstorms as main drivers. Mountain belts of beech-dominated forests mixed with Norway spruce may be vulnerable to bark beetle outbreaks and wind throws, particularly in upper mountain regions. Together with exogenous disturbance drivers such as wind, ice storms and drought, this may be a cause for the presence of larger canopy gaps and patches in mixed beech-fir forests (Firm et al., 2009; Trotsiuk et al., 2012; Hobi et al., 2015) When combined, low, intermediate, and rare high-severity disturbances events can result in mixed-severity disturbance regimes which may be comprised of numerous disturbance events driven by different disturbance agents and can create combinations of small and large patches affecting larger or smaller areas (Perry et al., 2011, Halofsky et al., 2011; Trotsiuk et al. 2014; Frankovič 2021). A mixed severity disturbance regime seems to be an essential natural element that frequently forms forest structure in temperate mountain forests in Europe and enhances structure diversity and biodiversity (Mikoláš et al. 2019; Meigs et al. 2017).

Mixed-severity disturbance can be found in some forest ecosystems as the result of the combination of a mixture of gap dynamics, intermediate-severity disturbance events and rare high-severity disturbances (Perry et al., 2011; Halofsky et al., 2011). This specific regime type was described mainly in connection to fire-prone forest ecosystems where the next criterium, aside from the spatial extent of the forest, is also the horizontal dimension of the burnt forest (crown or ground forest fires). Patches resulting from these disturbances can range from a few hundred to tens or hundreds of hectares in size, depending on local environmental and climatic factors. In coniferous forests of temperate Europe, complex spatiotemporal patterns of different disturbance severities were documented, creating a highly diverse forest structure and increasing its complexity (Janda et al., 2017). A single disturbance event can hit a large area with variable severities and create patches with different sizes within the landscape, or alternatively it can be the result of numerous disturbance events driven by different disturbance agents occurring in different parts within the studied landscape (Trotsiuk et al., 2014).

Studies focused on the spatial pattern of disturbances, such as gap dynamics studies, do not describe the vast temporal extent of disturbances (Drossler and von Lupke, 2005; Hobi et al. 2015; Kucbel et al. 2010; Bottero et al. 2011; Rugani et al. 2013) and some of them are using for a description of disturbance regime satellite imagery time series from last decades (Gao et al. 2020; Banskota et al. 2014; Kuenzer et al. 2014; Hirschmugl et al. 2017). In such studies are robust quantitative analyses of spatial scale present, which has a valuable effect on studying the current state of disturbance patterns or global climate change studies. However, these prior studies have predominantly focused on gap-generating processes (Šamonil et al., 2009, Kucbel et al., 2010, Drossler & von Lupke, 2005). Such analysis can determine the size of the disturbed area with a time series of longer periods, capturing the high-severity disturbance events that occur only episodically (Orman and Dobrowolska, 2017). Historical development of forests followed by disturbances and their characteristics, such as severity and frequency, can bring historical process reconstructions, which is key for disturbance regime description. However, robust quantitative analyses of disturbance intensity and severity over large temporal scales are lacking, particularly in the Western Carpathians (Szwagrzyk et al., 2001; Orman & Dobrowolska, 2017) The information about disturbance regime can bring us information about potential tolerance and resilience of forests in the connection to the potential rise of severities of disturbance because the global climate change (Kulakowski et al., 2017).

2.4.1 Forest disturbance agents

Natural disturbance agents such as windthrow, insect outbreaks, wildfires and others are key drivers affecting the composition, structure, and functioning of forest ecosystems and are related to climate and the sensitivity to its change. Evidence from observations all over Europe indicates that in the last few decades, disturbance regimes in forests have significantly increased, leading to a significant rise in damage caused by wind, bark beetles, and wildfires (Seidl et al. 2011). Discussion about disturbance agents and their synergising effect in the times of global climate change seems to be crucial to mitigate its acceleration (Jactel et al. 2017)

The major disturbance agents affecting tree forest cover are:

Windstorms: In European forests, wind is the main disturbance agent. More than half of the damage recorded in European forest areas each year - 18.6 million m^3 on average, is directly attributable to windthrow (Gardiner et al., 2010; Schelhaas, 2008). High winds can uproot trees or break branches, causing damage to forest stands. Windthrow, the process where the wind uproots trees, creates canopy gaps in various sizes from small to stand, replacing disturbances. One of the two meteorological factors contributing to strong winds in Europe is extratropical cyclones, which have the ability to affect forest areas larger than hundreds of square kilometres (Brázdil et al., 2004). Cyclones and their accompanying fronts can cause gradients in temperature, pressure, and humidity, resulting in winds exceeding 20 m/s over sizable impacted areas. The second major meteorological factor contributing to strong winds In Europe is atmospheric instability. It causes microbursts and occasionally tornadoes. Even though severe convective storms frequently occur in Europe (Taszarek et al., 2019). The convective storm elements can create higher-speed winds than extratropical cyclones but at smaller scales and for shorter periods. Strong winds, microbursts, and occasionally tornadoes are convective storm elements resulting from unstable atmospheric conditions (Brázdil et al., 2004; Pettit et al., 2021). Convective storms are generally less common in Southeastern Europe, but cyclone-induced windstorms are more common in the northwest region of Central Europe (Pettit et al., 2021).

Ice Storms: Ice storms occur when rain freezes on contact, coating trees and branches with a layer of ice. The added weight can cause branches to break or whole trees to topple, leading to disturbances in the forest structure.

Drought: Drought is a complex situation resulting from in low precipitation and low soil water availability. It is a major factor in the shifting of natural vegetation cover and the promotion of desertification, with water stress in forest ecosystems causing decreased growth and increased mortality. Prolonged periods of drought stress trees and can make them more susceptible to diseases and insect infestations. Specifically, warmer droughts can exacerbate the mortality of trees due to insects and intensify and expand forest fires (Seidl et al., 2017; Sommerfeld et al., 2018). Drought can lead to widespread tree mortality, especially in regions where water is already scarce. Future issues with water availability and forest response are considered to be among the main problems related to climate change scenarios. The combination of drought and heat can lead to deteriorating the health of trees, which can result in large-scale die-offs and these conditions can result in severe water stress symptoms. Forest water stress symptom is the condition of prolonged or severe water deficit resulting in disturbed forest ability to cope with it and leading to physiological stress followed by responses that can negatively affect forest health and productivity. Such responses to ecological effects include symptoms such as leaf discolouration, premature leaf-shedding, and mortality. Moreover, forest water stress can also increase the susceptibility of trees to biotic and abiotic stresses, such as insect attacks, disease outbreaks, forest fires, and extreme weather events.

Drought-related tree mortality pulses have recently been observed in forests worldwide, and the trend is increasing. In Europe, 500,000 hectares of forest mortality due to drought was recorded between 1987 and 2016 and the five highest fluctuations in the study were observed in 21. century (Senf et al., 2020), they are suggesting the increasing trend in European drought waves.

Wildfires: Wildfires are a natural part of many forest ecosystems. They clear out dead vegetation, promote seed germination, and help certain plant species to reproduce. However, human-induced climate change has led to an increase in the frequency and intensity of wildfires in some regions. Over a wide range of regions and biomes, fire is a major ecological disturbance that impacts a significant portion of the world's terrestrial ecosystems.

Fire can significantly affect important ecosystem processes, change the characteristics of the soil, and consume vast amounts of biomass. On a global biogeographical scale, fire is an important disturbance element in specific regions that has also played a role in plant evolution by promoting specific functional traits. Thus, fire also has very wide consequences on global patterns of biodiversity and vegetation distribution. Both ecosystem characteristics (such as fire-adapted versus fire-sensitive ecosystems) and fire characteristics (such as intensity, size, or recurrence) determine the precise effects of a given fire.

Fire may have bth, positive and negative effects concerning ecosystem services and was widely recognized as a key force affecting multiple ecosystem services. However, wildfires are frequently cited as one of the main disturbances that have a negative impact on ecosystem services in a range of terrestrial environments. Such negative impacts include soil erosion, runoff, and water quality decrease (Roces-Díaz et al., 2021).

Floods: Floods can inundate forests, leading to soil erosion, sediment deposition, and alterations in the composition of plant species. Floodplains are a classic example of forest ecosystems adapted to periodic flooding events.

Landslides: Slope failure can cause entire sections of forested slopes to move downhill, destroying everything in their path and creating new, disturbed areas where vegetation can recolonise.

Volcanic Eruptions: Volcanic eruptions can bury existing forests under layers of ash and lava. Over time, these volcanic soils can become fertile grounds for new plant growth.

Lightning Strikes: Lightning strikes can cause wildfires, but they can also directly damage or kill individual trees. This creates localised disturbances within the forest.

Avalanches: In mountainous regions, avalanches can mow down entire sections of forest, creating openings for new growth.

Insect outbreaks and radial increments: Insects, such as bark beetles, and diseases, like Dutch elm disease, can cause widespread forest damage. These disturbances can lead to tree mortality and, in some cases, may significantly alter forest composition. Periodic oscillations in abundance are among the most remarkable characteristics of animal population dynamics. While these cycles are not present in all species, they are common in many forest insect populations (Bjørnstad & Grenfell, 2001; Berryman, 2002). During peak activity, populations may reach very high densities over large areas, and the following episodes of massive defoliation and tree mortality are known as the essential forest disturbances that fundamentally affect ecosystem processes (Lovett et al., 2002).

Heavy defoliation by defoliating insects ordinarily results in an abrupt decrease in tree-ring width in the years of insect outbreak, followed by several years of growth suppression. (Speer 2010). In many cases, insect outbreaks are the result of the synergising effect of disturbances; for example, windthrow damage followed by drought because of the insolation in the sub-canopy and, consequently, insect outbreak in a generally weakened forest.

Mixed beech-dominated (*Fagus sylvatica* L.), fir (*Abies alba* Mill) and spruce (*Picea abies* L.) forests constitute one of the most widespread forest types in temperate Europe; therefore, insect species and specialists on individual tree species which may cause disturbance are very common. Mixed forests are more resilient to various disturbances and are more resistant to biotic stressors than monodominant forests, despite predictions that the severity and frequency of natural disturbances will increase (Seidl et al., 2017). This is especially the case regarding climate-related stressors like wind, bark beetle outbreaks, and drought (Bauhus et al., 2017; Jactel et al., 2017). . Thus, every tree species may depend on some of the numerous insect species, and most of them may cause a theoretical threat of insect outbreak. Individual description and ecology of most spread insect species related to tree species:

Fagus sylvatica **L.**

Young beech trees are susceptible to woolly aphids from subfamily Eriosomatinae (*Lachnus pallipes, Phyllaphis fagi*) (Gora et al., 1994). The large pine weevil (*Hylobius abietis*) is harmful for beech and markedly coexists with part of its natural niche. Herbivory by short-snouted weevils (*Strophosoma melanogrammum* and *Otiorhynchus scaber*) is another threat to beech (Löf et al. 2004). Next insect species which attacking European beech are: *Rosalia alpine, Cryptococcus fagi, Melolontha hippocastani, Xyloterus domesticus, Xylosandrus germanus, Ernoporicus fagi, Hylecoetus dermestoides, Hemicrepidius niger* L. Elateridae*: Adelocera murina* L.*, Selatosomus aeneus* L.*, Athous zebei.*

Abies alba **M.**

In the next decades, the climate of central and southern Europe is predicted to become warmer and somewhat drier, favouring diseases and plant pests. Insect pests such as mistletoe and bark beetles have already been responsible for a reduction of silver fir in the Mediterranean, especially in those areas where drought stress is more frequent (Barros et al., 2015). Phytophagous insects such as *Mindarus abietinus* and *Dreyfusia normannianae* are often the cause of infections to needles and bark. Other insects such as *Cinaria pectinatae* and *Epinotia nigricana* are affecting bark and buds. Silver fir is vulnerable to *Ips typographus* which is also associated to potentially harmful fungal assemblages (Giordano et al. 2013). The most important bark beetle species that live on fir are *Pityokteines spinidens, P. vorontzowi, P. curvidens, Cryphalus piceae*, and *Pityophthorus pityographus.* Documented pests' outbreaks from Dinaric mountains was caused by the needle mining moth (*Argyresthia fundella*) and budworm (*Choristoneura murinana*), which were reported to cause widespread damage to fir during the 1950´s in the Dinaric region of Croatia (Androič, 1960, Opalički, 1975).

Acer pseodoplatanus L.

Several species from the genus *Acer* are highly vulnerable to the Asian longhorn beetle (*Anoplophora glabripennis*), which is a large wood-boring beetle native of Asian countries, such as Japan, Korea and China (San Miguel Ayanz et al., 2016). The leaves may be severely affected by ascomycete fungi such as *Rhytisma acerinum* (Wulf, 1998).

Moreover, maple´s vulnerability is also connected to the activity of vertebrates and mammals as bark stripping by grey squirrels and damage by other browsing animals (Hein et al. 2008).

Fraxinus excelsior, L.

Due to the ash dieback phenomenon, which has spread to countries in eastern, northern, and central Europe, insect pest outbreaks on common ash are a relatively small problem in comparison to the death of over 90 % of all ash trees caused by the fungus *Hymenoscyphus fraxineus* (Skovsgaard et al., 2010). One of the most important pests hosted by common ash is the emerald ash borer *Agrilus planipennis* , which is a beetle native to Asia and eastern Russia (Straw et al., 2013). The most dangerous are emerald ash borer larvae, which feed on the phloem and can kill the tree and the adults graze on ash leaves. It was observed in western Russia and Sweden in 2007, which has caused concern that the species will spread to other European countries and cause damage to ash trees. The emerald ash borer was also discovered In North America in 2002, after probably entering from Asia in shipping material.

Ulmus glabra L.

Whole population of the Ulmus genus is affected by the two destructive epidemics, caused by the introduction of hyper-virulent fungal pathogens, *Ophiostoma ulmi* in the 1920´s and *Ophiostoma novo-ulmi* in 1970´s, usually called Dutch elm disease. Transmission of fungal pathogen is provided by the bark beetles of genus Scolytus (*Scolytus scolytus, Scolytus multistriatus, Scolytus laevis, Scolytus pygmaeus)* or throughout root connections, attacking principally other mature *Ulmus* genus species. *Ulmus glabra* is also susceptible to the fungal agent, but it remains unaffected, especially at higher latitudes, where the insect transmitting this pathogen cannot survive. There is an increasing possibility of the spreading of the genus *Scolztus* sp. attacking Elms in the mountains due to the changing environment in connection with climate change. Another threat of this serious disease is that elms are susceptible to the Asian longhorned beetle (*Anoplophora glabripennis*), which is a species native to mainland of China and the Korean peninsula (Hu et al., 2009) and is also connected to spreading in changing environment (Straw et al., 2014).

2.5 Forest biological diversity and disturbances

Forests are crucial for biodiversity conservation because they house a significant portion of terrestrial biodiversity. Biological diversity is usually positively related to habitat heterogeneity (Lindenmayer et al., 2006). Habitat heterogeneity occurs in forest ecosystems when stand composition or structure changes over time and space, and the availability of habitats within a forest is largely determined by the structural richness or complexity of the forest (Franklin & Van Pelt 2004). As a result, forest structure has been identified as a critical determinant of biodiversity and a variety of other ecosystem services (Paillet et al., 2018). Biodiversity measurement is an important step in preventing further losses. Single taxonomic groups have been found to be poor indicators of overall forest biodiversity. Aside from the low indicating quality, taxonomic measures to assess biodiversity can be time-consuming and highly subjective to the observer's knowledge, making them difficult to replicate or biassing biodiversity assessments. The focus has shifted from single-species inventory to evaluating structural elements supporting forest biodiversity, from fine-scale tree structures to landscape and stand-scales (Paillet et al., 2018).

These structural characteristics are mostly the results of natural disturbances, and they are an important part of structural variability and heterogeneity. With the intensity of forest management in a forest, the occurrence of such structures decreases. Most such structures are hostile in the managed forest due to the fact that many of them are closely connected to wood decay and pests, and generally are one of the factors that lead to the decreased quality of wood for industrial purposes. Thus, traditional forest management tries to avoid the development of such structures in the forest by using management techniques. Then, when most of the forest landscape is growing for forestry and industrial purposes, the problem of biodiversity loss may increase in a given locality.

The most important structural elements which are enhancing forest biodiversity are:

- **Deadwood:** Structure elements such as deadwood accommodate both saproxylic species (i.e. directly or indirectly dependent on dying or dead wood) and non-saproxylic species (Stokland et al., 2012). It is crucial for forest biodiversity because it offers high amounts of nutrients, energy, and habitat space. The amount of deadwood mostly affects the mortality rate. In natural forests, deadwood is frequently created by low or higher-severity disturbances. The senescence and natural disturbances can result in high deadwood volumes with many variations, including tree diameter, sun exposure, tree species, uprooted trees after windthrows, or rot holes in over-mature trees. More variation of deadwood is important for all variants of saproxylic species (Kozak et al., 2020).
- **Tree-related microhabitats:** TreM is a distinct, well-delineated structure occurring on living or standing dead trees that constitutes a particular and essential substrate or life site for species or species communities during at least a part of their life cycle to develop, feed, shelter, or breed (Kozak et al. 2018; Larrieu et al., 2018). TreMs are relevant to conservation efforts because they reflect a variety of resources available to forest creatures. Because of their diverse origins, substrates, and locations on the tree, forest stands' internal heterogeneity is significantly influenced by TreMs. Specialized species might find refuge, food, or breeding sources under their particular conditions-most notably, substrates and microclimates. The hierarchical approach to typology was described to identify seven general TreM forms based on methodology of Larrieu et al., 2018:

  Cavities: are holes or shelters formed in the wood either by cavity builders, decay processes, or morphological particularities on the trunk or collar.

  Injuries: that exposed sapwood and sometimes also heartwood. They are mainly created by mechanical impacts.

  Crown deadwood: dead branches that most often occur at the top of a tree. This often provides conditions for organisms that prefer open xero-thermophilous conditions due to its location in the canopy.

  Excrescences: their occurrence is mainly caused by reactive growth in response to increased light availability or to a parasitic or microbial intrusion (e.g. canker, burr).

Fungal fruiting bodies and slime moulds: the visible part of saproxylic fungi classified as a perennial or ephemeral structure.

Epiphytic and epixylic structures: encompass wide variety of structures in which the tree is merely the physical support on which the TreM grows or is located. These structures include different organisms growing on trees.

Exudates: Sap runs or heavy resinosis

- **Saproxylic beetles:** Saproxylic species are organisms that depend directly (obligatory) or indirectly (facultative) on deadwood. Saproxylic organisms are species that depend on the phloem or wood of wounded, dying, or dead woody plants during some parts of their life cycle (Stokland et al., 2012). Saproxylic beetles represent about 30% of the total biodiversity in temperate forests and about 50% of all forest beetles in Central (Seibold 2015).

2.6 Dendroecology methods for disturbance detection

Dendrochronological studies use correctly dated and measured tree rings to answer a variety of research problems, and dendrochronology has split into several sub-disciplines (Schweingruber, 1989). Disturbance reconstruction is very important for the explanation of forest dynamics which formed a current forest structure. Dendroecology is a subdiscipline of dendrochronology that studies the impact of environmental changes on tree growth, stand structure, and dynamics using historical variations in radial growth rates. Dendroecological approaches have recently increasing importance for identifying and recording historical disturbance regimes in forest stands. For the annual resolution of tree rings detection is the crossdating essential part of the matching of each tree ring propertiethe s to exact year of its increment. Variety of crossdating techniques and softwares have been developed (Douglass, 1920; Tsap Win software, RINNTECH, Heidelberg, Germany; COFECHA; Holmes, 1983; CDendro 7.1, Larsson, 2003). Increased precision in measuring, crossdating, and dating is the key to correctly identifying past disturbances and their agents (Black et al., 2016). Documenting disturbance with annual or ten-year resolution over centuries and at ranges ranging from tree to continental scales is a strong tool for understanding the mechanisms that drive forest dynamics. Disturbance dynamics in closed-canopy forests can have profound effects on annual radial-growth rates as growth releases and suppressions (Cook 1990; Nowacki, Abrams 1997). An abrupt, and sustained increase in tree- radial growth increases is referred to a release from the tree-to-tree competition and is taken as evidence of past canopy disturbance (Lorimer, 1980).

Dendroecological methods for identifying and describing disturbance histories are now widely used and a variety of strategies have been developed (Rubino and McCarthy, 2004; Trotsiuk et al. 2018).

2.6.1 Radial growth averaging method

The original technique calculated the percentage growth change (PGC) for each annual ring by averaging radial growth throughout the prior 15-year period M1 (containing the goal year t) and the succeeding 15-year period M2 (excluding the target year t) as follows:

$$PGC = [(M2-M1) / M1] \times 100.$$

To detect growth releases in understory trees, the original percentage growth thresholds were 100 percent for a "major, sustained" release and 50–99 percent for a "moderate" release (Lorimer, 1985; Lorimer and Frelich, 1989). To derive disturbance history from old-aged canopy oak trees, the initial window durations were decreased to ten years and the "moderate" release was reduced to a growth boost of 25%. (Nowacki and Abrams, 1997). To meet species- or site-specific criteria, different M1 and M2 window lengths, as well as growth thresholds, have been used (Rubino and McCarthy, 2004).

2.6.2 Boundary-line

It is the method where each tree's percentage growth change of each year is scaled by its greatest potential observable growth, as indicated by historical growth rates for that species growing at one or more locations. Releases were defined as growth pulses that exceeded 20% of the previous growth boundary line. In this case, the method should account for the influence of site conditions, species, size, and tree age on radial growth rates when normalising growth. Defining the boundary line demands a huge quantity of data from a single species in identical site conditions (up to 50,000 radial increments) in some situations, which may make the boundary line challenging to fit for some stands and species (Black and Abrams, 2003).

2.6.3 Absolute-increase method

The absolute-increase (AI) method (Fraver and White, 2005) subtracts the average pre-event growth rate (M1) from the average post-event growth rate (M2) using 10-year window lengths following formula:

$AI = M2 - M1$

If the difference in growth rate surpasses a predefined threshold for a given species, the growth increase is classified as a release. The method is similar to the major releases mentioned in radial-growth averaging and boundary-line methods in that it detects overhead canopy disturbances. The threshold value used to indicate the year of a release where knowledge of species’ growth potential is not available, they suggest selecting a threshold value equal to 1.25 of the standard deviation of all absolute increase values (tree ring growth changes) or somewhat less than the 90th percentile, of all absolute increases of the whole dataset or set of dataset in the fiven study (Fraver and White, 2005).

2.6.4 Time series method

Time-series analysis (TSA) is useful not just for reconstructing previous climates using tree rings, but also for reconstructing past ecological changes (Druckenbrod, 2005; Cook and Kairiukstis, 1990).

This release detection method removes a series' long-term growth trend, accounts for autocorrelation in sequential tree-ring width measurements, and employs intervention detection, allowing its release criteria to scale with a tree's growth rate, similar to the boundary-line and absolute-increase methods. Over time intervals of 9 to 30 years, release events are detected as series of abnormally large, positive departures from autoregressive residuals. The detection criteria classifies any sequence with a scale greater than 3.29 (or 99.95 percent of the observations in a one-tailed analysis) as an outlier, using Tukey's biweight mean as a reliable estimate of location and scale. At the start of the growth release, a Hugershoff curve is fitted. This curve's flexibility allows it to capture both transient and long-term release events. Unlike growth averaging methods, this curve intervention detection approach allows time-series analysis to reconstruct not only the year of release but also the magnitude and duration of the subsequent growth change caused by the disturbance event. (Druckenbrod et al., 2013).

3. Aims of the dissertation thesis

Natural disturbances are key factors in forming forest ecosystem structure and dynamics. Investigation of the spatial and temporal extent of disturbance regimes is critical for understanding forest structural heterogeneity, biodiversity habitats, and development stages. Natural and primary forests vary on a spatial and temporal level, and the main drivers of this heterogeneity are natural disturbances. We used a dendrochronological approach to analyse the disturbance regime, where we reconstructed tree growth trends of individual canopy trees. We compiled hierarchically scaled disturbance chronologies to reconstruct the overall regional disturbance regime and disturbance history. We studied the natural disturbance regimes of beech-dominated mixed-forest stands on the already existing network of permanent study plots across primary forest stands in the Carpathian mountains. We would like to bring new insight regarding the description of disturbance patterns and to try to evaluate the species-specific relationship between disturbances and stands.

Within first part of the dissertation thesis we compiled hierarchically scaled disturbance chronologies to reconstruct the overall regional disturbance regime and disturbance history. Specifically, we determined the timing, frequency and severity of past disturbances within three forest stands distributed across two landscapes in the western Carpathian ecoregion (Central Europe, Slovakia). Our goal was to estimate the range of past disturbance activity, as well as quantitatively describe the spatial and temporal variation in disturbance frequency and severity across the study stands – Kornietová, Šrámková and Šútovská valley in Western Carpathians, Slovakia. Specifically, we hypothesize that mixed-species primary forests are shaped by a range of processes, including local-scale gap-generating events, intermediate-severity windstorm-driven processes, and infrequent high-intensity disturbances that substantially disrupt forest structure and function over comparatively large spatial scales. To test this hypothesis, we looked for an approximately balanced or equal frequency distribution of disturbance severities over the studied time period, even though it is not possible to exclude gradations in both points of view, i.e. the size of gaps, patches, and time of canopy area removal. This part of study aims to describe the disturbance regime in the western Carpathian ecoregion and to evaluate the occurrence of high- and very high-severity disturbance events by addressing the following questions:

1. What is the range of past disturbance activity and description of the aspects of historical disturbance regime on stand level of the selected beech-fir forests reserves?

2. What are the spatial aspects and severity classes of historical disturbance regimes of the selected beech-fir forest reserves?

Moreover, to help shed light on the drivers and characteristics of disturbance regimes, and their changes across different regions, we expanded the study location, and we utilised data collected from temperate primary mixed beech-dominated forests in the Eastern and Western Carpathians. We again used a dendrochronological approach for the reconstruction of tree growth trends of individual canopy trees, from which we hierarchically compiled plot, stand, and regional-level disturbance chronology curves. These data were then used as proxy data for synchronicity analysis, size of disturbance patches, and proportion of plots disturbed (Schurman et al., 2018; Janda et al., 2017). Due to the broad consensus that forests with higher species diversity are likely to be more resistant and resilient to climate change stressors and ecological disturbances, we expect higher severity disturbances and higher synchronisation rates among stands in monodominant beech forests (Fares et al., 2015; Seidl et al. 2016). For this purpose, our goal was to compare two distinctive ecoregions and evaluate the exact value of this difference.

Our goal was to evaluate and describe the impact on spatial and temporal patterns of disturbance regime and compare results between the Eastern and Western Carpathians by addressing two main questions:

3. Is there a difference in the disturbance regimes (i.e. severity, patch sizes and proportion of disturbed plots) in the Western and Eastern Carpathian regions?

4. Is there evidence of disturbance synchronisation within stands, and is there a difference between the two distinct Carpathian regions with different species composition?

In addition to previous hypothesis, our further goal is to evaluate the relation between synchronicity rate and average species richness on the stands. We expect an increasing trend of synchronicity with the decreasing number of species per stand (e.g. higher synchronicity rate within monodominant species forest). For solution, we addressed one main question:

5. What is the statistical relationship between the rarified average species richness and the rate of Kendal´s W coefficient of synchronicity?

4. Methods

4.1 Study area characterisation

The research was realised within the REMOTE primary forests project (REsearch on MOuntain TEmperate forests; www.remoteforests.org). The project is a long-term international collaboration based on a network of permanent sample plots in central, eastern, and southern European forests. Primary forest is defined as a forest that has not been directly impacted by humans and where natural disturbances are the primary driver of forest structure and composition. These forests include both old growth and the early stages of seral development.

The thesis was based on research carried out in two distinct regions: Western Carpathian and Eastern Carpathian Mountains. The Carpathian Mountains are a range of mountains in Central and Eastern Europe. The mountains stretch in an arc from the Czech Republic in the northwest through Slovakia, Poland, Hungary, and Ukraine, and then Romania, Serbia, and Bulgaria in the southeast. The Carpathians are the second-longest mountain range in Europe, after the Scandinavian Mountains. Carpathians span over 220 000 km^2 and they represent the second largest mountain range in Europe. In the highest parts within the Carpathians mountains, altitudes of the highest peaks exceeed 2,500 m in the Southern Carpathians in Romania and in the Western Carpathians in Poland and Slovakia where altitude exceeds 2,600 m.

Division of Carpathians mountains usually includes three main parts (Oszlányi et al. 2004):

Western Carpathians: this section includes the mountains in the Czech Republic, Slovakia, Poland, and Hungary. Major ranges within the Western Carpathians include the Little Carpathians, White Carpathians, and the High and Small Tatra Mountains.

Eastern Carpathians: This section covers the Carpathians in eastern Slovakia, Poland, Ukraine, and Romania. The Eastern Carpathians are further divided into several subranges like the Beskids, Bukovec Mountains and the Ukrainian Carpathians.

Southern Carpathians: Also called the Transylvanian Alps, this section is located in central and southern Romania. It includes the Făgăraș Mountains, the Bucegi Mountains, and the Retezat Mountains.

The Carpathian Mountains range is one of the biodiversity hot spots of Europe with exceptional richness of plant and animal species. This region is home to around one-third of the vascular plant species found in Europe. The Carpathians are home to over 12% of the world's flora. Large predators such as brown bear (*Ursus arctos* L.), wolf (*Canis lupus* L.), and lynx (*Lynx lynx* L.) has one pf the last refugees in Europe in Capathians. Additionally, these mountains are home to several endangered species, including the golden eagle (Aquila chrysaetos L.), marmot (*Marmota marmota* L.), and chamoix (*Rupicapra rupicapra* L.).

For a long time, forests in the Carpathians were protected from human influence due to their remote location and poor accessibility. Lowland forests and forests located at lower elevations of the Carpathians were cleared because of their suitability for human settlement and agriculture. This process took place in different regions of the Carpathians in various historical periods but mainly throughout the Middle Ages (between 500 and 1 500 AD). The mountain forests located deep in the steep valleys and on the ridges remained mainly intact at that time. Until a few decades ago, a relatively continuous mountain forest cover was maintained in the Romanian and Ukrainian (partly also Slovakian) regions of the Carpathians because conducting logging in these forests was still not operationally or economically viable. Recently, however, due to the introduction of modern harvesting technologies, widespread destruction of many previously undisturbed sites has occurred across the Carpathians. As a result, primary forests are currently relatively rare in the Carpathians, and they make up only a small proportion of the total forest cover. Despite their scarcity, the size of primeval forests is still decreasing, mainly due the unawareness of their exact location (imprecise mapping) and the lack of effective protection measures. The primary forest stands studied in this dissertation thesis are in the Western Carpathian and Eastern Carpathian Mountains of Slovakia. From all identified primary forest sites in Slovakia, which include around 10,000 ha of forests (www.pralesy.sk, 2019), we selected together 14 stands and 174 study plots in beech dominated (*Fagus sylvatica* L.) forests for disturbance chronology analysis, disturbance regime description and spatial and temporal aspects and it´s comparison within the landscapes.

Moreover, forest stands are formed by the gradient of the mixed beech-dominated forest types accompanied by other typical tree species. While stands in the Western Carpathian region have higher tree species richness, the beech strongly dominated the forest tree species in the Eastern Carpathian region. Significantly occurring tree species in the forests are Fir (*Abies alba* Mill.) and Norway spruce (*Picea Abies* H. Karst.). Other more common types of trees species in mixed forest stands are maple (*Acer pseudoplatanus* L), European ash (Fraxinus excelsior L.) and Scots elm (*Ulmus glabra* Huds.), especially in the Western Carpathian part of the sites. Natural dynamics of temperate mountain beech-dominated primary forests in Central Europe.

4.2 Natural dynamics of temperate mountain beech-dominated primary forests in Central Europe

The primary forest stands are located in the Western Carpathian Mountains of Slovakia. This area is of particular interest for disturbance dynamics research because it is considered to be a biodiversity hotspot (Ujházyová et al., 2016, Jimenez-Alfaro et al., 2018) within the European temperate zone, with a large number of endangered species (Mikoláš et al., 2015). We identified stands based on a national inventory of primary forests in Slovakia, which was designed to identify stands where no human activity has directly affected the tree canopy layer. In primary forests in Central Europe, it is not possible to completely exclude any human influences on a forest stand, through, for example, grazing or selective logging. This forest inventory included a complex field survey, historical evidence from military maps of the Austro-Hungarian Empire from 1764 to 1768 and 1806 to 1869, and aerial images from the year 1950 (Mikoláš et al., 2019). From all identified primary forest sites in Slovakia, which includes around 10,000 ha of forests (www.pralesy.sk, 2019), we selected three beech (*Fagus sylvatica* L.) - fir (*Abies alba* Mill.) forest reserves for analysis. *Šútovská dolina* and *Šrámková* forest reserves in Low Fatra National Park and *Kornietová* forest reserve in Great Fatra National Park (Table 1). All three stands are protected through the highest category of protected areas according to Slovak legislation (Slovak national inventory of protected areas, 2002). The spatial distribution of the stands span from 49.192141°, 19.110292° on the north and 48.995117°, 19.103756° on the south, in two mountain ranges - Great Fatra and Low Fatra (Fig. 1).

Mountain range	Stand name	Number of plots	Number of cores	Area (hectares)	Elevation range (m a.s.l.)	Mean annual air temperature (C°)	Mean annual precipitation total (mm)	Bedrock	Soil group	Slope (min - max) (%)	Slope (mean) (%)
Great Fatra	Kornietová (KOR)	14	312	88.54	1012 - 1229	5 - 5.5	980	Limestone-sandstone	Cambisols - podzols	20-37	29,57
Little Fatra	Šrámková (SRA)	14	383	116.02	951 - 1117	5 - 5.5	1067	Granite	Cambisols	23-38	32,33
Little Fatra	Šútovská dolina (SUT)	14	329	197.23	785 - 1145	5 - 5.5	1067	Granite	Cambisols - podzols	24-40	32,36

Table 1: Characteristics of the study area. Mean temperature and total mean annual precipitation were calculated using data from the gridded CRU dataset (CRU TS Version 4.01; Harris, I., Osborn, T.J., Jones, P. et al., Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. Sci Data 7, 109 (2020). https://doi.org/10.1038/s41597-020-0453-3) from 1901 to 2016. Gridded data for our sites was obtained using the KNMI Climate Explorer (Van Oldenborgh et al., 2009).

4.2.1 Data collection

In each of the three forest stands, we established 14 circular permanent study plots (PSP) with areas of 0.15 ha, in the mapped primary forest polygons (www.pralesy.sk, 2019). For the selection of permanent study plots (PSPs), a polygon network (10 ha each) was created using the ArcView 9.3 Environment (ESRI ArcGIS, 2011). Within each polygon, we generated a random point. From the identified random points, we positioned a pair of plots along the contour, one on each side of the random point. Paired plot centres were 40 m from the random point and 80 m from each other (Figure 4). Each pair of plots consisted of two circular plots (horizontal radius 17.84 m).

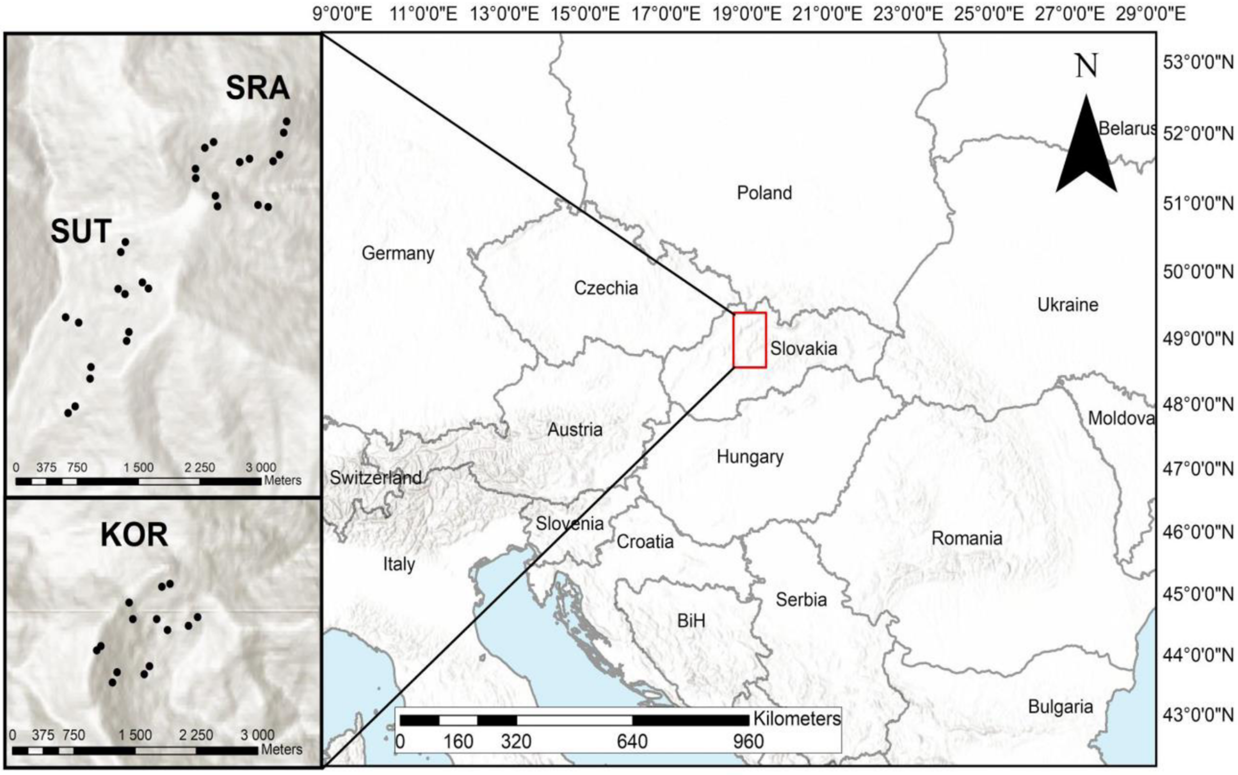

Figure 3: Spatial distribution of stands across Slovakia and design of permanent study plots within three study stands, including SRA, SUT, and KOR. The black circles represent study plots, indicating the design of their location within the study stand. The grayscale shade represents the elevation gradient. The red rectangle represents the location of the study region within Central Europe.

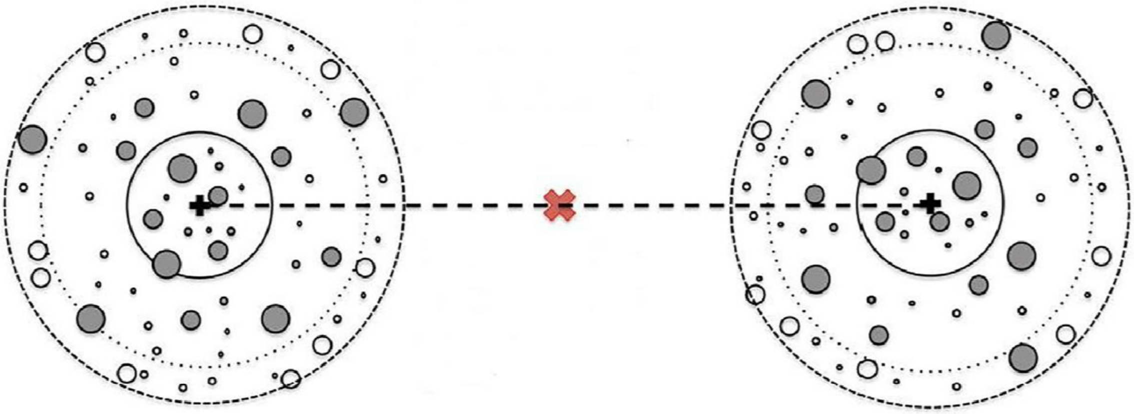

Figure 4: Example of the nested plot structure. The red cross indicates the randomly generated navigation point used to locate the pair of circular sample plots. The distance from the navigation point to the centre of

the plot is 40 m. Grey circles represent cored trees, and white circles represent non-cored trees. The dashed line represents the direction along the terrain contours.

Electronic and laser measuring devices linked to a GIS (Field–Map, IFER 2008) were used to map all trees with a diameter at breast height (DBH) over 6 cm within plots. To analyse disturbance history, we sampled all living canopy trees on each plot by collecting increment cores. We took one core from each tree extracted perpendicular to the terrain slope direction at a height of 1 m above the ground.

Tree ring cores were processed using standard dendrochronological techniques. Cores were measured using a LINTAB sliding table and TsapWin software (RINNTECH, Heidelberg, Germany, http://www.rinntech.com) with a resolution of 0.01 mm. In the case when the pith was missing from the core, the estimation of missing rings was done using Duncan's (1989) method. Cross-dating was verified using the software programs COFECHA (Holmes, 1983) and CDendro 7.1 (Larsson, 2003). To minimize potential dating errors, cores that could not be cross-dated with high confidence were excluded from further analysis. The current crown areas of 15 cored trees were also obtained from permanent study plots to quantify the relationship between crown area and diameter. Crown area was estimated by measuring the crown area of 15 individual cored trees in the field. After that, each crown area was predicted using a statistical relationship between the estimated crown areas of the cored trees, and DBH ($R^2 = 0.61$, $p < .001$). Then disturbance chronologies were reconstructed by linking current crown areas of released trees to the year when the detected release occurred, assuming that the crown area of trees that responded to the original gap formation approximates the size of the original gap (Lorimer and Frelich, 1989, Schurman et al., 2018). Finally, we recorded topographic attributes, including slope, aspect and altitude at each plot (Table 1).

4.2.2 Tree-level disturbance analysis

Using tree-ring width analysis we conducted disturbance history reconstruction based on two alternate patterns of radial growth: (1) abrupt, sustained increases in growth - referred to as growth-releases - which indicates the mortality of a former canopy tree (Frelich, 2002) and (2) rapid early growth rates which indicate historical recruitment or regeneration below a disturbance-generated canopy gap. For identification of release from suppression, we used the absolute increase method (Fraver and White, 2005), defined as the difference between the mean of the 10-year sequence prior to a focal year (M_1) and the 10-year sequence after (M_2).

$$AI = (M2) - (M_1)$$

The threshold value used to indicate the year of a release was calculated as 1.25 times the standard deviation of all absolute increase values (tree ring growth changes) in the whole dataset in this study. To prevent potential misidentification of disturbance events caused by extreme climatic fluctuation, the tree ring growth increases had to exceed the pre-event 10-year running mean for at least seven years and we excluded shorter periods of increases from the analysis. All the thresholds used were species and sub-region specific (Table S1). To minimise overestimation of disturbance extent or severity, we only used data from juvenile trees that occupied the actual area of the disturbance and responded to an increased amount of light attributed to canopy removal. Thus, we excluded neighbouring adult or canopy trees that occupied adjacent areas outside of the newly generated forest gap (Lorimer and Frelich, 1989). A specific threshold DBH limit was used to discriminate adult from juvenile trees at the time of the event (Appendix A1). This threshold size value was estimated from a regression model fitted with data from the measured known canopy and suppressed trees (Janda et al., 2017).

Gap recruitment (rapid early growth rates) was classified as trees which started to grow in former canopy gaps. We determined tree recruitment as evidence of a disturbance event when the mean width of the fifth to 15th ring exceeded the early growth rate threshold. This threshold was defined by comparing the growth rates of trees growing under open-canopy, to those growing under closed-canopy conditions (Svoboda et al., 2014, Trotsiuk et al., 2014, Janda et al., 2017). Larger juvenile growth rates indicate a change in the amount of resources available in the gaps after canopy removal. Each tree core potentially revealed evidence for multiple disturbance events. All the thresholds used were species and sub-region specific (Appendix A1). All detected events were converted to a percentage of canopy area disturbed in each plot to scale the evidence of disturbance according to each tree's current crown area. Because regenerating trees can take several years or decades to establish and grow to a coring height of one meter, and often show delayed growth responses in detecting releases, all records of disturbance events can oscillate in prolonged time periods.

4.2.3 Plot- and stand-level reconstruction of natural disturbance events

In order to examine disturbance trends across a larger spatial extent, we converted the evidence of tree-level disturbances to canopy area removed, and then used kernel density functions to aggregate tree-level to plot-level disturbance chronologies. Evidence of these were expressed as a proportion of canopy area affected by a disturbance event (for each cored individual tree on the plot from where the current crown area was obtained) which were weighted with disturbance evidence in individual chronologies obtained from each individual tree core (Lorimer and Frelich, 1989).

All disturbance histories identified for all plots were summed to stand disturbance chronologies. To minimize associated noise, we smoothed the chronologies by running a kernel density function (Trotsiuk et al., 2018). Kernel smoothing is a widely used non-parametric data smoothing technique to estimate the probability density function of a random variable (Duong, 2007). For all analyses, we used R software (R Core Team, 2019). The years with the maximum proportion of disturbed canopy area were identified as peaks in the smoothed values. Maximum disturbance severity was identified as the events with the maximum proportion of canopy area disturbed. The disturbance histories of the plots and stands were interpreted through graphs with an expression of disturbance severity, with dates of the event.

For the moving 30-year window we calculated the density with a smoothing bandwidth equal to five years. To estimate years of individual disturbance events we found peak years where the curve was increasing for at least five years. Coincident peaks in the function were aggregated unless separated by a minimum of 10 years. Minor random fluctuations in the function corresponding to gap sizes of less than 10% of canopy removed were considered to be unrelated to disturbance and were excluded from further analyses. The severity of disturbance events in the curve line was estimated as percentage of canopy area removed by summing relative canopy areas ten years around the peak. Summing the ten years area window around the disturbance peak is because ten years is the generally accepted time period for tree growth response (Fraver and White, 2005).

Stand-level disturbance events were subsequently reconstructed by aggregating plot-scale events with minimum severities of 10% canopy area removed. All detected years of disturbance events were plotted using a running kernel density function with the same coefficients. Peaks were again extracted as described previously for plot-level analyses.

Subsequently, we randomly selected 10 plots from each stand and using the kernel density function, we extracted the peak of the highest possibility of disturbance. Because the number of plots in each stand is variable, the process was repeated 1000 times to calculate peaks of the appearance of disturbance events (Čada et al., 2020). To smooth the resulting distributions of bootstrapped peaks, we used an 11-year window and bandwidth equal to 1. All extracted stand-level peaks were separated by at least 10 years. All plot-level event dates were assigned to the nearest stand-level disturbance event. The average difference between plot-level and stand-level disturbance events was 12 years and 95% of events were within 19.2 years.

4.2.4 Maximum severity and spatial distribution of disturbances

Four severity classes were defined based on the amount of canopy area removed: Low 0–20%, Moderate 20.1–40%, High 40.1–60% and Very high greater than 60% (Frelich and Lorimer, 1991, Janda et al., 2017). Due to the fact that regenerating trees can take several years or decades to grow to the coring height (Kulakowski and Veblen, 2002), we aggregated disturbance events with minimum severities of 10% of canopy area removed into nine 20-year long periods with the highest possibility of occurrence of disturbance activity: (1740–1760; 1760–1780; 1780–1800; 1800–1820; 1830–1850; 1860–1880; 1880–1900; 1920–1940; 1950–1970; 1970–1990). Maximum severity classes were calculated as the 20-year sum of all plot-level disturbances events with ≥ 10% severity in a given period.

4.3 Synchronicity and variation of natural disturbances across beech-dominated primary forests in the Carpathians

4.3.1 Study area

The studied primary forest sites are located within a network of existing permanent study plots established within the REMOTE project (https://www.remoteforests.org) that identifies and monitors primary forests in Central, Eastern, and Southeastern Europe. In this study, the stands are located in the Western and Eastern Carpathian Mountains of Slovakia. The stands were identified based on a national inventory of primary forests, which was designed to identify forests where no human activity has directly affected the locations. Because it is not possible to completely exclude all human past influences (extensive grazing and logging) in Central European primary forests, the inventory was designed to delineate localities where human activities have not directly affected the tree canopy layer. Field exploration to identify the sites was composed of a complex of forest surveys, historical evidence from military maps of the Austro-Hungarian Empire from 1764 to 1768 and 1806 to 1869, and aerial images from the year 1950 (Mikoláš et al. 2019). From all identified primary forest sites in Slovakia, which include around 10,000 ha of forests (www.pralesy.sk), we selected 14 stands and 174 study plots in mixed beech (*Fagus sylvatica* L.) - fir (*Abies alba* Mill.) forests for deep disturbance chronology analysis. The research area spans a broad elevation gradient (642 - 1284 m). The Western Carpathian research areas have higher ranges and altitudes, and border the upper mountain belts of Norway spruce (*Picea abies* L.) forests (Table 2). In the Eastern Carpathians, altitudes are comparatively lower, slopes are milder and bedrock differs. The spatial distribution of the stands spans from 49.19°N to 48.62°S, and from 19.01°W to 22.54°E (Figure 3). The study plots are located in areas which are part of forest reserves, and thus nature in the area is strictly protected and classified as non-intervention areas. They are generally considered biodiversity hotspots within European forests, hosting a large number of endangered species (Mikoláš et al. 2015, Ujházyová et al. 2016).

Region	**Landscapes**	**Stand name**	**Number of plots**	**Number of cores**	**Elevation range (m a.s.l.)**	**Slope (min - max) (%)**	**Slope (mean) (%)**	**BA (m2 ha-1) *Fagus sylvatica***	**BA (m2 ha-1) *Picea Abies***	**BA (m2 ha-1) *Abies alba***	**BA (m2 ha-1) Others**
Western Carpathians	**Vepor Hills**	Klenovský Vepor (VEP)	13	447	1107–1263	16–35	25,8	217	184	69	64
Western Carpathians	**Great Fatra**	Kornietová (KOR)	14	691	1012–1224	20-37	29,77	302	183	45	61
Western Carpathians	**Great Fatra**	Kundračka (KUN)	7	196	963–1193	25–44	3,14	161	63	37	15
Western Carpathians	**Great Fatra**	Padva (PAD)	7	188	1064–1270	21–35	28,43	145	60	4	15
Western Carpathians	**Great Fatra**	Skalná Alpa (SKA)	8	173	1106–1265	20–35	26,72	194	61	14	10
Western Carpathians	**Little Fatra**	Šrámková (SRA)	14	723	951–1117	23-38	32,57	324	51	129	43
Western Carpathians	**Little Fatra**	Šútovská (SUT)	14	723	785–1145	24-40	32,36	445	60	38	36
Western Carpathians	**Low Tatras**	Obrštín (OBR)	6	262	823–955	29–39	31,5	165	11	71	36
Western Carpathians	**Polana**	Poľana (POL)	20	626	1039–1284	17–33	24	460	145	83	99
Eastern Carpathians	**Vihorlat**	Vihorlat (VIH)	14	426	642–945	07-29	17,23	585	0	19	51
Eastern Carpathians	**Poloniny**	Havešová (HAV)	14	341	642–710	10.29	18	458	0	0	12
Eastern Carpathians	**Poloniny**	Stužica (STU1)	14	408	845–1020	10-26	18,14	571	0	5	1
Eastern Carpathians	**Poloniny**	Stužica (STU2)	14	428	822–1068	09-30	19,92	577	0	22	12
Eastern Carpathians	**Poloniny**	Stužica (STU3)	14	554	898–1053	23–38	28,43	641	0	41	8

Table 2*:* Characteristics of the study area.

4.3.2 Data collection and tree ring processing

In each of the 14 mapped primary forest stands, we established 6-20 circular permanent study plots (PSP) with areas of 0.15 ha. For their selection, a polygon network (10 ha each) was created using the ArcView 9.3 Environment (ESRI ArcGIS, 2011). Within each polygon, we generated a random point. From the identified random points, we positioned a pair of plots along the contour, one on each side of the random point. Paired plot centres were 40 m from the random point and 80 m from each other (Figure 4). Each pair of plots consisted of two circular plots (horizontal radius 21.84 m).

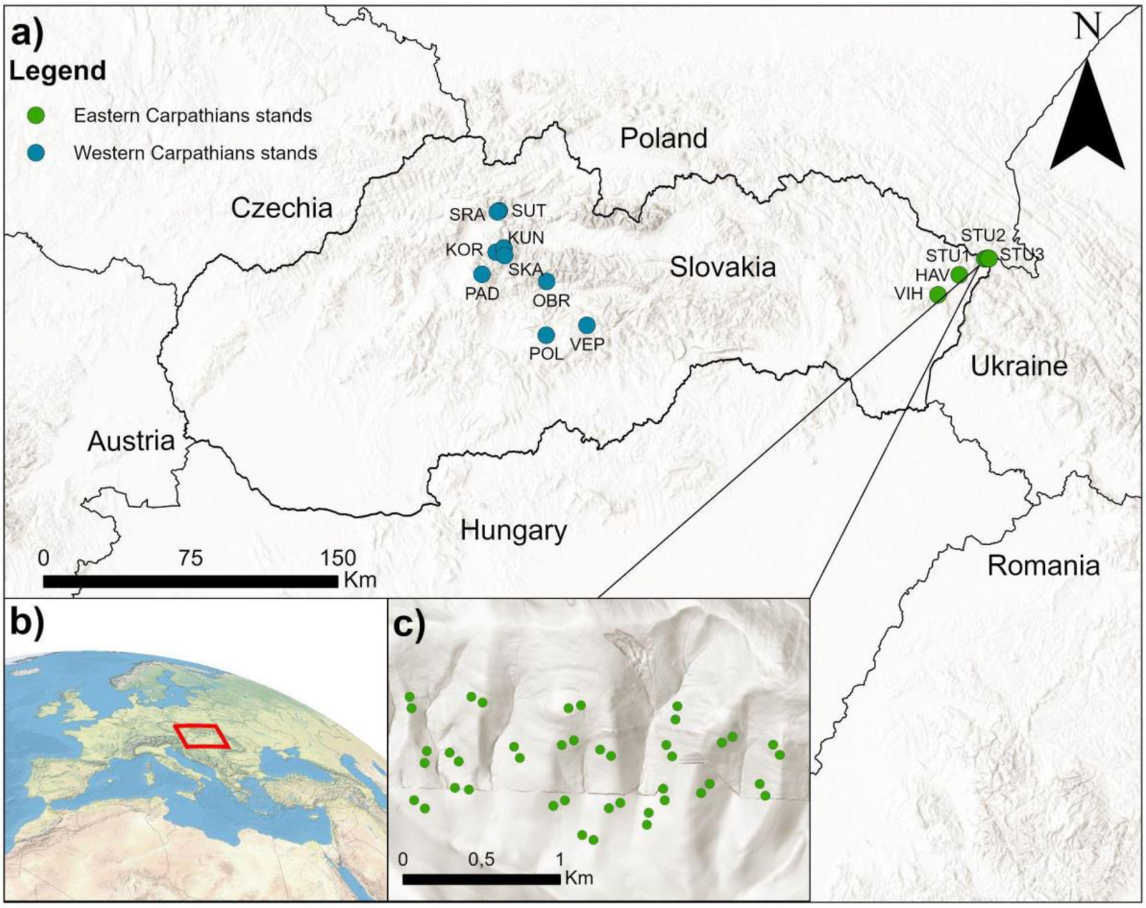

Figure 5: (a) Spatial distribution of stands across Slovakia; (b) location of Slovakia within Europe; (c) design of permanent study plots within stands. The colour of the circles represents the study region, divided into the Eastern (green) and Western Carpathian (blue) mountains. The grayscale shade represents the elevation gradient. Circles represent study plots, indicating the design of their location within the study stand.

Electronic and laser measuring devices linked to a GIS (Field–Map, IFER 2008) were used to map all trees within each plot with a diameter at breast height (DBH) ≥ 6 cm. To analyse disturbance history, we sampled living canopy trees on each plot by collecting increment cores, perpendicular to the terrain slope direction at a height of 1 m above the ground. Tree cores were collected following a hierarchical sampling design that considered tree size and its relative position on the plot. In the first circle (up to 0,05 ha, all trees ≥ 6 cm DBH were cored, in the second circle (up to 0,1 ha) all trees ≥ 20 cm DBH and 25% of the number of released trees with DBH 10-20 cm were cored, and in the third circle (up to 0,15 ha), only trees with up to 60 cm DBH were cored. In some of the stands in Western Carpathians, a slightly different coring design was used in which in the second circle all living trees with DBH ≥ 15 cm plus all released living trees with DBH ≥ 10 cm (+ randomly selected 3 suppressed trees with DBH 10 – 15 cm) were cored and in the third circle, up to 12 living released trees with DBH ≥ 10 cm within 12 regular quadrants were cored within a 0,2 ha area. Moreover, the current crown areas of 15 cored trees were also obtained by measuring the crown projections in the study plots.

After collection, the cores were dried, mounted on wooden boards and sanded using sandpaper (up to 1000 ANSI grit). They were measured using a LINTAB sliding table and TsapWin software (RINNTECH, Heidelberg, Germany, http://www. rinntech.de) with a resolution of 0.01 mm. When the pith was missing from the core, the missing rings were estimated using Duncan's (1989) method. The cross-dating was performed in the CDendro 7.1 program (Larsson, 2003). To minimise potential dating errors, cores that could not be cross-dated with high confidence were excluded from further analysis.

4.3.3 Tree level disturbance chronology reconstruction

Disturbance chronologies were reconstructed by linking the current crown areas of released trees to the year when the detected release occurred, assuming that the crown area of trees that responded to the original canopy opening approximates the size of the original canopy gap (Lorimer and Frelich, 1989; Schurman et al. 2018). Each crown area of the cored tree was predicted using a statistical relationship between the estimated crown areas of the cored trees and DBH with a regionally specific relation. Tree level disturbance chronologies were then calculated using tree-ring width analysis based on two patterns of radial growth: (1)

rapid early growth rates, which indicates historical recruitment or regeneration below a disturbance-generated open canopy and (2) abrupt, sustained increases in growth - referred to as growth-release - which indicates the mortality of a former canopy tree (Frelich, 2002). Open canopy recruitment was classified as rapid early growth rates of trees which started to grow in former open canopy conditions. We determined tree recruitment as evidence of a disturbance event when the mean width of the fifth to 15th ring exceeded the early growth rate threshold. This threshold was defined by comparing the early growth rates in young trees growing in gaps vs. those growing under a forest canopy (Appendix A1; Svoboda et al. 2014; Janda et al. 2017; Čada et al. 2020). Higher juvenile growth rates indicate higher resource availability in the gaps after canopy removal. Each tree core potentially revealed evidence for multiple disturbance events. For identification of release from suppression, we used the absolute increase method (Fraver and White, 2005), where the absolute increase is defined as the difference between the mean of the 10-year sequence prior to a focal year, and the 10-year sequence after. The year of a release event was identified as the year with an absolute increase value over a threshold defined as 1.25 times the standard deviation of all absolute increase values (tree ring growth changes) for the specific species group and location in the whole dataset in this study (Fraver and White, 2005). To prevent potential misidentification of disturbance events caused by extreme climatic fluctuation, the tree ring growth increases had to exceed the pre-event 10-year running mean for at least seven years and we excluded shorter periods of increases from the analysis (Fraver et al. 2009). All the thresholds used were species and sub-region-specific (Appendix A1).

To minimise overestimation of disturbance extent or severity, we used only data from juvenile trees that responded to an increased amount of light attributed to canopy removal. To exclude the potential response of neighbouring adult or canopy trees that occupied adjacent areas outside of the newly generated forest open canopy (Lorimer and Frelich, 1989), we calculated a species-specific DBH threshold (Appendix A 1). This threshold size was estimated as an optimal cutpoint separating canopy and sub-canopy trees. All detected events were converted to a percentage of the canopy area disturbed in each plot to scale the evidence of disturbance according to each tree’s current crown area.

4.3.4 Plot and stand-level disturbance chronology

The plot-level reconstruction of disturbances was compiled from the disturbance proxy evidence identified for each tree. The evidence of tree-level disturbances was converted to the canopy area removed, which was calculated from the relation between canopy diameter and DBH for all individual cored trees on the plot (i.e., current crown area of a tree for each year of disturbance chronology divided by the sum of current crown areas of all trees cored on the plot).

Then we used kernel density functions to calculate tree-level disturbance chronologies which were used for the calculation of plot-level disturbance curves, which were weighted with disturbance evidence in individual chronologies obtained from each individual tree core (Lorimer and Frelich, 1989; Čada et al. 2020). Kernel smoothing is a widely used non-parametric data smoothing technique to estimate the probability density function of a random variable (Duong, 2007) and we use it to minimise associated noise (Trotsiuk et al. 2018). The years with the maximum proportion of disturbed canopy area were identified as peaks in the smoothed values. Maximum disturbance severity was identified as the events with the maximum proportion of canopy area disturbed gained by kernel density estimation. For the moving 30-year window we calculated the density with a smoothing bandwidth of five years. The estimated years of individual disturbance events were identified as the peak of the smoothed curve, whereby the curve was increasing for at least five years prior to the peak. Coincident peaks in the function were aggregated unless separated by a minimum of 10 years. Minor random fluctuations in the function corresponding to open canopy sizes of less than 10% of canopy area removal were considered to be unrelated to disturbance and were excluded from further analyses. The severity of disturbance events was then estimated as the percentage of canopy area removed between five years before and after identified peaks (Fraver and White, 2005).

For an overall view of disturbance activity, plot-level disturbance chronologies were grouped into the stand-level disturbance chronology curves and were smoothed by kernel density estimation (Fig. 2). All disturbance histories identified for all plots were summed to stand disturbance chronologies and stand-level disturbance events were subsequently reconstructed by aggregating plot-scale events with minimum severities of 10% canopy area removed. All detected years of disturbance events were plotted using a running kernel density function again and with the same coefficients. Peaks were again extracted as described previously for plot-level analyses. Subsequently, we randomly selected ten plots from each stand and using the kernel density function, we extracted the peak of the highest possibility of disturbance. Because the number of plots in each stand is variable, the process was repeated 1000 times to calculate peaks of the appearance of disturbance events (Čada et al. 2020). To smooth the resulting distributions of bootstrapped peaks, we used an 11-year window and bandwidth equal to 1. All extracted stand-level peaks were separated by at least 10 years. All plot-level event dates were assigned to the nearest stand-level disturbance event.

4.3.5 Disturbance synchrony and regional differences

Kendall's coefficient of concordance W (Kendall, 1970) was used to quantify the level of synchrony among time series of disturbance chronologies of the plots within the stands and compared them between study regions.

The coefficient ranges from 0 (a lack of synchrony) to 1 (perfect agreement between ranked time series). We calculated stand-specific coefficients using plot-level time series representing kernel density estimates of disturbance chronologies. Since Kendall's W depends on the number of chronologies involved in the calculation (Gouhier and Guichard, 2014), we cannot directly compare synchrony among stands with a different number of plots (Table 1). Due to the sample depth which could be associated with noise in Kendall´s W calculation and objectivity, we removed plots with trees with a summary of the canopy area under the 10% of the area of the plot after the year 1850. Together we removed disturbance chronologies of 17 out of 174 study plots. To facilitate the comparisons, we employed m-out-of-n bootstrap (Bickel and Sakov, 2008) and resampled the original pool of chronologies 10,000 times while taking subsamples of size 4 at each iteration in each stand. Average stand-specific coefficients and their variances were calculated using the bootstrap samples.

The estimates of Kendall's W were further used to compare a degree of synchrony between the Western and Eastern Carpathian forest stands. We assessed differences between the regions employing generalised linear models (GLM) assuming Gamma distribution of the response (McCullagh and Nelder, 1989). To account for different precision in Kendall's W estimates, the values of the coefficient were inversely weighted by their variances in the GLM. Diagnostic plots of the residuals showed considerable heterogeneity which violates assumptions behind the GLMs and may lead to a biased statistical inference. To prevent misleading tests of the hypotheses, we used heteroskedasticity consistent estimators for the model covariance structure to provide standard errors that are asymptotically valid under heterogeneity of variances (Zeileis, 2006). Specifically, we employed a modified HC4 estimator which is particularly useful for small samples that contain high-leverage observations (Cribari-Neto and da Silva, 2011).

4.3.6 Disturbance severity, variation over space and regional difference

Patch size analyses were provided based on the assumption that the unsampled space between the neighbouring plots with similar evidence of disturbance events was also affected by this disturbance, so we estimated the sizes of disturbed areas based on the spatial distribution of the plots showing evidence of the event. Study areas were divided into a set of smaller polygons for each plot using Thiessen polygons in ArcGIS 10.5 (ESRI, Redlands, California, USA). Plot polygons were labelled by the stand-level disturbance year evidence and when two neighbouring polygons were sharing the same stand-level disturbance event, it was assumed as one patch and the total patch area was calculated. Based on the study plot density, we limited the patch size represented by a single plot to a maximum of 4 ha. We analysed patch sizes only in stands larger than 20 ha due to the irregular shapes and small areas of the stands. The assumption of the occurrence of patches between the study plots can lead to both negative and positive errors due to the irregular shapes of disturbance patches, thus we posit that this occurrence of irregular shapes balances out the estimations of the patch sizes following Čada et al. (2020). The analysis was not conducted for 2 out of 14 stands - Vihorlat in the Eastern Carpathians and Skalná Alpa in the Western Carpathians due to their small and irregular shapes. All the analyses were performed for the time period since 1850 with the same sample of plots as the synchronicity and Kendall´s W calculations.

The estimations of patch sizes were then supplemented by statistical estimation of spatial autocorrelation of disturbance events using Moran's I in the R software ncf package (Bjørnstad, 2018; R Core Team, 2018). We tested for the degree of spatial autocorrelation in disturbance events and how the spatial autocorrelation varied over time. Test for autocorrelation was provided after removing extreme values of disturbance years before 1740 and after 1990. To test the significance of spatial associations, 1,000 Monte Carlo permutations of the disturbance severities were provided within the 30-year window and in 50-metre distance classes. The measure of the distance threshold below which disturbances are spatially autocorrelated was the correlogram model's intercept following Čada et al. (2020).

The proportion of disturbed plots was then calculated as the number of contributing plot-level events within one stand-level event divided by the total number of plots in the stand. In the case when more than one event was recorded on a plot, we consider it as a single event and it was included in the calculations.

We provide a comparison of regional differences in disturbance characteristics. Generalised linear mixed models (GLMMs; Bolker et al. 2009) were used to compare patch area and proportion of plots affected by disturbances between the Western and Eastern Carpathian forest stands. The identity of the forest stands was included as a random effect in the models to account for repeated observations from the same stands. Non-negative continuous data on patch sizes were fitted using GLMMs with gamma error distribution and logarithmic link function. Because the model residuals showed large heterogeneity between the regions, we modelled the dispersion parameter of the GLMM as a function of the region (Brooks et al. 2017), which significantly improved the model fit (ΔAIC = 2.01). Proportions of plots affected by disturbances were modelled as binomial variates with logit link function. Also, in this case, the dispersion of the residual was higher than assumed by the model (ϕ = 1.84). Thus, the binomial GLMM was refitted with an added observation-level random effect to correct for the overdispersion (Harrison, 2014).

The analyses were performed in R (R Core Team, 2021) using the libraries DHARMa (Hartig, 2022), glmm TMB (Brooks et al. 2017), ggplot2 (Wickham, 2016), sandwich (Zeileis et al. 2020) and synchrony (Gouhier and Guichard, 2014).

4.4 Disturbance regime, synchronicity and species richness in the Western and Eastern Carpathian regions

4.4.1 Study area

For this study, we chose the same pool of the plots from stands located in the Western and Eastern Carpathian Mountains in Slovakia as in previous section (4.3 Synchronicity and variation of natural disturbances across beech-dominated primary forests in the Carpathians). Stands were identified based on a national inventory of primary forests and were designed to identify stands where no human activity has directly affected the locations.

Since it is impossible to totally rule out human impacts (such as heavy logging and grazing) on forest sites in Central European primary forests, the inventory was created to identify only areas where these activities have not had a direct impact on the tree canopy layer. Field survey data, historical information from military maps of the Austro-Hungarian Empire from 1764 to 1768 and 1806 to 1869, and aerial photos from 1950 were all combined to create this complicated exploration (Mikolaš et al., 2019).

From all identified primary forest sites in Slovakia, which includes around 10,000 ha of forests (www.pralesy.sk, 2019), we selected 14 stands and 174 study plots in beech (Fagus sylvatica L.) - fir (Abies alba Mill.) forests for deep disturbance chronology analysis with the altitude range from 642 to 1285 m (Table.1). In each of the 14 mapped primary forest polygons, we established 6-20 circular permanent study plots (PSP) with areas of 0.15 ha. For their selection, a polygon network (10 ha each) was created using the ArcView 9.3 Environment (ESRI ArcGIS, 2011) following section 4.3.

The primary forest sites are based on the existing primary forest study plots network of permanent study plots established within the REMOTE project (https://www.remoteforests.org). Research area is spanning a range of altitudes where, in most of the cases, is bordering with the upper mountain belts of Norway spruce forests (Tab. 1). In the Western Carpathian mountains, research areas spanning bigger altitude ranges and altitudes are higher than in the Eastern Carpathians, where altitudes are lower, slopes are milder and there are different bedrock (see methods). Moreover, stands differed in tree species diversity, Western Carpathians stands are more diverse in tree species richness then Eastern Carpathians, where the beech (*Fagus sylvatica* L.) and fir (*Abies alba* Mill.) are present as the most common combination of species in forests. Other the most common tree species admixtured in the forests are Norway Spruce (*Picea Abies* H. Karst.), Maple (*Acer Pseodoplatanus* L), European ash (*Fraxinus excelsior* L.) and Elm (*Ulmus glabra* Huds.) and it´s especially in Western Carpathian part of the plots (Figure 6; Figure 7).

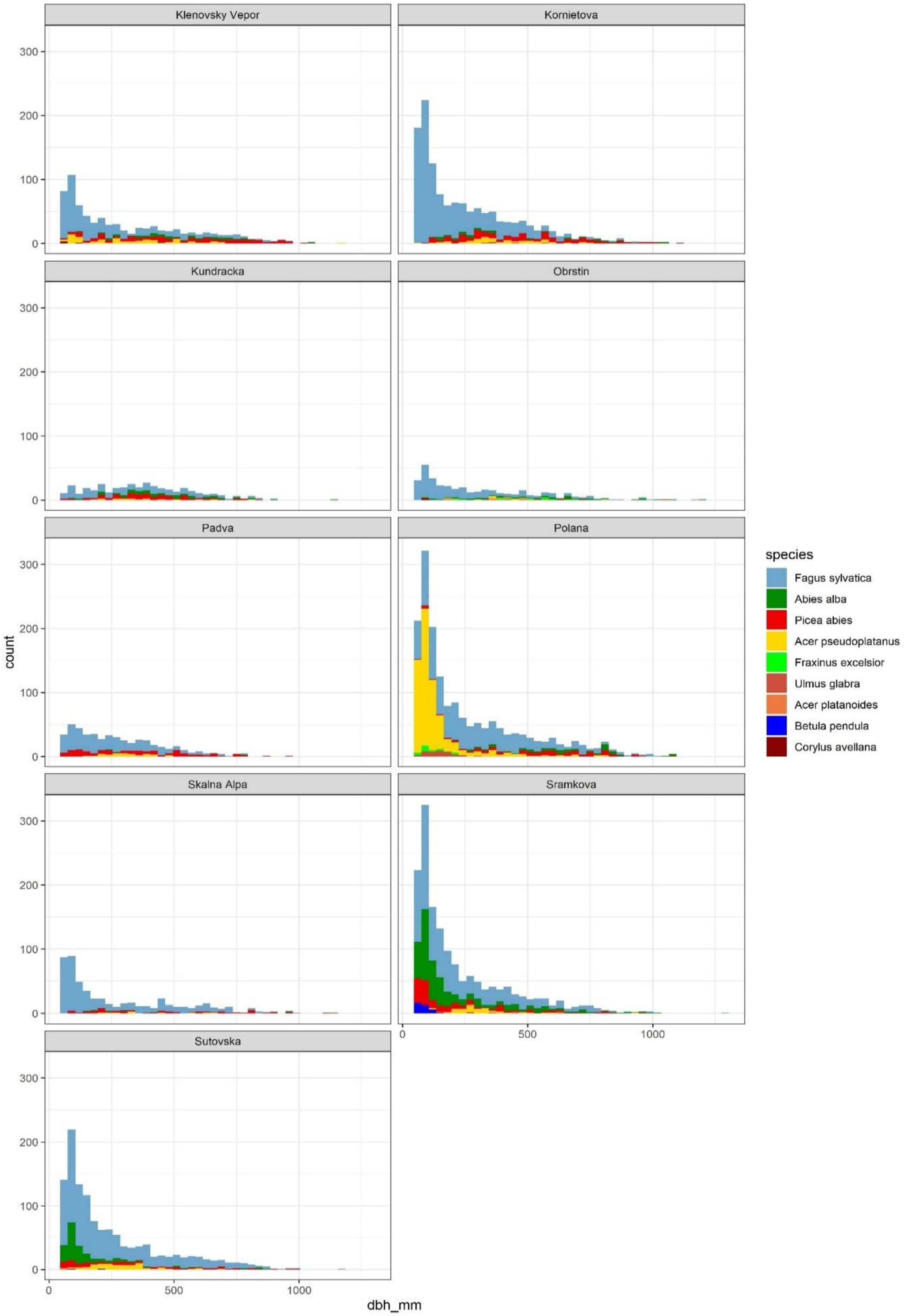

Figure 6: Species composition distributions on stand level for stands in Western Carpathian region. The high of columns are representing absolute number of trees with DBH ≥ 6 cm per species divided into DBH classes.

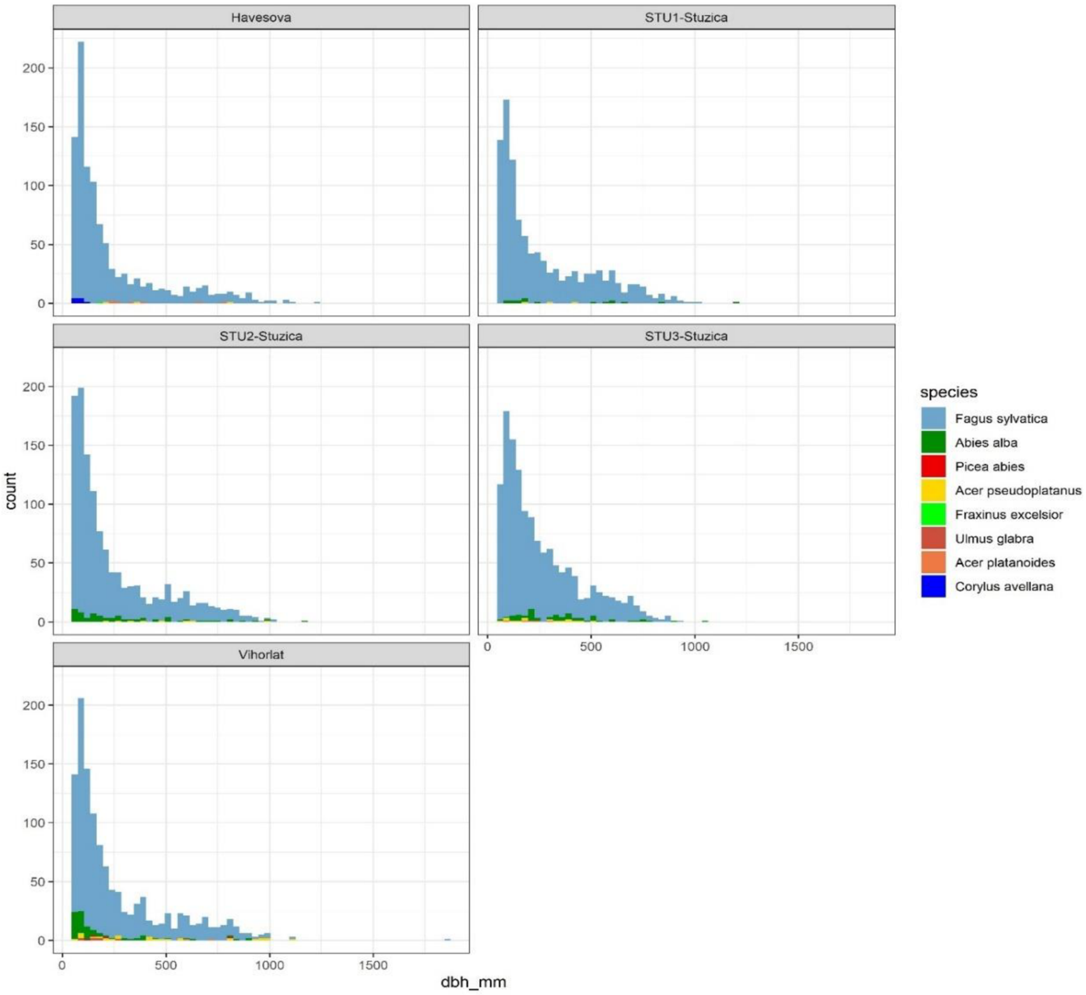

Figure 7: Species composition distributions on stand level for stands in Eastern Carpathian region. The high of columns are representing absolute number of trees with DBH ≥ 6 cm per species divided into DBH classes.

4.4.2 Data collection

For establishing permanent study plots (PSP) we generated a polygon network and using the ArcView 9.3 Environment (ESRI ArcGIS, 2011) we generated a random point from which were delineated centres of the plots in 40 m distance along the contours to both sides from the generated point following section 4.2. The data pool of the plots, their size and their number were identical as in section 4.3. Then, we mapped all positions of the trees over 6 cm within plots using laser measuring devices linked to a GIS (Field–Map, IFER 2008). Moreover, data about diameter distribution at breast height (DBH) and forest tree species were recorded to conduct disturbance history and tree species richness. The current crown areas of

15 cored trees were also obtained from permanent study plots to quantify the relationship between crown area and diameter. The crown areas was estimated by measuring the crown area of 15 individual cored trees in the field. After that, each crown area was predicted using a statistical relationship between the estimated crown areas of the cored trees, and DBH which is a regionally specific relation.

One core from the tree was extracted perpendicular to the terrain slope direction at a height of 1 m above the ground to avoid reaction wood (Speer, 2010). Each tree core was taken by the hierarchy of size classes within a circle around the plot centre which consisted of three nested circles with areas 500, 1000 m^2 and 1500 m^2. The scheme of taking the tree cores based on the distance from the plot centre was identical to that in section 4.2. However, the data pool of taken tree rings was not identical in this study because of the data limitations. For synchronisation and species richness analysis, many of the plots were excluded from the study.

Dendrochronology samples were measured and processed by classical dendroecology method as in sections 4.1 and 4.2 using a LINTAB sliding table and TsapWin software (RINNTECH, Heidelberg, Germany, http://www. rinntech.com) followed by cross- dating using the software CDendro 7.1 (Larsson, 2003).

4.4.3 Tree level disturbance chronology process

As in previous sections, for historical disturbance chronology creation we used tree-ring width changes to calculate the chronologies of tree-level disturbances which was later used as proxy data for plot and stand-level disturbances. Two growth patterns of radial growth were detected: abrupt, sustained growth increases known as growth releases that signify the death of a former canopy tree and rapid early growth rates that suggest past recruitment or regeneration below a disturbance-generated canopy gap (Frelich, 2002).

Consequently, we connected the current crown areas of a given year in the chronology with the year of the detected releases or recruitments, assuming that the crown area of trees responding to the initial gap formation approximates the size of the former canopy gap, (Lorimer and Frelich, 1989; Schurman et al., 2018).

To identify the release from suppression, We used the absolute increase method (Fraver and White, 2005). The absolute increase method (AI) is the difference between the mean of the 10-year series before a given year (M1) and the 10-year sequence after (M2).

(M2) - (M1) = AI

The threshold value which denotes the year of a release was determined by multiplying by 1.25 the standard deviation of all absolute increase values in the whole dataset examined in this work. We eliminated shorter periods of increases from the study in order to avoid the possibility of misidentifying disturbance events because the significant climate fluctuations. The tree ring growth increases had to surpass the pre-event 10-year running mean for a minimum of seven years.

All the thresholds used were species and sub-region specific (Appendix A1). To minimise overestimation of disturbance extent or severity, we only used data from juvenile trees that occupied the actual area of the disturbance and responded to an increased amount of light attributed to canopy removal. Thus, we excluded neighbouring adult or canopy trees that occupied adjacent areas outside of the newly generated forest gap (Lorimer and Frelich, 1989). A specific threshold DBH limit was used to discriminate adults from juvenile trees at the time of the event (Appendix A1). This threshold size value was estimated from a regression model fitted with data from the measured known canopy and suppressed trees (Janda et al., 2017).

4.4.4 Plot and stand-level disturbance chronology

As in other sections, the general principle of the creation of the disturbance curves was similar. A plot-level record of disturbances was created by compiling the disturbance proxy evidence found for every tree, and this record was used to evaluate the severity of disturbances. After that, the records of plot-level disturbance events provided proxy evidence for stand-level records of disturbance events calculation.

For the plot level disturbance curve, we used a running kernel density function to smooth the years of all the disturbance proxy data at each plot. The years were weighted based on the trees' relative current crown areas, which are calculated by dividing the current crown area of a tree by the total current crown areas of all the trees cored on the plot (Trotsiuk et al. 2018; Čada et al. 2020; Frankovič et al. 2021; Kameniar et al. 2023). For the Kernel density estimation, which is a non-parametric method to estimate the probability of density function, we set up the length of the moving window for 30 years and bandwidth equal to 5. We obtained the resulting disturbance curve and extracted years of the peaks with the highest probability of density, and we extracted only the peaks before which was curve was increasing for at least 5 yr. The next criterion was the minimum time period between two peaks was at least 10 years. The severity of the individual event was then calculated as the summary of all relative areas of a disturbed canopy of the trees on the plot whose evidence of disturbance occurred within an 11-year window. All used parameters were set based on the assumption that most trees respond to disturbances within a decade (Lorimer and Frelich 1989).

Further, stand–level disturbance years were calculated from the plot level and data were smoothed using a running kernel density function. All peaks were again extracted by the same method as at the plot level, using the same coefficients. Because of the different number of plots per stand, we used the bootstrapping method on random subsets of the plots with each stand. For randomly selected 10 plots per stand we calculated for 1000-time kernel density and extracted peaks. The resulting distribution we again smoothed by kernel density function. We used an 11-year window and bandwidth equal to 1, and we then extracted all stand-level peaks (i.e., stand-level years of disturbance events) separated by at least 10 yr. After that resulting stand–level peaks were associated with the nearest plot-level peaks from proxy evidence.

The study period of chronology was restricted to the years 1810–1990, because the sample size was often too small before 1810, and tree-ring data collected after 1990 are not representative since our data's minimum tree size leaves out more recent tree recruitment.

4.4.5 Disturbance synchrony and species richness

For synchrony evaluation we used Kendall’s coefficient of concordance W (Kendall, 1970). The level of synchrony of disturbance chronologies can vary from 0 (a lack of synchrony) to 1 (perfect agreement between ranked time series). As proxy data were used disturbance chronologies time-series of plots within the stands and for each stand were calculated Kendall’s coefficient of concordance W individually.

Since Kendall’s W depends on the number of chronologies involved in the calculation (Gouhier & Guichard, 2014), we cannot directly compare synchrony among stands with a different number of plots (see Table 1). To facilitate the comparisons, we employed m-out-of-n bootstrap (Bickel & Sakov, 2008) and resampled the original pool of chronologies 10,000 times while taking subsamples of size 4 at each iteration in each stand. Average stand-specific coefficients and their variances were calculated using the bootstrap samples.

The estimates of Kendall's W were further used to compare a degree of synchrony between the Western and Eastern Carpathian forest stands. We assessed differences between the regions employing generalised linear models (GLM) assuming Gamma distribution of the response (McCullagh & Nelder, 1989). Instead of the canonical inverse link function, we used a logarithmic link function that considerably improved the model performance. To account for different precision in Kendall's W estimates, the values of the coefficient were inversely weighted by their variances in the GLM. Since the stands differed in tree species diversity, we also linked the degree of disturbance synchrony with tree species richness. However, the number of cored trees ranged widely among plots (29–199 trees per plot), which may introduce a bias into the diversity estimates. Therefore, we simulated the same sampling effort ($n = 29$ trees per plot) and calculated expected species richness using rarefaction analysis (Chao et al., 2014). The rarefied species richness was then used as a predictor of disturbance synchrony in the GLM. Because the regions and the rarefied richness were strongly correlated (point-biserial correlation: $r = 0.88$, $p < 0.0001$), we did not combine both predictors in a single GLM but fitted two separate models. Diagnostic plots of the residuals showed considerable heterogeneity which violates assumptions behind the GLMs and may lead to a biased statistical inference. To prevent misleading tests of the hypotheses, we used heteroskedasticity consistent estimators for the model covariance structure to provide standard errors that are asymptotically valid under heterogeneity of variances (Zeileis, 2006). Specifically, we employed a modified HC4 estimator, which is particularly useful for small samples that contain high leverage observations (Cribari-Neto & da Silva, 2011). The predictive performance of the GLMs was compared based on leave-one-out cross-validated determination coefficients.

The analyses were performed in R (R Core Team, 2021) using the libraries DHARMa (Hartig, 2022), glmmTMB (Brooks et al., 2017), ggplot2 (Wickham, 2016), sandwich (Zeileis et al., 2020) and synchrony (Gouhier & Guichard, 2014).

5. Results

The results of the dissertation thesis consist of two primary and five side chapters, each of them representing different units based on the Aims of study from section 3.0. All results consist of the research that was published or will be published in scientific journals. The first chapter of the results (5.1) was published in a peer-reviewed, SCI-impact scientific journal covering forest management and ecology problematic *Forest Ecology and Management* entitled „Natural dynamics of temperate mountain beech-dominated primary forests in Central Europe". The chapter (5.2.3) was published in the peer-reviewed scientific journal *Zprávy lesnického výzkumu* entitled „Disturbance regime, synchronicity and species richness in primary beech-dominated (*Fagus Sylvatica* L.) forests in Central Europe". Publication named „Synchronicity and variation of natural disturbances across beech-dominated primary forests in the Carpathians" will be resubmitted in *Forest Ecology and Management* journal.

The first part focuses on the general description and reconstruction of historical disturbances and forest structure and high-severity disturbances in beech-fir forests in the Low Fatra (N=28 plots) and Great Fatra (N=14 plots) was found. It covers a 250 year long time period and is explaining prevalence of mixed severity disturbance regime. Moreover determines the spatial extent of the disturbance regimes in the region (Section 5.1). explaining the difference between disturbance regimes, synchronicity and spatial extent of disturbances between the stands in the Western and Eastern Carpathian regions (Section 5.2). The third part explains species specific relationship between species composition and synchronicity between the stands within the Western and Eastern Carpathian regions (Section 5.3).

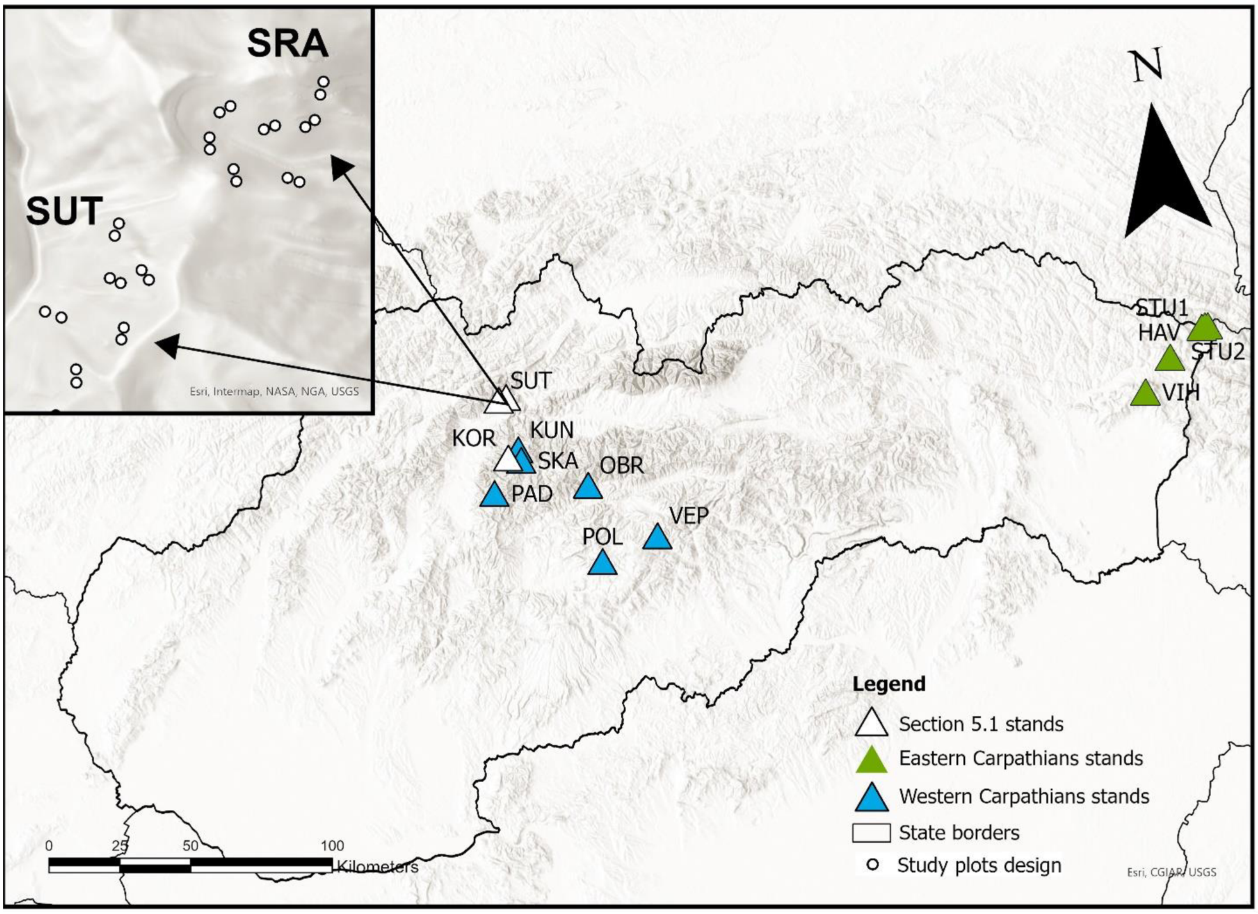

Figure 8: The system of data collection within the sections of results. Section 5.1 (non - colored triangles) consists of three stands. Other two sections studies were extended to 14 stands across Carpathian mountains within Slovakia.

5.1 Natural dynamics of temperate mountain beech-dominated primary forests in Central Europe

5.1.1 Temporal aspects of historical disturbance regime of the beech-fir forests in Western Carpathians

Our reconstructed disturbance chronologies for the stands in Low Fatra (N=28 plots) and Great Fatra (N=14 plots) spanned a 250 year long time period. A total of 1139 tree cores were collected. The summarized disturbance chronology of all three stands (Figure 15; Figure 16) shows variability in disturbance severity in time, with periods of escalation. The escalation of stand-level disturbance events - identified by the kernel density function estimation of disturbances - occurred in the individual stands (Kornietová, Šramková, Šutovská) in roughly regular time periods. On the 42 permanent study plots, we identified a total of 144 disturbance events with severities exceeding at least 10% of canopy area removed.

We observed that disturbance frequency peaked over regular time periods. We selected periods with the highest frequency of disturbance activity to assess disturbance synchronicity in time. Twenty-year long time periods of disturbance chronology were derived visually, as they represent periods with the highest amount of disturbance events. Disturbance activity was clumped in all three stands, with major peaks appearing largely around the middle of the 19th century in the periods 1830-1850 and 1860-1880.

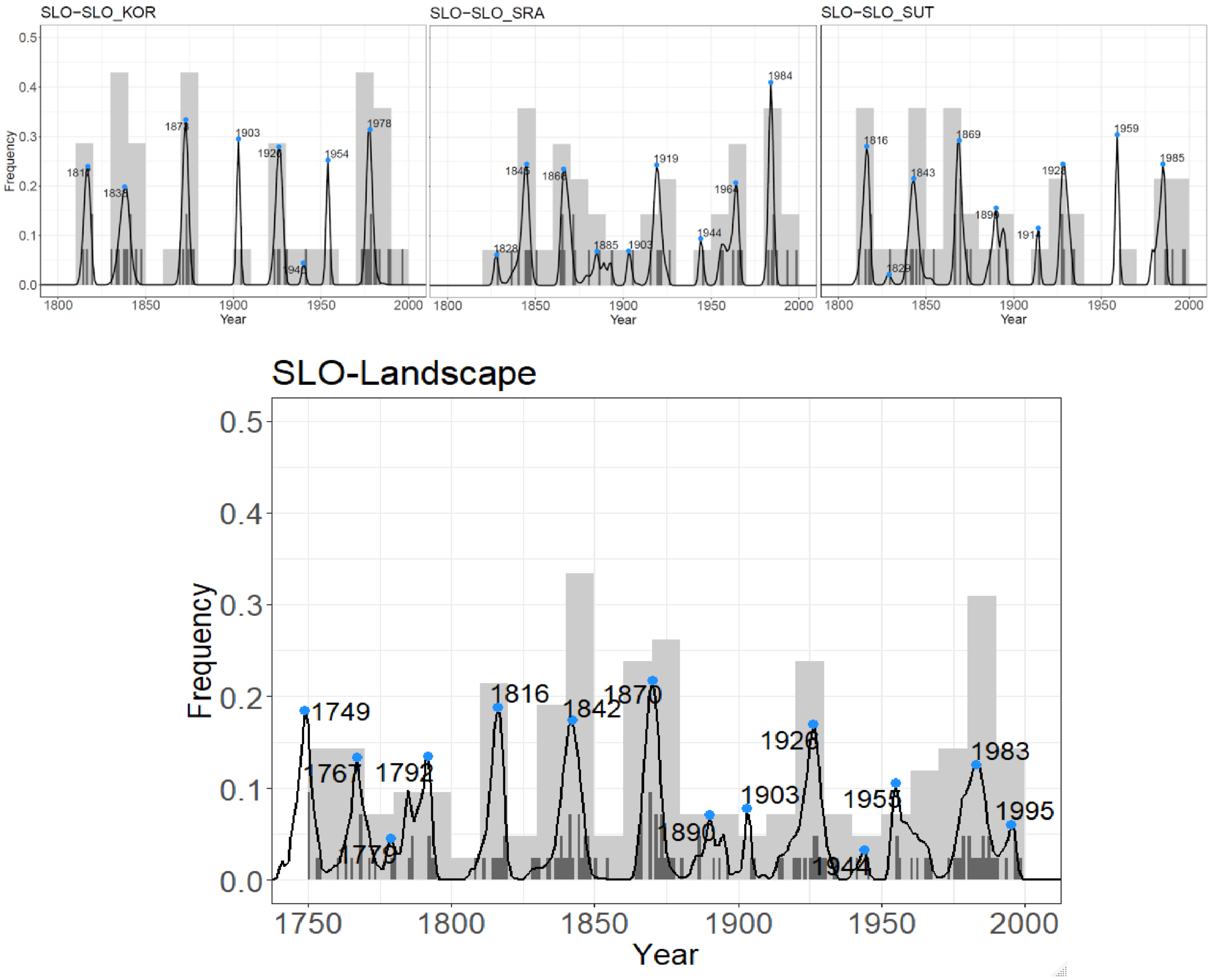

Figure 9: Stand-level (upper panel) and landscape-level (lower panel) reconstruction of disturbance history, using plot-level disturbance events with ≥10% canopy area removal (severity). Their distribution is represented by the height of the black bars (smoothed by kernel density function, black curve). The grey bars represent the sum of the disturbance events at the end of a given decade (smoothed by a kernel density function). The kernel density was fitted to the random subset of 10 plots per stand 1000 times (bootstrapped), and the peaks (blue dots) in the resulting distribution (black line) were attributed to the years of stand-level disturbance events.

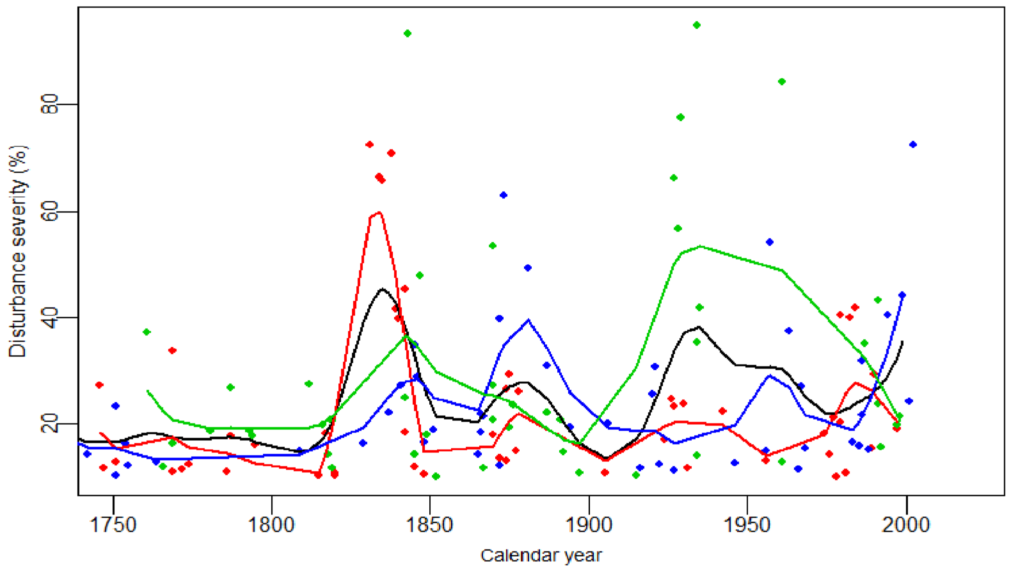

Figure 10: Temporal distribution of disturbance events. Each dot represents a plot-level disturbance event with ≥10% of canopy area removal (severity), smoothed by spline function (lines). The black line represents the smoothed function of all plot–level disturbance events. The coloured lines represent the smoothed functions of plot–level disturbances for each of three stands: KOR - red, SRA - blue, SUT - green.

Tree ring evidence of disturbance events were comprised of gap recruited and released trees in approximately equal proportions (52% were gap recruited), which indicated fast growth rates of juvenile trees and growth in open canopy conditions. Release was detected by identifying the discrete event of growth change, but regenerating trees can take several years or decades to establish and grow to a coring height. Due to this fact and also due to delayed growth response, all records of disturbance events can oscillate over prolonged time periods. Reconstructed disturbances were highly variable in terms of severity, with low to moderate events, as well as a few occurrences of extreme disturbances that removed > 60% of the canopy area of a site (Figure 10). In most records, we detected no evidence of very high-severity disturbance events. The majority of events (N=65) were low-severity, with less than 20% of the forest canopy removed in all of the stands, which suggests that lower-severity and smaller-scale events were more frequent (Figure 10). Based on the number of events, the evidence shows differences between the proportion of lower- and higher-severity disturbance events in the periods with the highest total number of disturbance events (1830-1850, 1860-1880, 1920-1940 and 1970-1990). While events with low- and moderate-severity disturbances were prevailing in the time period 1860-1880, there was no event with very high severity (Figure 11).

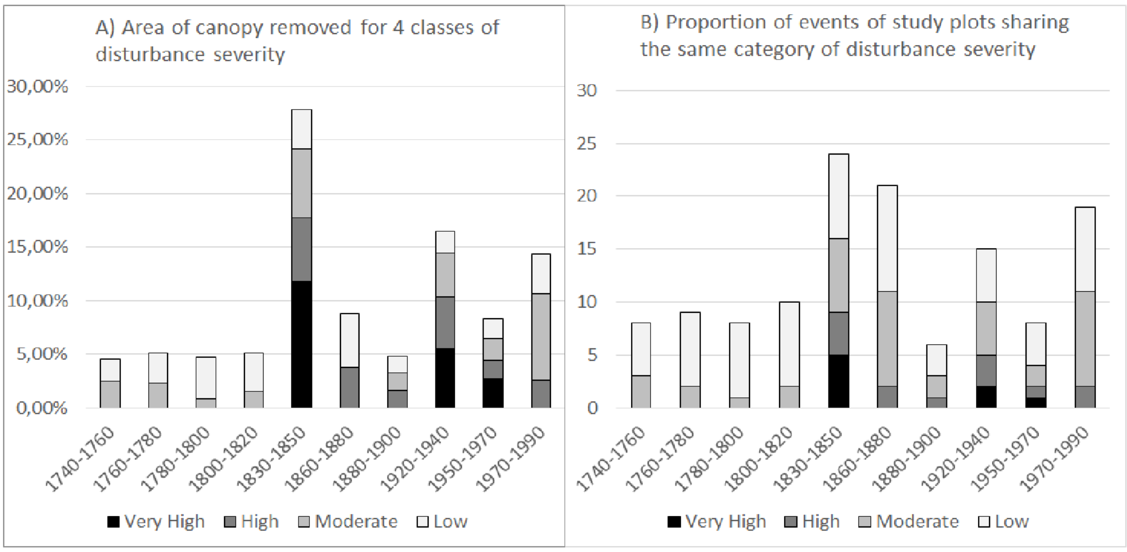

Figure 11: The number of events as a percentage of the total on all permanent study plots sharing a similar maximum disturbance severity in a given period, by canopy area removed (A) and the number of events in the whole study region (B). Maximum-severity disturbance events are classified into four categories (Very High ≥ 60%, High 59-40%, Moderate 39-20 % and Low ≤ 20%).

The period between 1830-1850 was characterized by the largest proportion of very high-, high- and moderate-severity disturbances in terms of both canopy area removed and also frequency of events, while the period between 1860 - 1880 - which had the second largest number of events - was not disturbed as much in regard to the amount of canopy area removed (Figure 11A).

In general, the highest proportion of canopy area was removed by high-severity and moderate-severity disturbances. Our results show that there is unequivocal evidence for past occurrences of severe disturbances across all studied forest stands. In the Kornietová stand, all of the detected very high-severity disturbances events occurred within the time period 1830-1850 within the plots close to each other, with the exact years and percent of canopy area removed being: 1831 - 72%; 1838 - 71%; 1834 - 66% and 1835 - 66%, which suggests a gradation of disturbance events in this part of the stand, which creates patchy forest disturbance dynamics. In Šramková, one very high plot-level disturbance event was detected in 1873 with 63% of canopy area removed, and one recent disturbance event from 2002 with 72% of canopy area removed. In the Šútovská stand, the high-severity disturbance events detected and percent of canopy area removed were: 1934 - 95%; 1843 - 93%; 1961 - 84%; 1929 - 78%.

5.1.2 Spatial aspects of historical disturbance regimes of the beech-fir forests in Western Carpathians

Between the stands, the spatial pattern of canopy area removed in disturbance events classified into the four severity classes was more similar between the Kornietová and Sutovská stands, where the sum of canopy area removed in the strongest events were substantially larger than in Šramková stand (KOR 22% and SUT=27% vs. SRA=11%). The highest proportion of very high- and high-severity disturbances occurred in Sutovska (Figure 12). A series of disturbance events occurred in the time period 1920-1940, affecting the stand with a higher number of events of high- and very high-severity. Specifically, two disturbance events resulted in more than 60% canopy area loss on the study plots, and two additional disturbance events caused more than 80% canopy removal in this time period on the plot-level (Figure 10). There was also the occurrence of other disturbance events with over 80% of canopy removal in this study stand, approximately in the years 1843 and 1961.

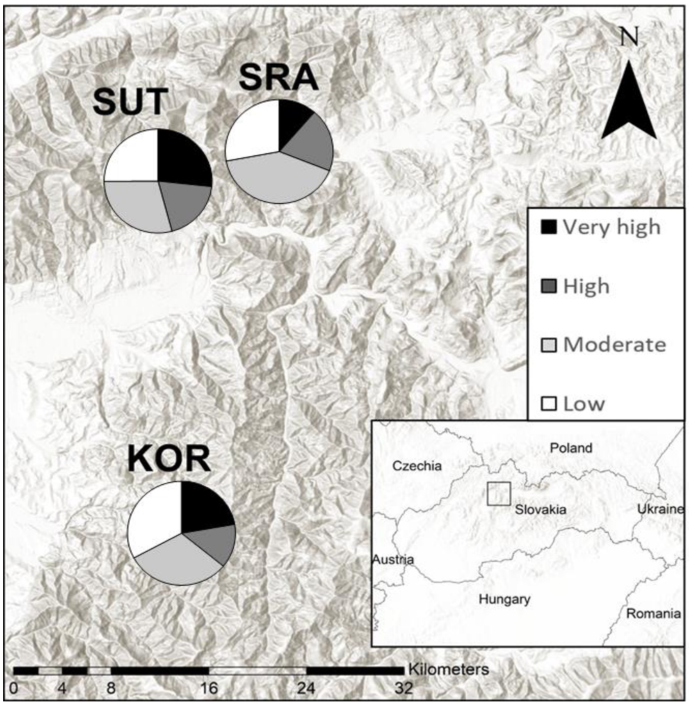

Figure 12: The number of events on all plots sharing a similar maximum disturbance severity, by study stands and their spatial distribution. The maximum severity of disturbance events were classified into four categories (Very High ≥ 60%, High 59-40%, Moderate 39-20 % and Low ≤ 20%.

The spatiotemporal maps of maximum severity disturbances within the stands - based on the maximum severity events within the given 20-year periods - showed the whole range of canopy area removal on the study plots. Synchronicity varies from low-synchronicity of maximum-severity values to higher degree of synchronicity (Figure 10). In the time period 1920-1940 in the Sutovska stand, there was evidence of very high-severity plot-level disturbance events, while in the Šramková stand, such evidence was lacking. Due to the fact that both of the stands are close to each other, the evidence of a high-severity disturbance event in the Sutovska stand in the year 1934 suggests that it was a local-scale disturbance event, which was probably associated with a local thunderstorm, or another specific event including drought, bark beetle outbreaks or ice storms (Nagel et al., 2017; Dobrowolska et al. 2017).

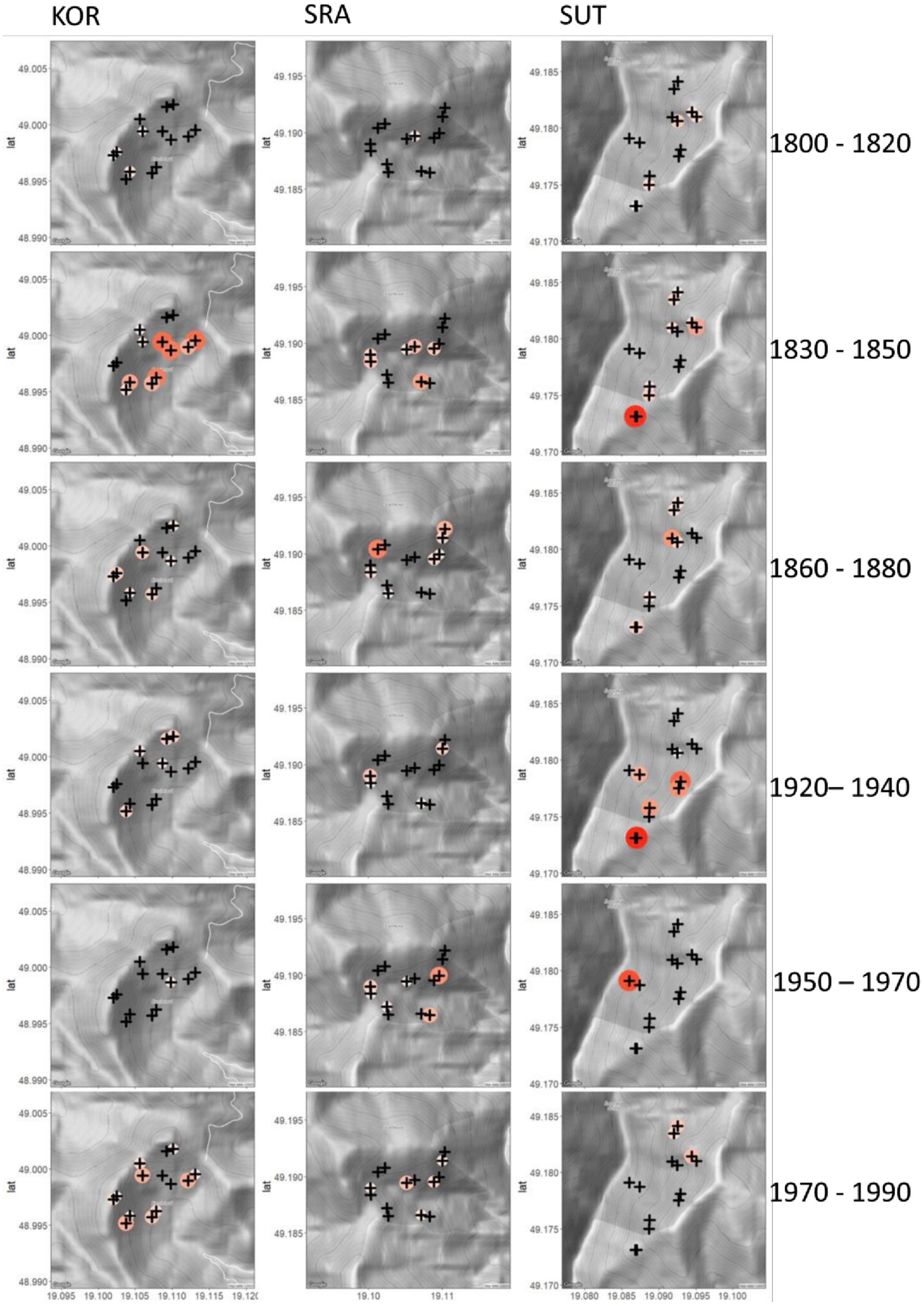

Figure 13: Maps of time-lapse collection of disturbance rates in Kornietova, Šramková and Sutovska for the periods with the occurrence of the largest amount of disturbance events, following Fig. 2 and 3. To capture prolonged recruitment periods, disturbance rates were summed in two consecutive decades for selected periods. The size of the circle represents each disturbance class, with the circle size increasing with the amount of disturbed canopy, categorized into the following: Very High ≥ 60%, High 59-40%, Moderate 39-20 % and Low ≤ 20% of canopy area disturbed per plot. The crosses represent the position of the study plots with no evidence of disturbance events in a given time period.

5.2 Difference in the disturbance regime, synchronicity and species richness in the Western and Wastern carpathian region

5.2.1 Difference in the disturbance regimes and components (i.e. severity, patch sizes and proportion of disturbed plots) in the Western and Eastern Carpathian region

We collected 6186 tree cores in total and identified 517 plot-level disturbance events with severities exceeding at least 10% of canopy area removed between the years 1800 - 2000. The summarised 200-year-long time period of disturbance chronology of all plots shows high temporal variability in disturbance severity, with periods of stand and region-level escalation (Figure 14). Plot-level disturbance chronologies show evidence of high and very-high severity disturbance events with more than 60% canopy area removed, especially on the plots in the Western Carpathians forests.

The Kernel´s density smoothed compilation of the disturbance regimes of the Carpathian stands shows evidence of high and very-high disturbance severity (40-60% canopy area removed) peaks. The most affected plots with evidence of high-severity disturbances occurring in the smaller period (30 years) were found on several study plots, especially in the Western Carpathians. We observed a small difference between disturbance regimes in the Western and Eastern Carpathian plot level chronologies. In the Western Carpathians a bigger synchronisation is present, which suggests different disturbance agents from the point of atmospheric processes and maybe other environmental factors. The stands in West and East differ in local environmental conditions such as topography factors (Tab. 1) and species composition. However, stand-level smoothed lines do not show very big difference between Western and Eastern Carpathian regions (black lines), while the individual study plots chronologies show very high variability and slightly bigger pulsations of high severity disturbance events (coloured lines, Figure 15, Figure 16).

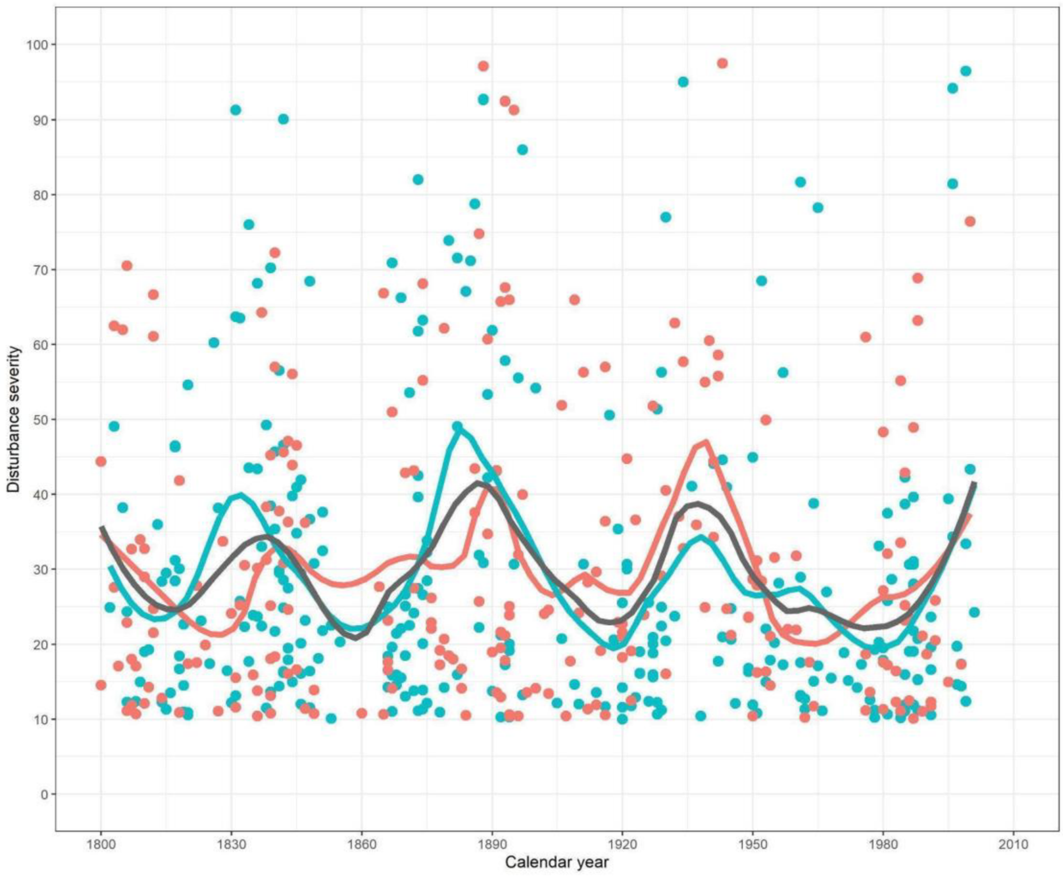

Figure 14: Temporal distribution of disturbance events. Each dot represents a plot-level disturbance event with ≥ 10% of canopy area removal (severity), smoothed by local regression polynomial function (lines). The black line represents the smoothed function of all plot–level disturbance events, blue colour represents data from the Western Carpathians and red colour from the Eastern Carpathians.

The forest in the Kornietova (KOR) stand was affected by a group of high-severity disturbance events when the 6 of 14 study plots were affected, with a mean value of disturbance severity of approximately 60% of canopy area removal, with peaks in period 1825-1835 (Figure 15; Figure 16). This was followed by more recent moderate and high-severity disturbances that occurred in 1980 with a wider mean of disturbance severities. Sutovska (SUT) stand experienced the peak of disturbance severity approximately at the same time as in Kornietova (KOR), which can be connected to one of the atmospheric patterns of windstorms. Evidence of individual plot level extreme high-severity events also occurred in Sutovska (SUT) with the highest values of 92% of canopy area removed in 1934. The Kundracka (KUN) stand was also affected by high- and intermediate-severity disturbance events in the same time as the Kornietova (KOR) stand which can suggest the spatial proximity. Polana (POL) stand was affected by the most severe disturbance events, synchronised into the two peaks. The first peak was detected approximately between 1860 - 1890 with mean values of 63% of canopy area removed, with the highest value of 90%. The subsequent peak occurred more recently on different study plots, with a mean disturbance severity of 85% on 9 study plots, suggesting that older, larger trees were disturbed (Figure 15).

Western Carpathians

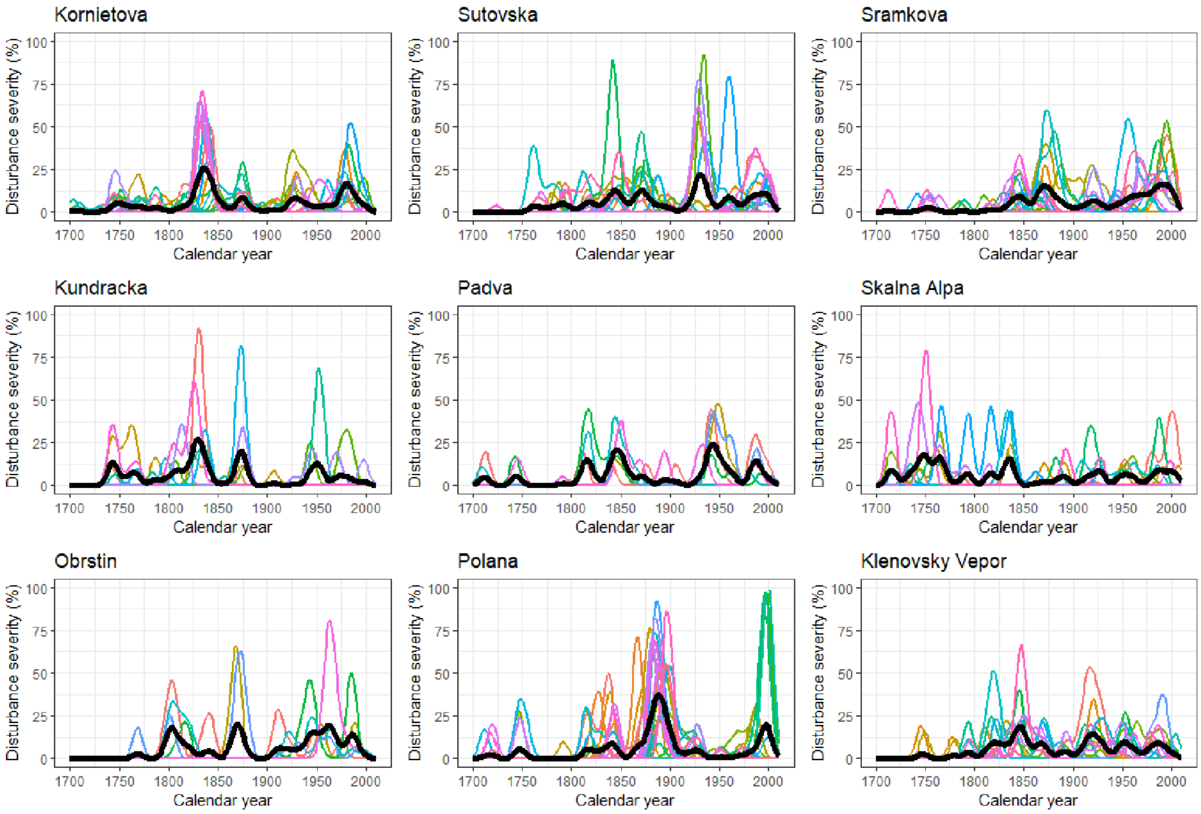

Figure 15: Plot- and stand-level disturbance chronologies of the Western Carpathians study stands, composed from stand-level chronologies (black lines) which were derived from plot-level chronologies (colored lines) calculated using kernel density estimation (KDE) of disturbed area. These chronologies reflect a temporal range of annual rates integrated into point estimates by a Gaussian kernel.

The Eastern Carpatians forests were affected by less severe disturbance events, which affected study plots individually (Figure 16). The highest number of plots affected by high- and very-high severity disturbances were four in the case of the Vihorlat (VIH) study site. Here, a disturbance peak was detected in 1890 in four plots; these were affected by disturbances with a mean severity of 75% of the canopy area removed. In the Stuzica stand (which was subdivided into three stands: STU1, STU2, STU3), several plot-level disturbances were detected, but only in STU3, rather than across the entire stand.

Eastern Carpathians

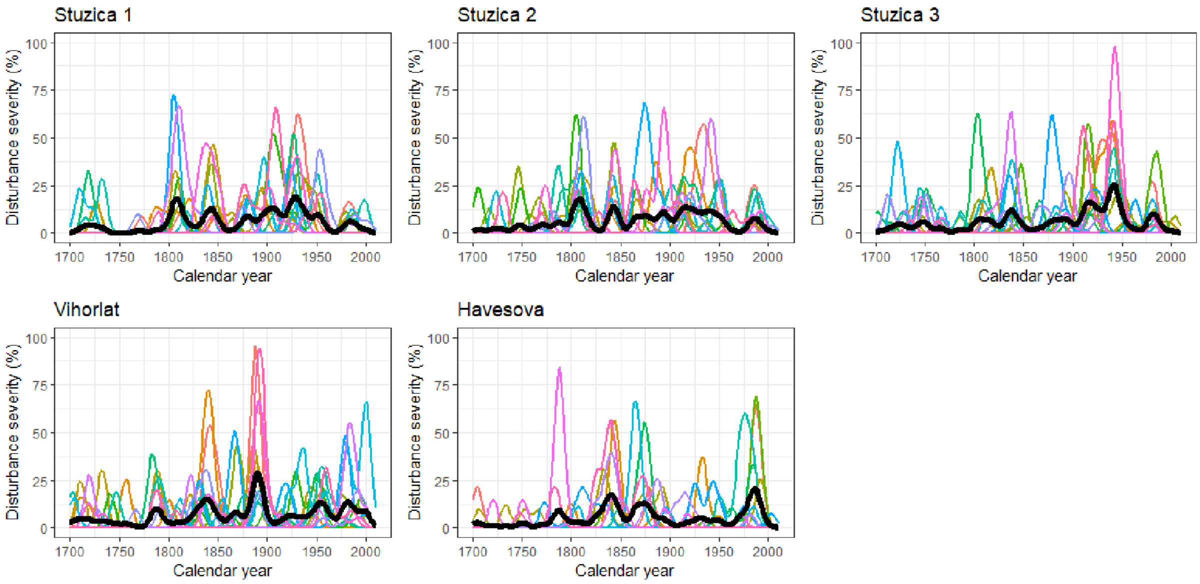

Figure 16: Plot- and stand-level disturbance chronologies of the Eastern Carpathians study stands, composed from stand-level chronologies (black lines) which were derived from plot-level chronologies (colored lines) calculated using kernel density estimation (KDE) of disturbed area. These chronologies reflect a temporal range of annual rates integrated into point estimates by a Gaussian kernel.

Stands in the Western Carpathians overcame high-severity disturbance stand-level events, which drove forest development and shape. Synchronicity between peaks of plot-level disturbance events on one stand can suggest that it was one event, while a group of peaks can suggest that a forest was affected by several disturbance events in a smaller period. The fluctuations of disturbance gradation are visible in the peaks in years: 1830; 1890 and 1935 (Figure 14).

Waves of high stand-level disturbance severity were documented in Kornietova (KOR) stand, with 27% of the canopy area removed in 1836, and in Kundracka (KUN), where 26% of the canopy area was removed in 1830. The biggest fluctuation of the smoothed kernel density stand-level disturbance severity event was detected in the Polana (POL) forest in the Western Carpathians, which was caused by high-severity plot-level disturbances accumulated in one time period. (Figure 17). The Eastern Carpathian forests were affected by less severe stand-level disturbance events because the study plots were affected individually. The highest number of plots affected by high- and very-high severity disturbances were four in the case of the Vihorlat (VIH) study site in the Eastern Carpathians (Figure 17).

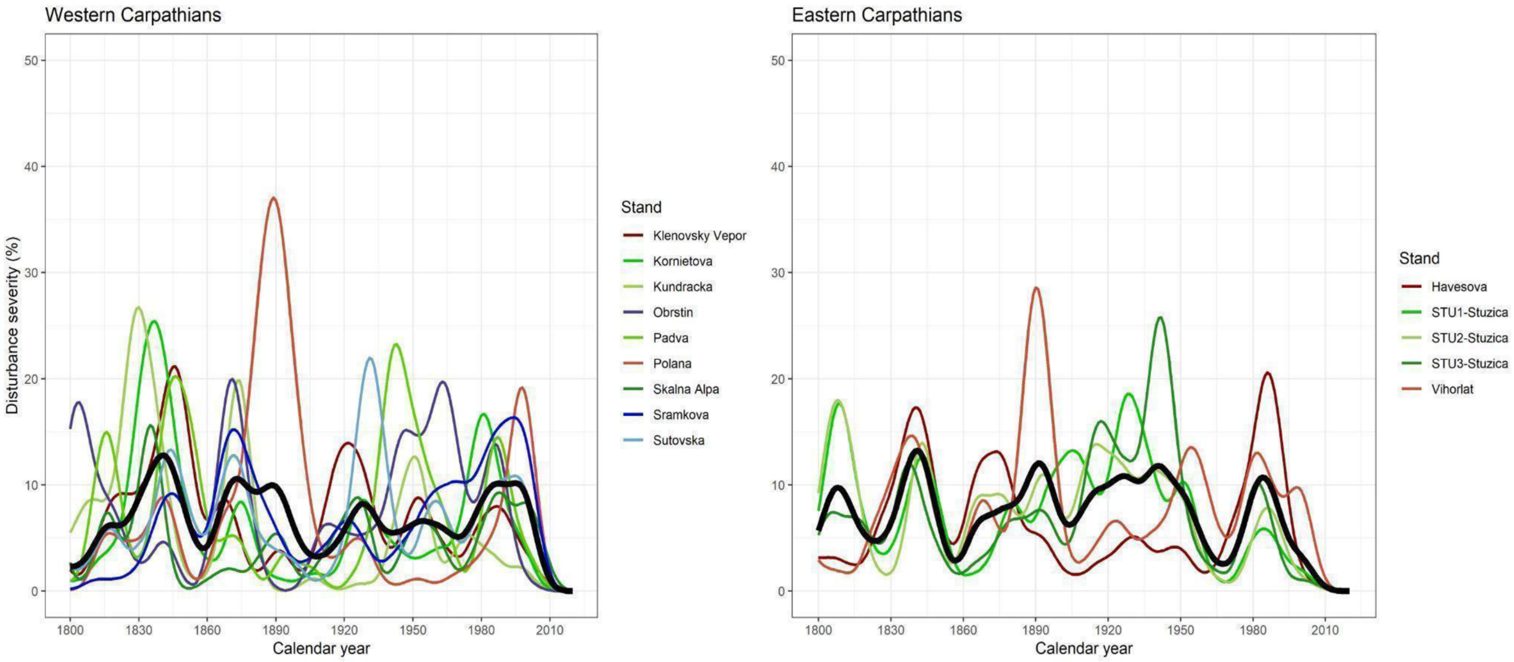

Figure 17: Landscape-level disturbance chronologies divided into the Western and Eastern Carpathians, composed from stand-level chronologies lines (coloured lines) which were calculated using kernel density estimation (KDE) of disturbed areas. Each colour represents one stand. The black line represents smoothed landscape-level chronologies for the whole landscape. These chronologies reflect a temporal range of annual rates integrated into point estimates by a Gaussian kernel.

The landscape level disturbance analysis shows differences between the Eastern and Western Carpathians. The proportion of releases vs. gap recruitment events that detected disturbances shows a significantly higher proportion of releases in the Eastern Carpathians (69.4% of releases presented) than in the Western Carpathians, where 56.8% of events were driven by releases (Figure 18). Reconstructed disturbances were highly variable in terms of severity, with low to moderate events, as well as a few occurrences of extreme disturbances that removed > 60% of the canopy area of a plot. In most records, we did not detect evidence of very high-severity disturbance events i.e. with > 60% of plot-level canopy area removal (only

56 of 517 events). However, the ratio of releases vs. gap recruitment indicates that higher severity disturbances occurred in the more mixed species forests in the Western Carpathian region, while the Eastern part was driven by disturbances of smaller scales which contradicts the hypothesis.

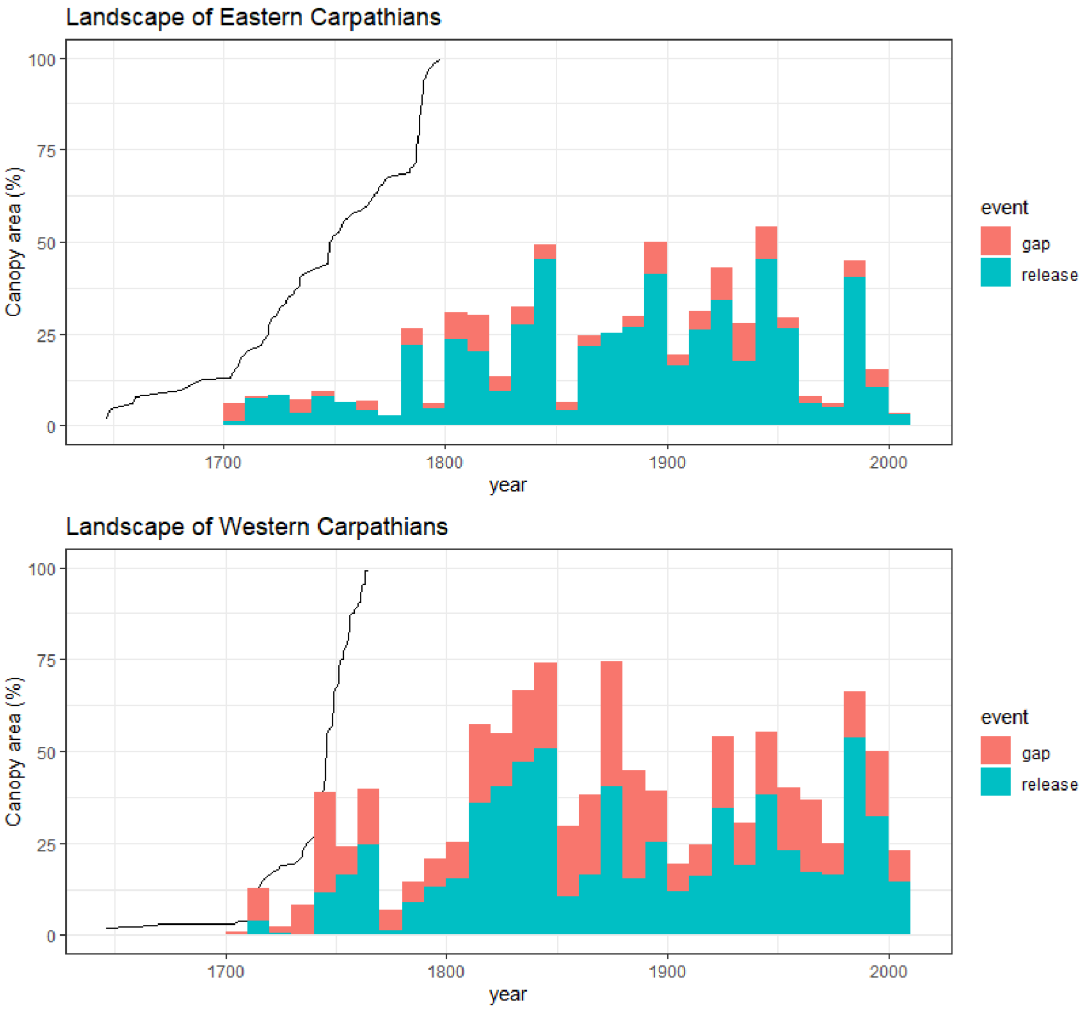

Figure 18: Proportion of events which were detected disturbances (gap origin vs. releases) and sample depth (solid line).

However based on the patch size analysis we did not find significant differences in mean patch area (gamma GLMM: z = -1.41, p = 0.158) and mean proportion of disturbed plots (binomial GLMM: z = 1.01, p = 0.313) between the Western and Eastern Carpathians (Figure 19). However, the patch size data were more heterogeneous in the east than in the west (z = 2.00, p = 0.046).

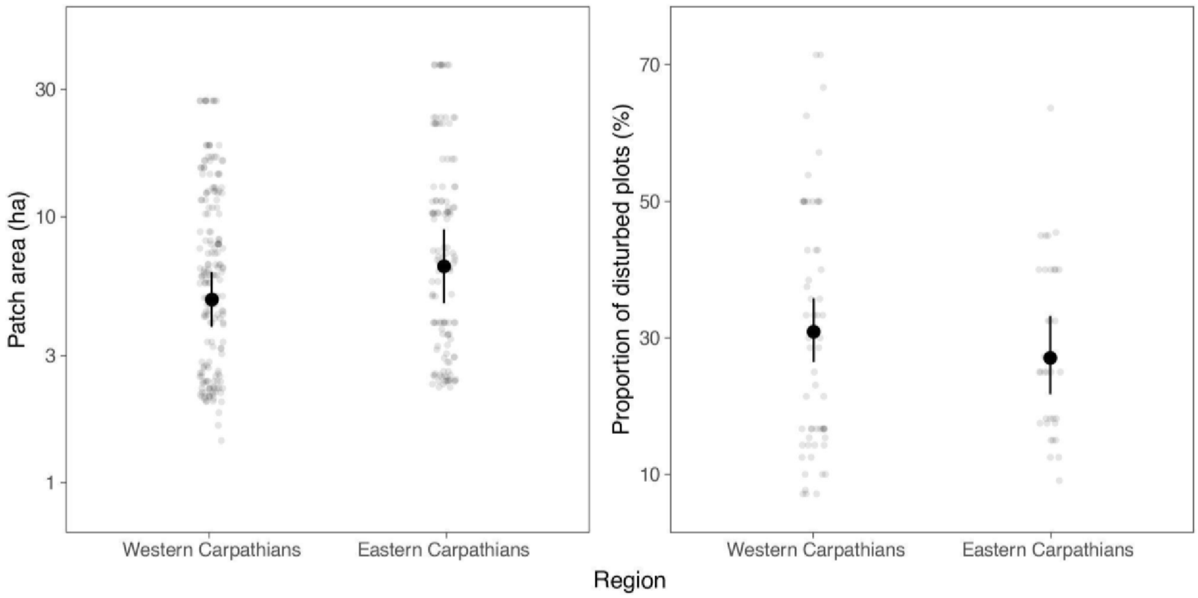

Figure 19: Differences in disturbance patch area and proportion of disturbed plots between the Western and Eastern Carpathians. Observed values (grey dots) are shown along with GLMM-based estimates (black dots) and their 95% confidence intervals (error bars).

5.2.2 Disturbance synchronicity and regional differences

We recorded gradations in disturbance activity across both regions. Kendall's W coefficients between plot-level disturbance histories showed some degree of synchronicity within all of the stands and ranged from 0.33 to 0.58 (Figure 20).

Comparison of regions using GLM models showed a significantly higher degree of synchronicity between plot-level disturbance histories within the stands in the Western Carpathians than in the Eastern Carpathians (GLM: b [se] = 0.24 [0.06], z = 3.65, p = 0.0003). The western portion of the forests is significantly more admixtured by Norway spruce and other tree species (). Patches of Norway spruce may act as a trigger of higher severity disturbances in the Western region due to its vulnerability to windthrow and bark beetle outbreaks.

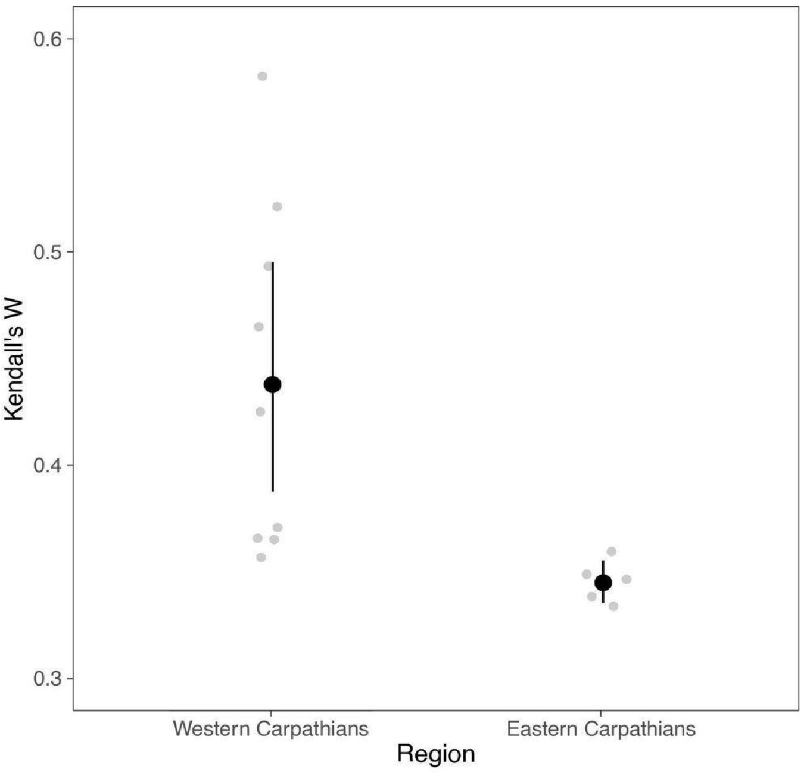

Figure 20: Differences between disturbance synchrony in Western and Eastern Carpathian forest stands. Gamma GLM-based estimates (black dots) and associated 95% confidence intervals (error bars) are displayed along with observed values (grey dots).

5.2.3 Disturbance synchronicity and species richness

As was highlighted in previous chapter, Kendall´s coefficient of concordance revealed the stand-level disturbances within the stands. The highest synchrony of disturbance chronologies in Obrštín stand (W = 0.58) and the lowest in Havešová (W = 0.33). The disturbances were significantly more synchronised in the Western Carpathians than in the Eastern Carpathians. Moreover, we tested disturbance synchrony results (Kendal´s W values for individual stands and tree diversity (average rarefied tree species richness of species occupying canopy area per stand). Disturbance synchrony was also significantly linked with tree diversity (GLM: b [se] = 0.14 [0.07], z = 1.99, p = 0.0464). The level of synchrony increased with the average number of tree species per plot. However, the predictive performance of the GLM involving regions (cross-validated R2 = 0.19) was slightly better than that of the diversity model (cross-validated R2 = 0.10).

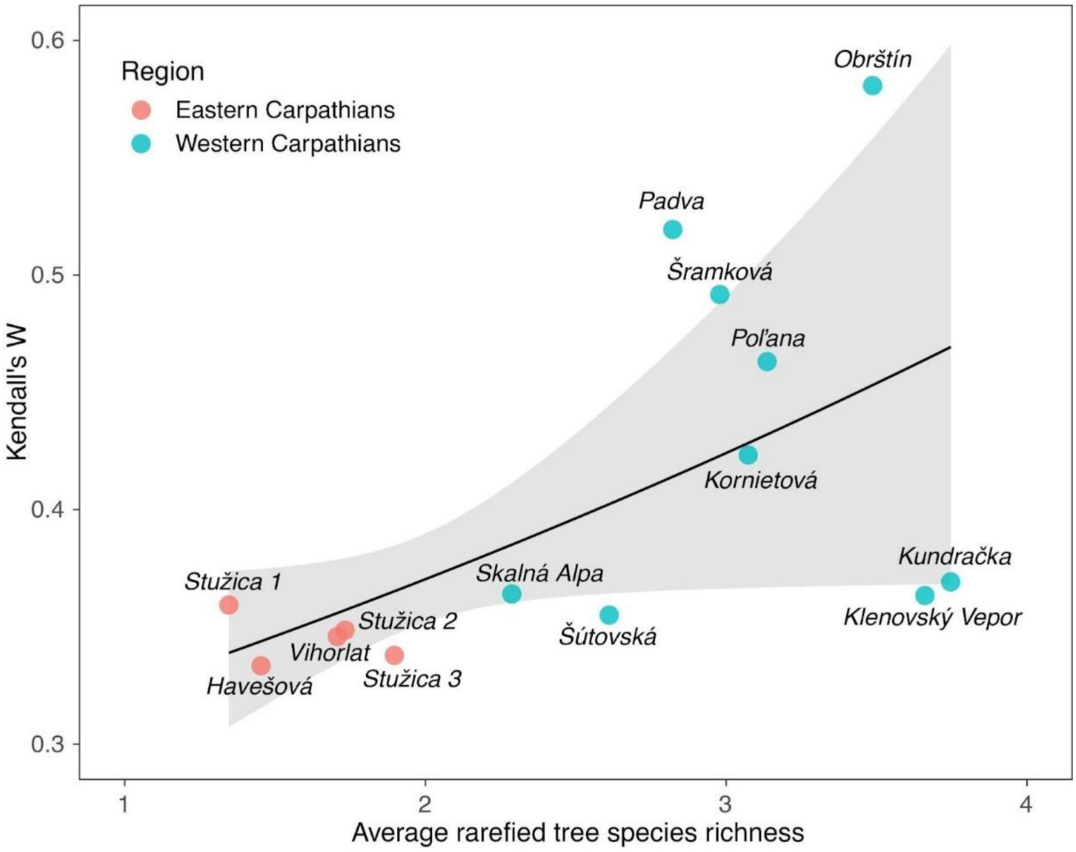

Figure 21: Relationship between tree diversity and disturbance synchrony in Western and Eastern Carpathian forest stands. GLM-based prediction (line) and associated 95% confidence intervals (grey band) are displayed along with observed values (points). labelled by the stand names. Colour of the points is representing the study region (blue dots – Western Carpathian forest stands; red dots – Eastern Carpathian forest stands)

6. Discussion

6.1 Natural dynamics of temperate mountain beech-dominated primary forests in Central Europe

We reconstructed the spatiotemporal patterns of natural disturbance regimes in a primary beech-fir forest region within Central Europe. We used an innovative method based on the number of plots with more than 10% severity in a given year to capture disturbance regimes in the study plots. We identified 144 plot-level disturbance events, which we grouped to stand-level disturbance events by the number of plots affected and by the amount of canopy area removed. We found continuous variations from low- to high- and very high-severity disturbance events.

Low- and moderate-severity disturbance regimes in beech and beech-fir forests were dominant in our study (Fig. 11B) and create a spatial structure of canopy gaps with an area of dead trees embedded within a matrix of intact forest cover (Drosser and von Lupke, 2005). Gap sizes can reach from several tens to several hundred square meters in extent (Bottero et al., 2011, Zeibig et al., 2005, Nagel & Svoboda, 2008).

For simple illustration we divided all plot-level disturbances into four severity classes (Janda et al., 2017; Frelich & Lorimer 1991). Although low-severity events (under 20% of canopy area loss) account for the largest proportion (N = 65) of disturbed area in our study plots, there is also evidence of disturbance events in the highest severity class (Very High ≥ 60%) on eight plots across all three of the studied stands. Spatial and temporal expression (Figure 12) shows synchronicity within the value of maximum severity of disturbance events divided into 20-year periods, due to capturing prolonged recruitment periods (Svoboda et al. 2014). Evidence of events of higher severity (high and very high) and their temporal synchronicity occurred in the study region.

Past research has found that in the nearby Dinaric ecoregion - where montane primary beech-fir forest is also found - higher severity disturbances are mostly related to strong winds associated with local thunderstorms. These conditions are amongst the primary agents of stronger and intermediate-severity disturbances that removed >40% of the canopy area (Nagel and Diaci, 2006; Nagel et al., 2014). Nevertheless, it seems that no single disturbance agent dominates the regime of beech-fir forest in the Dinaric ecoregion (Nagel et al. 2017). Although it is more likely that high-severity disturbance events associated with local thunderstorms impact smaller spatial scales of the study areas (for example stand or group of plots), the extratropical cyclone systems affecting larger areas in Central Europe in winter are also accompanied by strong winds (European windstorms), and can affect a larger proportion of the study plots with scattered or clustered damage patterns (Martínez-Alvarado et al., 2012; Zeibig et al., 2005). In mixed beech-fir forests, it is worth noting that summer thunderstorms may disproportionately kill broadleaf trees, while conifers would be more susceptible to winter storms. Oscillation of disturbance events and their gradation could be related to some abnormal meteorological situation in a given area of the Carpathians (Seidl, 2011). Due to limitations of dendrochronological reconstruction, such as whether peak disturbance chronologies are related to single and stronger events, or to multiple disturbances with lower severity within a short time is still a question. The results indicate gradation periods, with the three largest peaks in the disturbance chronology around 1830-1850, 1860-1880, and 1920-1940.

On the plot-level we found seven very high- and 21 high-severity disturbance events, with severities of more than 60% and 40-60% of canopy area removed, respectively. Their occurrences show slight temporal synchronisation, mainly within stands, but also within the region. Due to the problem with growth response to disturbance - which can take from several years to nearly a decade (Frelich, 2002; Jones et. al. 2004) - and because the problem with core height, such events could be the same plot-level event within a given stand (Trotsiuk et al., 2012). Due to the fact that the most likely type of event was thunderstorms, this hypothesis of one and the same severe storm event is acceptable.

The occurrence of high-severity disturbances can be affected by physiographic attributes such as slope, bedrock and topography (Rebertus et al., 1997; Kulakowski and Veblen, 2002). For example, disturbances on the upper part of the slopes are generally more severe (Svoboda et al., 2012). However, we found that the majority of plots that were disturbed during the severe disturbance period between 1830 and 1850 were located at lower slope positions, at least within the stand Kornietová. We suggest that the divergent disturbance patterns in KOR may be influenced by the unique physical and compositional features found there. Specifically, altitudinal gradients, which are more severe, as well as differences in tree species composition, with spruce being substantially more abundant in KOR. Therefore, although Norway spruce has previously been recognized as a common gapmaker (Orman and

Dobrowolska, 2017), this species contributed minimally to expanding gap area in this study. The morphology of spruce crowns is typically narrower than beech or other deciduous species so that the relative contribution of disturbance-killed spruce individuals to total canopy area removed is comparatively lower (Kenderes et al., 2008; Kucbel et al. 2010). However, differences in mortality rates between tree species also influences their contribution to gap area. For example, Norway spruce is relatively more susceptible to uprooting by wind due to shallow rooting depths. Further, spruce is the only host species for the spruce bark beetle (*Ips typographus*, L.), and is thus vulnerable to localized, periodic beetle-induced tree mortality. We therefore argue that some of the divergent historical disturbance patterns observed in this study may be attributed to spatial differences in species composition. We further argue that these discussed interactions between species-specific physiognomy and disturbance type may affect analysis of results at local plot scales but will not bias larger stand or regional scale disturbance chronologies.

6.1.1 Conclusions and management implications

Our goal was to capture the range of past disturbance activity, as well as comparing the variation in disturbance frequency and severity across three primary beech-dominated forests. We reconstructed the overall disturbance history in some of the best preserved remnants of primary forests in the Central European region. The study gave us insight into the past regimes and processes in the forests. Low- and moderate-severity disturbances prevailed, but the occurrence of plot-level high- and very-high severity disturbances were also documented. Disturbances affected several plots simultaneously over short time periods, thus creating a coarse-grained forest structure.

In contrast with the heterogeneity and diversity found in primary forests, the most common commercial harvesting practices in the region leads to simplified forest stand structures and the homogenisation of forest landscapes, with a consequential shift in species composition and a decrease of diversity in those of early- and mid-seral stages (Seymour 1999; Mikoláš et al., 2015; Michalová, Svoboda 2017, Ujházy et al., 2017). Thus mimicking observed natural disturbances patterns in a given area through management, together with sufficient retention of deadwood and other structural elements, is important for maintaining a forest without substantial biodiversity loss (Lindenmayer et al., 2006). The mixed-severity disturbance regime patterns observed in this study may further provide a reference system for such ecological forestry practices aimed to increase structural heterogeneity and essential forest functions (Seymour et al., 2002; Trotsiuk, 2014; Khakimulina et al. 2016). Thus forest management should recognize natural disturbances - including the high-severity events - as an integral part of the dynamics of mixed beech-dominated forests in Central Europe.

6.2 Synchronicity and variation of natural disturbances across beech-dominated primary forests in the Carpathians

We reconstructed disturbance histories across primary beech-fir forests of Central Europe and compared the disturbance regimes in two distinct regions - the Western and Eastern Carpathians. The summarised disturbance chronology of all 14 stands shows temporal variability in disturbance severity, with periods of escalation (Figure 15). On the 174 permanent study plots, we identified a total of 517 disturbance events with severities exceeding at least 10% of the canopy area removed (Figure 10). We observed a small difference between disturbance regimes in the Western and Eastern Carpathian regions and we evaluated the degree of synchronisation. In the Western region, bigger synchronisation is present. It may suggest different natural conditions such as altitude (Tab.1) and species composition, which can result in different recorded observations of temporal and spatial variables of disturbances such as severity and synchronisation.

Because the studied primary forests have diverse structure and growth reaction varies between individual trees, proxy disturbance data can be dispersed over two consecutive decades. This is because the tree ring signals of releases and gap recruitments can last several years, therefore, traditional dendroecological methods relying on decadal binning of the data can lead to the false identification of multiple disturbance events instead of a single severe one (Lorimer and Frelich 1989; Čada et al. 2020). To avoid this situation, we used a continuous data smoothing method instead of decadal binning, which can provide us with information about individual discrete disturbance events in time based on Kernel density estimation (Trotsiuk et al. 2018; Čada et al. 2020; Frankovič et al. 2021; Kameniar et al. 2023). The method allowed us to determine individual disturbance events which are important for accessing the synchronicity of disturbance regimes between studied stands and regions.

6.2.1 Disturbances and the effect of climate processes

As in other mixed-beech-dominated forests in Europe, low- and moderate-severity disturbance events are prevalent in our study region (Trotsiuk et al.2012; Hobi et al. 2015; Feldmann et al. 2018; Orman and Dobrowolska, 2017; Frankovič et al. 2021), and the structure of the studied forests were likely driven by mixed-severity disturbance regimes. However, evidence of high and very high severity disturbance events was also detected. In the resulting plot-level disturbance chronology curves, occasional temporal synchronicity between the individual peaks is evident, which is an important temporal pattern, and it may also be one of the key elements involved in the formation of forest structure. Synchronicity between peaks of plot-level disturbance events within one stand suggests that it was one event, while a group of peaks suggests that a forest was affected by several discrete disturbance events in a shorter time span. Less synchronised disturbances create a more diverse forest structure, while more synchronised disturbances lead to the creation of biological legacies.

The resultant chronologies indicate that the disturbance events were more synchronised in the Western Carpathians, whilst the Eastern Carpathian forests were more characterised by unsynchronised events. Climate-induced atmospheric processes are a key factor driving the synchronicity of natural disturbances at stand, regional and landscape scales. In Central Europe, this often pertains to strong winds related to extratropical cyclones (Pettit et al. 2021). Large-scale cyclone-induced windstorms are well known to affect forests in Europe, with past research indicating that the overall area of affected forests can cover thousands of ha (Pettit et al. 2021). Therefore, the detected regional synchronicity of disturbance events across the Western Carpathians suggests that the region was affected by fronts associated with cyclones. In addition to windstorms, ice storms, heavy snow or drought can also cause intermediate severity disturbances across large landscapes (Pederson et al. 2014; Nagel et al. 2017; Synek et al. 2020). However, synchronised disturbances within regions can have different spatial extents; scattered damage patterns are more frequent, and occasionally, some very high-severity stand-level disturbances can appear in a similar time period (Martínez-Alvarado et al. 2012; Zeibig et al. 2005). Thus, considering this likely influence of atmospheric conditions, it appears the Western Carpathians are more influenced by extratropical cyclones, while the Eastern Carpathians may be more affected by small-scale convective instability summer storms, which can cause severe, but unsynchronised windthrows. These are more common in Southeastern Europe than in

Central Europe, where extratropical cyclones are more common (Nagel et al. 2017; Furtuna et al. 2018; Pettit et al. 2021).

Although higher disturbance synchronicity was detected predominantly in the Western Carpathians, evidence of unsynchronised disturbance activity was also detected in both regions. High and intermediate-severity unsynchronised plot-level disturbances which remove > 40 % of the canopy area can be related to strong winds, likely resulting from unstable local atmospheric conditions such as strong thunderstorms. Such events have been documented in the Dinaric ecoregion of the Balkan peninsula, where old-growth beech-dominated mountain forests are also present (Nagel et al. 2017). Unsynchronised smaller-scale disturbances can be driven by background mortality or the death of several trees per plot. Such smaller-scale disturbances are also often the result of convective instability, which can cause localised thunderstorms; these affect smaller spatial scales than disturbance agents related to extratropical cyclones. Thus, the differences in the detected temporal peaks in the disturbance regime over a large proportion of study areas may be driven by convective instability-induced windthrow events, which affect chronologies on individual plots or groups of plots, rather than entire landscapes or regions (Frankovič et al. 2021; Pettit et al. 2021). Although such evidence was limited at the stand scale, the influence of these small-scale storms in driving forest processes cannot be ignored. Disturbance patterns that create patchy and coarse-grained structures can also be connected to atmospheric patterns such as convective instability; local thunderstorms can affect several trees, or several plots per stand, which then results in high spatiotemporal variability in forest structure.

Physiographic attributes such as slope gradient, orientation and topography also affect disturbance regimes by altering exposure to some of the atmospheric conditions. In the upper part of slopes and on mountain ridges, atmospheric conditions such as wind can be more severe and general forest damage can be higher (Svoboda et al. 2012). Past research has already found that landscapes with more complex topography show higher variation in patch fragmentation after a disturbance (Kitagawa et al. 2015; Senf & Seidl, 2018). The Western Carpathian stands are characterised by a larger altitudinal gradient and steeper slopes than the Eastern Carpathians; this difference in physiographic features is likely a contributing factor driving the observed higher disturbance synchronicity in the Western studied regions.

6.2.2 Disturbances and the effect of species composition

Specific physical and compositional landscape features can also influence the severity of disturbances through their effect on tree species composition. Complex landscapes often have higher variability in tree species richness than flat areas where environmental gradients are lower (Kitagawa et al. 2015; Senf & Seidl, 2018). Tree species composition also changes with elevational gradients. The Western Carpathian forest stands have significantly more admixture tree species - predominantly Norway spruce and silver fir (Tab. 2) - in comparison with the Eastern Carpathians, which are largely beech-dominated. Norway spruce is a very common admixture species growing together with European beech and silver fir (Pividori et al. 2016). The abundance of this species can vary based on local natural conditions and can be dominant in some patches. The presence of spruce in mixed-beech forests is most often related to elevation; they become more common at around 1100 m a.s.l., with mixed-beech forests bordering the upper montane tree belt dominated by Norway spruce. Norway spruce has previously been recognized as a common gap maker vulnerable to windthrow and bark beetle outbreaks (Winter et al. 2015; Orman and Dobrowolska, 2017). In particular, low water availability and high temperatures can increase bark beetle development and survival through an increased probability of the completion of a second or third generational cycle per year, significantly affecting the severity of an outbreak (Marini et al. 2017; Jakoby et al. 2019). Therefore, yearly differences in weather patterns can significantly affect bark beetle-driven disturbances, thereby influencing the temporal variability of disturbance in spruce-dominated patches. Although mixed-species forest stands are generally more resilient to disturbances than those of single species, the regional context of landscape properties can have a key effect on the synchronisation and severity of disturbances. Thus, species compositional changes on the upper belt of beech-dominated montane forest can have a significant effect on the temporal and spatial disturbance patterns, and regional-scale drought patterns can significantly affect bark beetle population dynamics across larger study areas (Marini et al. 2017). Hence tree species composition of the regions is most likely a driver of the differences in disturbance synchronisation (Kameniar et al. 2023). Therefore, the higher proportion of spruce characterising the Western Carpathians likely contributed to the higher disturbance synchronicity in comparison with the beech-dominated Eastern Carpathian forests.

6.2.3 Patch sizes

Despite differences in the degree of disturbance synchronisation, no significant differences in the sizes of patches between the Western and Eastern stands were detected. However, in the Eastern Carpathians, the distribution of patch size within individual stand-level disturbances was slightly bigger and more heterogeneous. This may be associated with a higher occurrence of local thunderstorms, which create unsynchronised peaks across regions and the size of removed canopy area may differ. Nonetheless, the proportion of disturbed plots was higher in the Western Carpathians. This can be associated with the synchronicity of disturbances caused by extratropical cyclones and fronts associated with them. As aforementioned, there are likely more reasons behind these patterns; the more complex topography and diverse relief characterising the Western Carpathians (Tab. 1) could have also likely contributed to the observed diversification and fragmentation of the disturbed patches. Furthermore, the plot area is 0.15 ha and plots cover a limited area of the stands, thus in some cases could be insufficient to transfer the signal of plot-level disturbance to stand level.

6.2.4 Study limitations

Our large database of dendrochronological data provides valuable insights into the disturbance history of some of the best-preserved primary forests in Central Europe. However, a mathematical description of the nature of the past can bring many questions. This is because the tree ring signals of releases and open canopy recruitments can last from several years to decades because surviving trees can have snapped branches and can be damaged in different ways based on the type of disturbance. Consecutive competition of open canopy-recruited trees can also cause late growth reactions. Thus, the disturbance chronology is particularly shaped by the methodological decisions in setting parameters and thresholds for releases and gap-recruited trees.

Growth release detection in the absolute-increase method is influenced by the window length of comparison of tree ring widths. Shorter window lengths can lead to false positives, while longer window lengths can lead to false negative detections of disturbances. However, to avoid such errors, we established an additional criterion of at least seven years of sustained increased growth (Fraver et al. 2009). Further, the method used here for recalculating disturbance relies on the canopy area removed which thus depends on the number of trees available for analysis for a given time period. In general, the further we delve into the past, the fewer tree cores are available for analysis. It means that a disturbance chronology may be less accurate further in the past. This was addressed by the setting threshold of the canopy area accessible for the study to 10% of the study plot area.

It is also worth noting that the recruitment of new trees in an open canopy can take over a decade until a tree reaches the size for coring (height 1 m above ground) and several years of age of the tree can be lost in the first several tree rings next to the pith (Svoboda et al. 2014). For these reasons, all the mentioned absolute areas and percentages should be taken with caution and should be taken proportionally and contextually for the purpose of forest ecology and forest dynamics processes.

We must also add that although both landscapes were likely affected by multiple disturbance agents, uncertainties in pinpointing the exact drivers of disturbance patterns are connected with methodological limitations. Dendroecology can detect growth changes in the past, but cannot detect exact disturbance agents, except fires, landslides and rock falls (Svoboda et al. 2014; Speer; 2010).

6.2.5 Management implications

Ongoing climate change will most likely alter disturbance regimes worldwide in terms of the frequency and severity of disturbance events. Therefore, regional scale reconstruction and comparisons of historical natural disturbance regimes in primary mixed forests have the potential to improve current climate change mitigation policies (O'Brien et al. 2021). Our findings therefore provide valuable information which could be used for a sophisticated spatiotemporal forest management strategy that mimics natural disturbance processes to promote biodiversity in forest landscapes.

Based on the results, temporal synchronisation of disturbances seems to be the inherent element of the processes in the forests. Different disturbance agents with the interaction of local environmental conditions can quickly lead to disturbances scattered over the landscapes in relatively short time periods. This effect can enrich forest development cycles by creating naturally shifting mosaics of different development stages. Therefore, management mimicking these processes may help to maintain biodiversity through disturbance-induced forest structure.

Further, due to the high variability of disturbance severities over the individual events, we suggest protecting large continuous areas with high altitudinal gradients, including various forest landscapes for the implementation of all-natural types of disturbances and their variability.

Salvage logging often leads to homogenisation and simplification of forest structure (Lindenmayer et al. 2017). The mosaic of development stages is then replaced by even-aged cohorts of trees in salvaged areas. Homogenisation and simplification of forest structure may lead to the loss of specialised forest species and important ecosystem services (Thom and Seidl 2016). Therefore, salvage logging of disturbed forest stands impairs conservation-related efforts.

To mimic local disturbance regimes in forest management in non-protected areas we suggest creating as diverse-sized patches as is technically possible to diversify forest structure with preference given to the creation of smaller patches (0.1-0.3 ha) to imitate the prevalence of low-severity disturbance events. Further, logging should imitate synchronous and asynchronous disturbance events of lower severities to ensure the continuum of all forest development stages to imitate the stochastic distribution of asynchronous disturbances in time and space.

6.2.6 Conclusions

The resulting disturbance chronologies indicate that higher severity disturbances were more common in the forests in the Western Carpathian which are characterised by a higher admixture of Norway spruce, while the Eastern region was driven by smaller disturbances. We did not find a large difference in the sizes of the disturbance patches between the Western and Eastern stands. However, the patch size data were more heterogeneous in the east, while the proportion of disturbed plots was higher in the Western Carpathians. We found higher synchronicity of disturbances in the more species-mixed forests of the Western Carpathians than in the Eastern Carpathians. This may be an effect of species composition and topographic complexity, where the presence of Norway spruce may act as a trigger for the severity of disturbances in the Western portion of the mountains. Both results may be an artefact of the more diverse relief and more heterogeneous species composition in the West. This research suggests that the main disturbance agents in beech-fir forests are derived from the atmospheric conditions, which is in line with past research (Pettit et al., 2021; Nagel et al. 2017). Based on the disturbance temporal patterns and synchronicity we assume the Western Carpathian stands were more affected by extratropical cyclone frontal systems, while the Eastern Carpathians were affected by convective instability during summer storms.

6.3 Disturbance regime, synchronicity and species richness in the Western and Eastern Carpathian regions

We detailly characterised the disturbance regime of mountain beech-dominated forests of Western and Eastern Carpathians in Central Europe using the dendroecology approach. We used an innovative method based on the number of plots with more than 10% severity in a given year to capture disturbance regimes in the study plots. In contrast to many dendroecological studies, using decadal binning, we smoothed the disturbance proxy data using a kernel density function. Decadal binning may often lead to overestimating the number of disturbance events or underestimating their severity. It allowed us to extract plot-level and stand-level peaks of disturbance activity with the exact resolution and use the data further to analyse the relationship between synchronicity and species composition – disturbances.

As was mentioned in the previous chapter, we identified 517 plot-level disturbance events, which we grouped into stand-level disturbance events by the severity of the plots affected (Figure 14; Figure 15).

The results of the general description of the disturbance regime are comparable to previous studies, where the low severity disturbance events were prevalent (Zeibig et al., 2005; Šamonil et al., 2009; Wagner et al. 2010; Trotsiuk et al., 2012; Hobi et al., 2015; Feldmann et al. 2018; Orman & Dobrowolska 2017; Frankovič et al. 2021). However, high structural complexity is evident across the landscape, and the evidence of moderate and high-severity disturbance events was recorded, despite being less frequent than small-scale events. We found continuous variations from low - to high - and very high-severity disturbance events. Low- and moderate-severity disturbance regimes in beech and beech-fir forests were dominant in our study (Figure 15) , and they can help to create a spatial structure of canopy gaps with an area of dead trees embedded within a matrix of intact forest cover (Drosser and von Lupke, 2005). Gap sizes can reach from several tens to several thousand square metres in extent (Bottero et al., 2011, Zeibig et al., 2005, Nagel and Svoboda, 2008). However, it is not only small-scale disturbances that are affecting forest cover in mixed beech-dominated forests. Evidence of higher severity disturbance events (high and very high) and their temporal synchronicity occurred in the study region (Figure 8; Figure 16; Figure 17). Disturbance patterns that create patchy, coarse-grained structures can be connected to atmospheric patterns such as convective instability; local thunderstorms can affect several trees or plots per stand, resulting in a highly diverse structure in the sense of time and space. The influence of small-scale convective storms has been recorded in the forests of the Dinaric Mountains of Southeastern Europe (Nagel et al., 2017), the Romanian Carpathian Mountains (Furtuna et al., 2018), and in the deciduous forests of North America (Canham et al., 2001).

However, the complex of properties affecting spatiotemporal aspects of disturbance regimes remains unclear. Physiographic features, including elevation, slope gradient, and orientation, influence a disturbance regime’s exposure to certain atmospheric conditions. Overall, forest damage can be higher and more severe atmospheric conditions, such as wind, can appear on mountain ridges and in the top half of slopes (Svoboda et al., 2012). At higher elevations, the composition of tree species often changes, with spruce being substantially more abundant (Winters et al., 2015). Norway spruce was previously recognized as a common gap maker, vulnerable to windthrow (Orman and Dobrowolska, 2017). Therefore, one driving feature of disturbance severity can also be the species composition of the forest. Hence, the results of this research, along with past studies, highlight the complexities pertaining to forest disturbance regimes and their driving forces. Species composition may be affected by disturbance regimes, but the vulnerability of individual species may affect disturbance regimes. Thus, the relation may be reciprocal.

Therefore, one driving feature of disturbance severity can also be the species composition of the forest. The presence of spruce as a gap maker can result in higher severity rates in the zone of the upper mountain belt of beech-mixed forests bordering with spruce forests (Loch & Armatys 2014). At higher elevations in mixed beech forests in Europe (about 1100 m), Norway spruce is a very common species growing together with European beech and silver fir in mixed beech forests (Chwistek 2008; Różański et al. 2006). Occurence of this species can vary based on local natural conditions and on some patches, can be dominant. Moreover, spruces are more susceptible to wind damage due to more shallow rooting systems (Knoke et al. 2008). The problem can also be the presence of foliage throughout the year, which increases the size of the crown area exposed to the wind (Dhôte et al. 2005).

The species composition of mixed beech-dominated forests in the Carpathians can vary based on natural conditions, and the gradient can be wide. From the monodominant species forests dominated by beech to mixed forests composed of beeches, spruces, maples and firs. There is a difference between the natural environment of forests between Western and Eastern Carpathians. In the west, the altitude gradient is bigger, slopes are steeper and species composition is more diverse, while in the East it is almost dominant beech forest.

We observed a significantly higher portion of the spruce on the study stands in the west than in the east. Mixed-species forests have often been shown to be more resilient than monodominant forests. However, the results observed in the studies conducted in the Carpathians show different trends. The resulting disturbance chronologies indicate that higher severity disturbances were more common in the forests in the Western Carpathian mountains, and the synchronicity in the stands with the higher number of the species (Figure 18). All of these can indicate more considerable disturbances in the more mixed forests, which contradicts the general assumption that mixed-species forests are more resilient (Fares et al. 2015; Seidl et al. 2016).

However, based on the idea of lucky monocultures and unlucky mixtures theory, we can assume that not everything mixed with more tree species is more resilient. Forests in the Western Carpathians are enriched with more tree species, such as maple, fir, or European ash. Diverse forest structures may mitigate the disturbance effects in forests. The spruces often appear in this forest in patchy patterns, and their proportion is growing with altitude. Thus, the overall disturbance severity rates may be strongly affected because many of the plots have a high proportion of spruce. Pure beech forests, or forests with a low admixture of spruce, may have lower disturbance severity rates and also lower synchronisation because the beeches are more prone to the wind; moreover, beeches have no leaves in the winter, which is one of the riskiest parts of the year when a European windstorm may occur (Brazdil et al. 2004). Thus, disturbances may have patchy or gap patterns and overall severity rates after strong winds may be lower.

Because the statistical relation shows the slightly better predictive performance of the GLM involving regions (cross-validated R2 = 0.19), we assume the factor of the patchy occurrence of the spruces in Western Carpathian may be the reason behind this pattern. Other environmental factors may also play role. The higher positions of the mountains are more exposed to the wind. We assume that the overall diversity of forests may have only a positive effect on the better resistance of forests. However, species composition and structural diversity n stands behind this resistance.

6.3.1 Conclusion

Natural and primary forests play an irreplaceable role in mitigating climate change and preserving biodiversity. Describing natural processes directly influenced by humans can enhance the understanding of the functioning of original forest ecosystems and assist in planning the management of protected areas, or even in planning nature-friendly active management in commercial forests. Research results suggest that not only species composition but also the diversified structure of a forest can significantly contribute to its resilience (Fares et al., 2015; Meigs et al., 2017; Bauhus et al., 2017; Jactel et al., 2017).

Effective forest management in Central Europe should take into account the significance of natural disturbances caused by wind, insects and their temporal and spatial aspects. Studying these disturbances is essential for understanding the structural heterogeneity and dynamics of forests. The synchronization of these natural disruptions is a crucial factor, with our study results indicating that disturbances in Western Carpathian forests are more synchronized than in Eastern Carpathians. Forest ecosystem management should be appropriately adapted to the considerable variability in the frequency and severity of disturbances.

Dominant disturbances types in mixed beecg dominated forests are those with low to intermediate severity, which should be accounted in the planning of forest recovery and protection strategies in response to changing environmental conditions. The species composition of forests should also be considered, as the results show that disturbances are more synchronized in forests with a higher representation of spruce. The significant impact of a higher proportion of spruce presence in the Western Carpathians, which is less resistant to disturbances than deciduous species, should be considered in planning and implementing measures for sustainable forest use.

7. References

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Appendix

Appendix 1. Species- and region-specific parameters and threshold values for the calculation of disturbance proxy evidence in individual tree-growth series (tree level).

Location	**Species group**	**Absolut increment threshold (mm)**	**Early growth rate threshold (mm)**	**dbh_mm**	**Diameter threshold for release calculations (mm)**
Great Fatra	Abies	1,00450538	2,1	200	(0.0055748*dbh_mm+3.2118573)^2
Great Fatra	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Great Fatra	Fagus	0,6174379	1,4	230	(0.0109108*dbh_mm+3.7376647)^2
Great Fatra	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Great Fatra	Picea	0,76084121	2,2	200	(0.0051325*dbh_mm+2.7436641)^2
Little Fatra	Abies	1,00450538	2,1	200	(0.0055748*dbh_mm+3.2118573)^2
Little Fatra	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Little Fatra	Fagus	0,6174379	1,4	230	(0.0109108*dbh_mm+3.7376647)^2
Little Fatra	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Little Fatra	Picea	0,76084121	2,2	200	(0.0051325*dbh_mm+2.7436641)^2
Low Tatras	Abies	1,00450538	2,1	200	(0.0055748*dbh_mm+3.2118573)^2
Low Tatras	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Low Tatras	Fagus	0,6174379	1,4	230	(0.0109108*dbh_mm+3.7376647)^2
Low Tatras	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Low Tatras	Picea	0,76084121	2,2	200	(0.0051325*dbh_mm+2.7436641)^2
Polana	Abies	1,00450538	2,1	200	(0.0055748*dbh_mm+3.2118573)^2
Polana	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Polana	Fagus	0,6174379	1,4	230	(0.0109108*dbh_mm+3.7376647)^2
Polana	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Polana	Picea	0,76084121	2,2	200	(0.0051325*dbh_mm+2.7436641)^2
Poloniny	Abies	0,94490456	1,8	200	(0.004872*dbh_mm+3.358116)^2

Location	Species group	Absolut increment threshold (mm)	Early growth rate threshold (mm)	dbh_mm	Diameter threshold for release calculations (mm)
Great Fatra	Abies	1,00450538	2,1	200	(0.0055748*dbh_mm+3.2118573)^2
Great Fatra	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Great Fatra	Fagus	0,6174379	1,4	230	(0.0109108*dbh_mm+3.7376647)^2
Great Fatra	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Great Fatra	Picea	0,76084121	2,2	200	(0.0051325*dbh_mm+2.7436641)^2
Little Fatra	Abies	1,00450538	2,1	200	(0.0055748*dbh_mm+3.2118573)^2
Little Fatra	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Little Fatra	Fagus	0,6174379	1,4	230	(0.0109108*dbh_mm+3.7376647)^2
Little Fatra	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Little Fatra	Picea	0,76084121	2,2	200	(0.0051325*dbh_mm+2.7436641)^2
Low Tatras	Abies	1,00450538	2,1	200	(0.0055748*dbh_mm+3.2118573)^2
Low Tatras	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Low Tatras	Fagus	0,6174379	1,4	230	(0.0109108*dbh_mm+3.7376647)^2
Low Tatras	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Low Tatras	Picea	0,76084121	2,2	200	(0.0051325*dbh_mm+2.7436641)^2
Polana	Abies	1,00450538	2,1	200	(0.0055748*dbh_mm+3.2118573)^2
Polana	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Polana	Fagus	0,6174379	1,4	230	(0.0109108*dbh_mm+3.7376647)^2
Polana	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Poloniny	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Poloniny	Fagus	0,6286624	1,1	230	(0.0091012*dbh_mm+3.4721892)^2
Poloniny	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Vepor Hills	Abies	1,00450538	2,1	200	(0.0055748*dbh_mm+3.2118573)^2
Vepor Hills	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Vepor Hills	Fagus	0,6174379	1,4	230	(0.0109108*dbh_mm+3.7376647)^2
Vepor Hills	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Vepor Hills	Picea	0,76084121	2,2	200	(0.0051325*dbh_mm+2.7436641)^2
Vihorlat	Abies	0,94490456	1,8	200	(0.004872*dbh_mm+3.358116)^2

Location	Species group	Absolut increment threshold (mm)	Early growth rate threshold (mm)	dbh_mm	Diameter threshold for release calculations (mm)
Great Fatra	Abies	1,00450538	2,1	200	(0.0055748*dbh_mm+3.2118573)^2
Great Fatra	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Great Fatra	Fagus	0,6174379	1,4	230	(0.0109108*dbh_mm+3.7376647)^2
Great Fatra	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Great Fatra	Picea	0,76084121	2,2	200	(0.0051325*dbh_mm+2.7436641)^2
Little Fatra	Abies	1,00450538	2,1	200	(0.0055748*dbh_mm+3.2118573)^2
Little Fatra	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Little Fatra	Fagus	0,6174379	1,4	230	(0.0109108*dbh_mm+3.7376647)^2
Little Fatra	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Little Fatra	Picea	0,76084121	2,2	200	(0.0051325*dbh_mm+2.7436641)^2
Low Tatras	Abies	1,00450538	2,1	200	(0.0055748*dbh_mm+3.2118573)^2
Low Tatras	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Low Tatras	Fagus	0,6174379	1,4	230	(0.0109108*dbh_mm+3.7376647)^2
Low Tatras	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Low Tatras	Picea	0,76084121	2,2	200	(0.0051325*dbh_mm+2.7436641)^2
Polana	Abies	1,00450538	2,1	200	(0.0055748*dbh_mm+3.2118573)^2
Polana	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Polana	Fagus	0,6174379	1,4	230	(0.0109108*dbh_mm+3.7376647)^2
Polana	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Vihorlat	Acer	0,75393957	2,2	230	(0.0108999*dbh_mm+2.7622634)^2
Vihorlat	Fagus	0,6286624	1,1	230	(0.0091012*dbh_mm+3.4721892)^2
Vihorlat	Others	1,22986045	2,2	220	(0.009335*dbh_mm+3.332423)^2
Vihorlat	Picea	0,76084121	2,2	200	(0.0051325*dbh_mm+2.7436641)^2