Czech University of Life Sciences Prague
Faculty of Forestry and Wood Sciences
Forestry Engineering

Mortality, dynamics and structure of mountain forests in Central Europe

Mortalita, dynamika a struktura horských lesů Střední Evropy

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Ph.D. THESIS ASSIGNMENT

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Mortality, dynamics and structure of mountain forests in Central Europe

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Objectives of thesis

One of the most suitable approaches for studying primary forest dynamics is through the observation of stand structure, and its changes, on permanent study plots. A re-census of study plots after a period of time allows for an analysis of changes in the dataset. Besides stand structure itself, such analyses can be focused on tree mortality during the re-census interval. The data obtained from permanent sample plots can also be useful for evaluating of the role of stand structural characteristics (e.g., basal area) and topographic parameters (e.g., slope, aspect) in stand development. The repeated inventory data also provide the option to assess the patterns of tree mortality on different spatial scales.

Methodology

1) Search for relevant scientific literature

2) Literature review

3) Preparation of methodology for field data collection and processing

4) Collection of field data

5) Data processing

6) Preparation of scientific outputs

The proposed extent of the thesis

150 pages

Keywords

Tree mortality, Disturbances, Forest dynamics, Stand structure

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Recommended information sources

BORMANN F. HERBERT, – LIKENS GENE E. *Pattern and Process in a Forested Ecosystem. Disturbance, Development and the Steady State Based on the Hubbard Brook Ecosystems Study.* NEW YORK: SPRINGER, 1979.

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Zadání disertační práce

Mortalita, dynamika a struktura horských lesů Střední Evropy

Cíle práce

Jednou z možností náhledu do dynamiky původních horských porostů je sledování změn struktury na trvalých výzkumných plochách během určitého časového úseku. Tedy porovnání struktury porostů po několika letech a analýza změn pozorovaných v získaných datech. Tato analýza může být konkrétněji zaměřena nejen na samotnou strukturu, ale také na mortalitu pozorovanou v daných porostech. Data získaná na trvalých výzkumných plochách mohou být použita k vyhodnocení role strukturních charakteristik (například výčetní kruhová základna) a topografických parametrů (například orientace svahu) ve vývoji porostu. Zároveň by mělo být možné posoudit, jestli mezi sledovanými plochami nebo porosty existují obecné vzorce výskytu a míry mortality, případně v jakém měřítku jsou tyto vzorce sledovatelné.

Metodika

1) Vyhledání relevantní zahraniční a domácí literatury
2) Vypracování rešerše na dané téma
3) Příprava metodiky sběru a zpracování dat
4) Sběr dat v terénu
5) Zpracování dat
6) Příprava vědeckých článků

Doporučený rozsah práce: 150 stran

Klíčová slova

Mortalita, disturbance, dynamika lesa, struktura lesa

I hereby confirm that this Ph.D. thesis “Mortality, dynamics and structure of the mountain forests in the Central Europe” was elaborated independently with the usage of quoted literature and based on consultations and the recommendations of my supervisor.

I agree with publishing this Ph.D. thesis according to Czech law n. 111/1998 Sb. about the universities in its current valid wording. This agreement is independent from the results of defense.

November 30th, 2021, Beroun

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Abstract

Natural tree mortality, driven by disturbances, their legacies and climate, represents a key process shaping forest dynamics and influencing forest structure. Shifting tree mortality rates are a global-change syndrome influencing forests across the world. However, determining whether environmental changes are altering mortality rates is complicated by the fact that tree mortality inherently changes through time as forests develop following natural disturbances. Exploring the mortality patterns in primary forests in the context of their disturbance regimes and stand structure provides information on natural dynamics of the forests under ongoing climate change.

Different mortality agents leave various biological legacies that influence future stand structure and sensitivity to disturbances. The composition of mortality agents across different tree species and sizes is therefore crucial for stand development. The thesis aims to 1) evaluate the mortality rates and composition of mortality agents in the context of stand structure in primary mountain Norway spruce forests (Chapter 5.1), 2) explore the relationship between disturbance history and current mortality (Chapter 5.2), 3) evaluate the overall and species-specific mortality rates and mortality agents' composition in primary European beech-dominated mixed stands (Chapter 5.3), and 4) analyze the main drivers of basal area variability in primary forests (Chapter 5.4). An extensive database of permanent study plots from primary forests in the Carpathian Mountains was used for these studies. Structural, dendrochronological, and re-census-based mortality data from a total of almost 700 sample plots were used to achieve the goals. The main findings of this thesis are:

1) The estimated overall annual mortality rate in primary Norway spruce stands was within the previously published range of background mortality, however, substantial variability was detected on both stand and plot levels. The overall distribution of mortality was balanced up to 50 cm DBH, however, the distributions for individual mortality agents were different,

because some mortality agents are prevalent in certain size classes. Bark beetle (*Ips typographus* L.) was the most frequent mortality agent even in stands with low overall mortality. The results suggest the role of bark beetle as a mortality agent does not equate to severe mortality at large scales (Chapter 5.1).

2) Recent mortality was highest in the historically least disturbed plots. The strongest relationships were observed for the 120-year period immediately preceding the inventory-based observation of current mortality at the stand level. The patterns varied among subregions. The stronger results on stand level than plot level, coupled with the absence of significant results for some subregions, indicate an important role of scale when assessing the relationship of past disturbances and current tree mortality. The results suggest not only intensity, but also variability through time, are parameters of disturbance regimes which shape current forests. The past disturbance period with the strongest relationship to mortality rate in the target decade is shifting (Chapter 5.2).

3) The estimated overall annual mortality rate in mixed stands was well within the previously reported range of background mortality. Stand- and plot-level mortality rates varied, although, not as much as has been reported from other forest types in the Carpathians. Most recently dead trees were found in the smallest size classes, pronouncing the effects of competition. However, individual mortality agents have different distributions across the size classes. Climatic extremes as a major mortality agent were reported for only a limited number of trees, despite the fact that most study stands are experiencing drought conditions. Competition and abiotically caused damage are prevalent mortality agents overall, however, insect infestation is the most frequent mortality agent in Norway spruce. The significant differences in mortality rates among regions and species and species-specific distributions of mortality agents emphasize the importance of structural and compositional heterogeneity of forest stands (Chapter 5.3).

4) We found that the basal area of Norway spruce forests varies on multiple spatial scales. Climatic drivers are most important at coarse scales while natural disturbances represent the primary driver of forest heterogeneity at fine scales. Finer-scale variability is driven by local disturbances (mostly bark beetle and windstorms) and the legacies of disturbances that occurred more than a century ago. Climate change can increase the basal area of northern sites, however, a potential increase in disturbance frequency and severity can disrupt environmental responses (Chapter 5.4).

Additionally, based on our results and their context within published literature, the thesis provides general recommendations and guidelines for forest management and conservation.

Keywords: Annual mortality rate, Disturbance legacies, Forest dynamics, Forest structure, Mortality agents, Natural disturbances, Primary forest

Abstrakt

Přirozená mortalita stromů, ovlivňovaná disturbancemi, jejich biologickým dědictvím a klimatem, je klíčovým procesem dynamiky lesa a ovlivňuje strukturu porostu. Měnící se míra mortality je syndromem globálních změn a ovlivňuje lesy celého světa. Jednoznačné určení zda klimatické změny způsobují změny v míře mortality je však komplikováno jejími přirozenými změnami v průběhu vývoje porostu po přírodních disturbancích. Výzkum vzorců mortality v původních lesích v kontextu jejich disturbančních režimů a porostní struktury poskytuje cenné informace o přirozené dynamice lesů v důsledku klimatických změn.

Rozdílné příčiny mortality zanechávají charakteristická biologická dědictví, která ovlivňují následnou strukturu porostů a jejich následnou citlivost k následným disturbancím. Skladba příčin mortality v rámci druhů a velikostí jedinců je tedy významným aspektem dalšího vývoje porostu.

Tato práce si klade za cíl: 1) vyhodnocení míry mortality a skladby jejích příčin v původních horských smrkových lesích v kontextu jejich struktury (Kapitola 5.1), 2) prozkoumání vztahu mezi disturbanční historií a současnou mortalitou (Kapitola 5.2), 3) vyhodnocení celkové a druhově-specifické miry mortality a skladby příčin mortality v původních bukových a smíšených lesích (Kapitola 5.3) a 4) analyzovat hlavní factory řídící variabilitu výčetní kruhové základny porostů v původních lesích (Kapitola 5.4). K těmto účelům byla využita rozsáhlá databáze trvalých výzkumných ploch v primárních lesích Karpatského řetězce. Byla použita strukturní a dendrochronologická data spolu s daty o mortalitě založenými na opakovaném měření z téměř 700 trvalých výzkumných ploch.

Hlavní zjištění práce:

1) Vypočtená roční míra mortality v primárních horských smrkových lesích je v rozsahu dříve publikované pozaďové mortality. Na úrovni ploch a porostů byla však detekována značná variabilita. Zaznamenané recentně mrtvé stromy náležely rovnoměrně do tloušťkových tříd až do 50 cm výčetní tloušťky. Tloušťkové rozdělení se však výrazně lišilo pro jednotlivé příčiny mortality, jelikož konkrétní příčiny převažují u jedinců určitých velikostí. Napadení lýkožroutem (převážně Lýkožrout smrkový, *Ips typographus* L.) bylo nejčastější příčinou mortality I v porostech s nízkou celkovou mírou mortality. Výsledky studie naznačují, že výrazná role lýkožrouta se nemusí nutně rovnat extrémní mortalitě na velkém území (Kapitola 5.1).

2) Současná mortalita byla nejvyšší v rámci historicky nejméně narušených ploch. Nejsilnější vztah byla nalezen na úrovni porostu pro 120 let dlouhé období předcházejí opakované inventarizaci. Pozorované vzorce se však liší mezi dílčími regiony. Silnější vztah pozorovaný na úrovni porostu v porovnání s úrovní plochy, a dále podpořený absence statisticky významných vztahů v rámci některých regionů, indikuje důležitou roli měřítka při vyhodnocování vztahu historických disturbance a současné mortality. Výsledky take naznačují, že nejen pouhá intenzita, ale též proměnlivost v čase jsou zásadními parametry disturbančních režimů formujících dnešní lesy. Délka období historických narušení s nejsilnějším dopadem na mortalitu se v průběhu času mění (Kapitola 5.2).

3) Vypočtená celková meziroční míra mortality ve smíšených lesích je bezpečně v publikovaném rozsahu pozaďové mortality. Míra mortality na úrovni porostů a ploch je variabilní, ačkoliv ne tolik jako v případě horských smrčin ve stejném region. Většina recentně udumřelých stromů spadala do nejnižších tloušťkových tříd, což zdůrazňuje efekt kompetice. Jednotlivé příčiny mortality mají odlišná rozdělení mezi tloušťkovými třídami.

Přestože vliv klimatických extrémů byl v roli příčiny mortality zaznamenán v omezeném množství případů, většina sledovaných porostů byla ovlivněna suchem. Kompetice a abiotickými vlivy způsobené mechanické poškození jsou nejčastějšími příčinami mortality. V případě smrku je však převažující příčinou napadení lýkožroutem. Statisticky významné rozdíly v míře mortality na úrovni region a druhů a druhově-specifická skladba příčin mortality podtrhují význam heterogenní porostní struktury a druhové skladby (Kapitola 5.3).

4) Bylo zjištěno, že výčetní kruhová základna smrku ztepilého je proměnlivá na několika prostorových škálách. Při velkých měřítkách je nejzásadnější vliv klimatu, zatímco v menších měřítcích mají na heterogenitu porostů největší vliv přírodní disturbance. V menších měřítcích je variabilita řízena disturbancemi (převážně způsobenými větrem a hmyzem) a biologickými dědictvími disturbancí, keteré se staly před více než stoletím. Klimatická změna může vest ke zvýšení průměrné výčetní základny v severnějších oblastech, zároveň však potenciální zvýšení četnosti a síly disturbancí může narušit obvyklé a předpokládané reakce prostředí (Kapitola 5.4).

Dále tato práce předkládá obecná doporučení pro ochranu a management lesů, založená na výsledcích výzkumu a jejich kontextu v další publikované literatuře.

Klíčová slova: Roční míra mortality, Biologická dědictví disturbancí, Dynamika lesa, Struktura lesa, Příčiny mortality, Přírodní disturbance, Původní lesy

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1. Introduction

Disturbances significantly influence forest dynamics (Turner 2010, Čada et al. 2016) and are considered among the most important processes influencing forest structure and species composition via altering availability of resources and opportunities for recruitment (Denslow 1995, Oliver and Larson 1996, Canham et al. 2001). Variation in disturbance area, frequency, and severity plays an essential role in shaping forest structural and compositional heterogeneity at the landscape scale (Fraver et al. 2009, Donato et al. 2012). Due to their direct and indirect effects, disturbances are recognized as major cause of tree mortality (Turner 1987, Seidl et al. 2007, Fraver et al. 2009, Sproull et al. 2015, 2016, Das et al. 2016).

Tree mortality processes, rates and mortality agents are important for understanding forest dynamics (Franklin et al. 1987, Das et al. 2016) because they strongly influence further stand development (Bircher et al. 2015), and they are crucial for predicting forest structural and compositional changes in response to global change (Bonan 2008, Adams et al. 2010, Allen et al. 2010, Dietze and Matthes 2014). Tree mortality is a key factor in modelling carbon residence time, yet it remains one of the highest uncertainties in large-scale models of vegetation dynamics (Friend et al. 2014, Bugmann et al. 2019). Quantifying the composition of different mortality agents in the context of disturbances and stand conditions remains critical to study, to help link tree, stand, landscape, and global processes (Franklin et al. 1987). Different mortality agents affect trees in various ways and results in different mortality modes (Larson and Franklin 2010, Holzwarth et al. 2013). The mortality modes in turn affect stand structure through biological legacies, therefore the composition of mortality agents is important for subsequent stand development (Das et al. 2008, Schurman et al. 2018, Esquivel-Muelbert et al. 2020). The role of mortality agents is assumed to be species-specific (Holzwarth et al. 2013, Vanoni et al. 2016) and influenced by stand conditions (Das et al. 2016).

Stand structure in primary forests is shaped by disturbances varying in area, frequency, and severity, which results in structural and compositional heterogeneity at the landscape scale (Fraver et al. 2009, Donato et al. 2012). Stand structure affects resilience or susceptibility of the stand to future disturbance events (Johnstone et al. 2016, Schurman et al. 2018). While local disturbances are likely the most influential factor on a fine scale, climate is the main driver of structural variability on coarse scales (Janda et al. 2019). With expected increases in the frequency, scale and severity of drought- and insect-related disturbance events following climate change (Seidl et al. 2007, Allen et al. 2010, Lindner et al. 2010, Jonsson et al. 2012, Vanoni et al. 2016, Seidl and Rammer 2017, Seidl et al. 2017) it is imperative to improve our ability to disentangle the effects of climate and developmental drivers within forest stands (Lindner et al. 2010, Jonsson et al. 2012, Vanoni et al. 2016, Kulakowski et al. 2017, Seidl and Rammer 2017, Seidl et al. 2017).

Primary forests present a unique opportunity to study natural processes in stands developing for extensive periods of time with little to no human impact, driven by their natural disturbance regimes and characteristic by high structural heterogeneity (Franklin et al. 2007, Kuuluvainen and Aakala 2011). The Carpathian Mountains represent one of the largest forested regions in Europe and contain relatively large tracts of primary forests (Veen et al. 2010, Knorn et al. 2012, Sabatini et al. 2018) therefore for research, they offer ideal study sites. Studying the complex relationship of natural disturbances, tree mortality and forest structure poses an important challenge in improving our understanding of forest dynamics and our ability to model or predict impacts of global changes. Research conducted in primary forests provide important reference baselines for forest management practices as they represent intact ecosystems, thus our results may serve as a guidance for forest management and conservationists to maintain the conditions which support biodiversity, structural heterogeneity, and the continuity of temperate forest ecosystems.

2. Literature review

2.1 Primary forests

Based on the definition by the Food and Agricultural Organization (FAO, 2015), primary forests are naturally regenerated forests of native species with no clearly visible indications of direct human activities, and where ecological processes have not been significantly disturbed. However, it would not be proper to completely deny a certain level of human intervention in the past, as it might not be documented and after prolonged period the impacts cannot be detected or at least reliably identified. A definition presented by Kraus and Krumm (2013) is based on natural processes: primary forests are forests that were initiated under a regime of natural disturbances and have developed with limited direct human influence. A crucial factor of primary forests is the absence of direct human operations that disturb ecological processes but, like all forests, even the primary ones are subject to indirect impacts of human activity, such as climate change, air pollution or altered population densities of ungulates. Primary forests can also be defined as dynamic ecosystems driven by disturbances of various scales, diverse developmental pathways, shifting microenvironments, and competitive interactions governing spatial patterns of mortality and recruitment (Donato et al. 2012, Svoboda et al. 2012). Because the stands have developed under their natural disturbance regimes and there is limited evidence of past human impacts, the old-growth stage of development is not a required condition and early seral stages might be present as well (Sabatini et al. 2018, Svoboda et al. 2014) promoting their structural heterogeneity. The natural disturbance processes maintain spatial heterogeneity, which in turn affects the spatiotemporal distribution of associated organisms (Lindenmayer et al. 2006). Primary forests also generally contain substantially higher amounts of deadwood than managed forests (Siitonen 2001). Deadwood that arises as a legacy of various disturbance and mortality processes is diverse in forms and sizes (Larson and Franklin 2010, Holzwarth et al. 2013, Esquivel-Muelbert et al. 2020). With these unique qualities, primary forests significantly contribute to biodiversity conservation (Lachat and Müller 2018), thus their protection should be a global concern (Mackey et al. 2015). In regions with highly fragmented forests, the ecological value of these diverse forests is of even greater importance (Vandekerkhove et al. 2009) as they serve as refugies and reservoirs for rare and/or endangered species, especially taxa sensitive to human disturbance that are unable to survive in managed and highly altered forests (Peterken 1996, Paillet et al. 2015).

Primary forests represent a suitable model for studying natural disturbances and successional dynamics (Kuuluvainen and Aakala 2011), especially under the ongoing climate change (Allen et al. 2010), and provide valuable information about ecosystem services under unmanaged conditions, including carbon stocks and sequestration (Burrascano et al. 2013). Furthermore, primary forests allow us to better assess human impacts on forest ecosystems and to evaluate the potential and limits of management practices in forestry (Bauhus et al. 2009, Kuuluvainen and Aakala 2011). Since ancient times, the temperate forests of Europe were used for many purposes including gathering fuel wood, pasture, and timber extraction (Veen et al. 2010). Like in other long-settled regions, historical deforestation and forest exploitation came close to eliminating European primary forests (Potapov et al. 2017). As such, the last tracts of primary forests are located in remote and/or hardly accessible mountain regions of Eastern and Southeastern Europe (Veen et al. 2010, Knorn et al. 2012). The Carpathian Mountains contain a large share of Europe's remaining temperate primary forests (Sabatini et al. 2018, Mikoláš et al. 2019). These remnants of undisturbed forests are heavily fragmented, and reportedly there are no intact forest landscapes exceeding 500 km^2 except for European Russia and boreal Northern Europe (Potapov et al. 2017). The remaining primary forests occur in remote, sparsely populated regions, mostly in difficult to access mountain areas (Fraver et al. 2009), where landuse has a shorter history and/or lower intensity than in the rest of Europe (Kulakowski et al. 2017).

2.2 Disturbance and disturbance regimes

Disturbances are considered a key component of ecological systems and the main drivers of spatio-temporal heterogeneity (Turner 2010). Disturbances – discrete events changing resource availability and disrupting an ecosystem or community (Pickett and White 1985), that occur over a short period of time but have long-term affects on the system (Turner 2010) – and their patterns on both the spatial and temporal scale influence the stand in its structure, composition and even function (Fraver and White 2005, Turner 2010). The origin of disturbances may be abiotic or biotic, or a combination of these. In contrast to a discrete disturbance event, a disturbance regime describes the spatial and temporal dynamics of disturbances in a respective forest stand over time. Disturbance regimes are characterized by the spatial distribution of disturbances, disturbance frequency, return interval, size, intensity, and severity (Turner 2010). As mentioned, natural disturbances represent one of the main drivers of primary forest dynamics. Variability in disturbance area, frequency, and severity plays an essential role in shaping forest structural and compositional heterogeneity at the landscape scale (Fraver et al. 2009, Donato et al. 2012). Due to this variation on different spatial and temporal scales, forest ecosystems are dynamic; their structure and composition are in a continuous state of change (Kraus and Krumm 2013). Disturbances might alter the age structure of forest landscapes, promote early seral species, and influence the development trajectories in forest ecosystems, leaving legacies that affects the forests for decades or even centuries (Frelich 2002, Nagel et al. 2014).

The intensity, frequency, and severity of natural disturbances in primary forests have a major effect on the quantity and quality of available habitats (Lachat and Müller 2018). Thus, disturbances play a key role in maintaining biodiversity in temperate forest ecosystems through their biological legacies, such as increased quantity and quality of deadwood, and increased light availability in the understory (Hanson and Lorimer 2007, Woods 2004). The concept of the "historical range of variability" proposed by Keane et al. (2009) suggests a specific regime of past disturbances as the primary driver of forest conditions that native forest species have adapted to over extensive periods of time (McPeek and Holt 1992, Gauthier et al. 2015) and from which they are likely to benefit in the future (Drapeau et al. 2016, Mikoláš et al. 2017, Betts et al. 2019).

Severe windthrows connected with the direct disturbance of canopy trees are considered the most important type of disturbance in the temperate forests of Central Europe (Ulanova 2000, Schelhaas et al. 2003). Most primary forests in the Carpathians are considered subject to mixed-severity disturbance regimes (Panayotov et al. 2011, Svoboda et al. 2014, Trotsiuk et al. 2014, Janda et al. 2017, Schurman et al. 2018), however, the role of intermediate disturbance events (i.e., single events that cause stand-level damage ranging from scattered single tree falls to larger openings several thousand square meters in size (Woods 2004)) should not be neglected. The major impact of recent high severity disturbances, predominantly caused by windstorms and subsequent bark beetle (most frequently *Ips typographus* L.) infestation, on Norway spruce (*Picea abies* (L.) Karst.) stands (Schurman et al. 2018, Čada et al. 2020) has been repeatedly reported from various areas of their natural range (Čada et al. 2016, Lausch et al. 2011, Svoboda et al. 2012; Mezei et al. 2014, Sproull et al. 2015, 2016). Both windstorms and insect outbreaks influence stand structure on multiple temporal and spatial scales (Grodzki et al. 2004, Jonášová and Prach 2004, Krumm et al. 2011, Panayotov et al. 2011). Bark beetle outbreaks often follow major windthrow events, because they provide large amounts of breeding material (Wermelinger 2004). Bark beetles predominantly attack, but are not limited to, trees suffering from other stress factors (e.g., drought or structural failure). Spruce trees that are not weakened by other means are generally resistant to bark beetle attacks through their resin defenses (Stokland et al. 2012). Larger, older trees are usually preferred (Schroeder and Lindelow 2002, Křístek and Urban 2013, Nelson et al. 2014, Seidl et al. 2015, Sproull et al. 2015, 2016). However, when the population reaches outbreak levels the selective behavior plays a minor role as the numbers of individuals boring into each tree surpasses the natural defenses of the tree and large scale, sweeping mortality might occur. Even under such conditions complete stand-replacing disturbances are rare (Sproull et al. 2015, 2016). Primary mountain Norway spruce stands in the Carpathians are affected by broad spectrum of disturbances ranging from low to high severity, however, synchronicity of these events on the stand or landscape scale is often limited (Svoboda et al. 2014, Trotsiuk et al. 2014). Moderate-severity and moderate-scale disturbances are reported to be the most common (Čada et al. 2020). This finding supports the suggested particular importance of such events in forests mostly driven by wind- and insects-related disturbances (Fraver et al. 2009), and highlights the importance of the spectrum of disturbances (Angelstam and Kuuluvainen 2004) between the traditional fine-scale gap dynamics (Seymour et al. 2002) and stand replacing disturbances (Kuuluvainen and Aakala 2011). Studies conducted in primary and natural beech and beech-dominated mixed forests indicate that periodic intermediate-severity damage caused by wind disturbances is an important component of the disturbance regime in this region (Nagel et al. 2014, Frankovič et al. 2021). The disturbance dynamics in mixed stands are expected to be less turbulent than in spruce stands (Motta et al. 2011).

Due to their direct and indirect effects on forest ecosystems, disturbances are recognized as a major source of tree mortality (Turner 1987, Seidl et al. 2007, Fraver et al. 2009, Sproull et al. 2015, 2016, Das et al. 2016). Understanding disturbance characteristics is key to disentangling the effects of environmental changes and developmental drivers of temporally variable mortality rates (Lindner et al. 2010, Jonsson et al. 2012, Vanoni et al. 2016, Kulakowski et al. 2017, Seidl and Rammer 2017, Seidl et al. 2017).

2.3 Mortality and mortality rates

Tree mortality and its rates are crucial for understanding forest dynamics (Franklin et al. 1987, Das et al. 2016) because they strongly influence future stand development (Bircher et al. 2015) and are a key factor for predicting forest structural and compositional changes in response to global climatic and environmental change (Bonan 2008, Adams et al. 2010, Allen et al. 2010, Turner 2010, Dietze and Matthes 2014, Thom et al. 2017). Tree mortality rates represent a major factor in modelling carbon residence time, yet they remain one of the critical uncertainties in large-scale models of vegetation dynamics (Friend et al. 2014, Bugmann et al. 2019). A number of studies have been conducted in forests with consistently low annual mortality rates (e.g., Stephenson and van Mantgem 2005, Das et al. 2016). It has been documented that in such forest ecosystems, even slight changes to background mortality rates, as low as 0.5 to 2% per year (Stephenson and van Mantgem 2005), could ultimately have a bigger impact than a severe disturbance event (van Mantgem et al. 2009). Another considerable effort has been made in studying stands recently affected by high-severity disturbances, most frequently windthrows and insect outbreaks, with reported high mortality rates (e.g., Bréda et al. 2006, Sala et al. 2010, McDowell et al. 2011, Anderegg et al. 2015, Sproull et al. 2015, 2016). With expected increases in the frequency, scale and severity of drought and insect outbreak events under climate change

(Seidl et al. 2007, Allen et al. 2010, Lindner et al. 2010, Jonsson et al. 2012, Vanoni et al. 2016, Seidl and Rammer 2017, Seidl et al. 2017), the value of the information obtained by both groups of studies becomes even more relevant. However, the mortality scenarios form a continuum from regular (non-catastrophic) to irregular (catastrophic) mortality (Monserud 1976, Hawkes 2000). Disturbances are an integral part of the dynamics even in low mortality stages (Turner 2010). Mortality can vary substantially on both temporal and spatial scales (Sproull et al. 2016, Čada et al. 2020), which might be linked to composition of mortality agents and stand structure. As aforementioned, disturbances significantly influence forest structure and dynamics (Turner 2010, Čada et al. 2016), and represent one of the key processes affecting forest structure and composition via altering resource availability and opportunities for recruitment (Denslow 1995, Oliver and Larson 1996, Canham et al. 2001), therefore, they are recognized as major drivers of tree mortality (Turner 1987, Seidl et al. 2007, Fraver et al. 2009, Sproull et al. 2015, 2016, Das et al. 2016). The close and intertwining connection of disturbances and mortality processes is evident, however, our understanding of the connection on different spatial scales and its extent remains insufficient. Since there are studies linking disturbance history with contemporary forest structure (e.g., Zenner 2005, D'Amato et al. 2008, Janda et al. 2017) or current structure with observed mortality (Clyatt et al. 2016), evaluation of the relationship between past disturbances and contemporary mortality seems to be a desirable next stage.

Individual-based forest models often generalize mortality into two major groups, using "vigor-related" mortality and "ambient" (or "background") mortality. Vigor-related mortality assumes an inverse relationship between tree growth and mortality probability (Shugart 1984, Bugmann 2001, Bircher et al. 2015), which roughly reads that trees limited in growth, for whatever the reason, are more prone to mortality. Ambient mortality in general is somewhat random and not related to growth. Abiotic factors such as wind, fire, or lightning, are commonly considered to be the drivers behind ambient mortality. Intrinsic biotic factors might also contribute to mortality and there are concerns about their underestimation in many models (Das et al. 2016). Many individual-based models, however, have been developed for managed, even-aged forests, and thus often consider only one generation of trees, which makes them inappropriate for complex, uneven-aged structures, that are common in primary forests (Bircher et al. 2015).

2.4 Mortality agents and mortality modes

Our understanding of tree mortality processes is incomplete because of the problem that tree mortality can rarely be observed and attributed to unequivocal causes (Adame et al. 2010, Das et al. 2016, Vanoni et al. 2016). Concerns regarding accuracy of identifying the mortality agents for some trees - mainly large, fast-growing trees - have been raised (Das et al. 2016). These concerns are based on the complicated evaluation of signs in parts of trees that are difficult to view, determination between a combination of agents, and the complicated differentiation of primary and secondary (after tree death) occurrences of fungi and insects (Das et al. 2016). Quantification of the contribution of different mortality agents in the context of disturbances and stand conditions, however, presents a key step to link tree, stand, landscape, and global processes (Franklin et al. 1987).

Mortality can be greatly variable through space and time (Sproull et al. 2016, Čada et al. 2020), which might be linked (among other factors) to the mortality agents. The consequences of different processes ultimately leading to tree mortality are various mortality modes (Larson and Franklin 2010, Holzwarth et al. 2013, Nagel et al. 2021). These different modes create different biological legacies and therefore have different impacts on structure and further stand development (Das et al. 2008, Schurman et al. 2018, Esquivel-Muelbert et al. 2020). The combination of mortality agents and their respective contribution is dependent on species composition (Holzwarth et al. 2013, Vanoni et al. 2016), stand structure (Das et al. 2008), and local topography (Das et al. 2008, Senf and Seidl 2018). Several studies have highlighted the predicted increases in the scale and severity of drought and insect outbreak events related to ongoing climate change (Seidl et al. 2007, Jonsson et al. 2012, Vanoni et al. 2016, Seidl and Rammer 2017, Seidl et al. 2017), which may also alter the relative prevalence of mortality agents. Combining empirical mortality data with demographics and mortality agents and collecting extensive datasets from various forest types represents a relatively simple, yet crucial way to improve our understanding of forest mortality.

Grouping the factors of mortality based on their role in the mortality process provides a more complex scheme than simple “vigor related” or “random” division often used by older individual-based models. The concept uses three categories of factors: predisposing, inciting, and contributing (Manion 1991). Predisposing factors, such as climate or competition, influence stands over the long term (Allen et al. 2010). Agents operating in the short term with highly variable intensities are part of the inciting factors group; this group includes acute drought and frost, insect or pathogen attacks and generally random events of abiotically-caused physical damage (Anderegg et al. 2015). Effects of inciting factors can be followed by subsequent agents. Insects and fungi are considered the most frequent contributing factors, which encompass agents that are frequently part of the mortality process, but they might not induce tree death and their impacts are often uncertain (Allen et al. 2010). Some agents can act as different factors depending on given scenario.

Mortality modes have an obvious limitation as they are only an approximate reason of tree death (Larson and Franklin 2010, Holzwarth et al. 2013), therefore they provide less precise information than an assessment of the cause of mortality of each tree shortly after its death (Das et al. 2016) as it is in many cases problematic to distinguish which of the contributing factors were involved in the mortality process (Allen et al. 2010, Das et al. 2016). Additional information on the year of tree death (which can be subtracted from a dendrochronological series), can potentially help to link individual tree death to a larger scale event however, it is also reliable only to some extent as many trees show abrupt growth decreases several years or even decades prior to death (Vanoni et al. 2016). Despite these limitations, mortality modes allow us to evaluate the main mortality agents. Evaluating the relative frequency of different mortality agents or modes on landscape and species levels in primary forests should provide further insight on how disturbance regimes may interact with climate change (Turner 2010).

The accuracy of assessing mortality agents or causes of mortality, depending on the followed approach, decreases with time since tree death, thus technically with extending time period between observations (Das et al. 2016). Due to the amount of time and work required to assess the mortality agents or modes in the field, studies dealing with huge datasets usually simplify the categorization, up to the level of distinguishing standing dead trees and trees affected by structural failure or physical damage (e.g., Esquivel-Muelbert et al. 2020). However, this still provides substantial information about the mortality dynamics.

A more detailed categorization, allowed by the relatively short remeasurement period – as used by REMOTE (Remote Primary Forest, 2021) - in combination with the roles of mortality factors according to Manion (1991), lists the following major groups of mortality agents:

Climatic extremes. This pertains to mortality induced or directly related to acute drought, frost, or similar deviations from climatic standards of a studied region. Due to difficulties in defining the exact driver, which is most frequently assumed to be drought, the category is defined as a broader group covering all the climate-related extremes. Climate can operate as both predisposing (long-term effects) and inciting (acute events) factors. It is complicated to identify this category of mortality agents in the field when subsequent mortality agents occur on the target tree. Through this cause of mortality, the dead trees are often left standing and mostly intact. The impacts of climate are expected to be large scale and affect the majority of a stand, therefore, it is assumed that this agent should be generally reported for multiple trees per sample unit.

Competition. This group is mostly associated with competition for light, as limitations for growth by other resources are extremely hard to ascertain in many cases. For the agent to be considered significant, the trees should have at least half of their crown directly shaded by neighbouring trees. Competition is regarded as a predisposing factor with or without subsequent mortality agent. In certain situations, the struggle of an individual for resources might be induced by prior structural damage (e.g., partial crown loss).

Fungi. Often followed by physical damage due to structural failure, fungi are considered one of the most frequent contributing mortality factors. This agent is, in many cases, difficult to identify in the field, because without a subsequent agent the presence of fungi might not be detectable (root rot, rot inside the stem) and a subsequent agent can destroy or mask the evidence.

Insects. Insect infestation might affect the tree as an inciting (with or without subsequent agent) or a contributing factor. In non-outbreak conditions the insects are assumed to be non-lethal in most cases, however, with population densities exceeding certain thresholds, the mortality probability steeply increases. Trees usually die standing, and structural damage might occur later because of wood decay, which can be accelerated by fungi associated with the infesting insects.

Physical damage. Physical damage, also reported as structural failure (e.g., Esquivel-Muelbert et al. 2020), mostly operates as inciting factor, often without any subsequent agent. Depending on the damage, the other agent might just speed up the decline, play no role at all, or be the factor ultimately resulting in tree death. In cases of limited damage to the crown, which makes the tree vulnerable to other agents (e.g., insects or fungi) or results in increased competition for resources (mostly light), this category can also be considered a contributing factor. The category can be divided to three main sub-groups based on the character of the damage. Crown breakages refer to limited damage to the crown which might or might not be lethal depending on the broader context. Stem breaks result in tree death in the majority of cases, as most or all photosynthetically active parts are removed. Uprooting is a result of structural failure in the below-ground parts of the tree (root system) or by movement of the substrate in which the tree is anchored. The damage can be caused directly by wind, heavy snow or another falling tree. This category also includes specific and rare cases induced by landslides, avalanches, or lightning.

Others. It is impossible for any methodology to systematically cover all the rare scenarios that might transpire. This group includes, for example, potential severe damage caused by animals (e.g., fraying, browsing) that might in the presence of other agents which ultimately result in tree death. In such cases the agent can operate as inciting or contributing factor depending on the context.

Since different mortality agents have various dispersion across the size, species, and social status spectrum it is crucial to evaluate the composition of mortality modes, or agents, in order to improve our understanding of tree mortality and forest dynamics in general (Das et al. 2016, Esquivel-Muelbert et al. 2020).

2.5 Stand structure

Primary forests and forests in general are important for the conservation of biodiversity because they host a substantial array of species (Lindenmayer et al. 2006). Biological diversity positively relates to habitat heterogeneity (Huston 1994) and habitat heterogeneity is driven by compositional or structural variability over time and space (Franklin and Van Pelt 2004). Forest structure is therefore considered a key determinant of biodiversity and many other ecosystem services (McElhinny et al. 2005, Paillet et al. 2018). Structural variability and features, like various volumes and forms of deadwood and large old trees, are mostly legacies issued from natural disturbances (Franklin et al. 2002), and thus are usually infrequent in managed forests.

Primary forests are composed of a mosaic of developmental stages with complex vertical and spatial structure (Franklin et al. 2002). In comparison with even-aged production forests they therefore provide better opportunities for natural regeneration and become more ecologically resilient. The complex structure is dependent on species composition, characteristics of individual species present (longevity, typical growth rates and strategies), climatic conditions, and disturbances – their type, frequency, scale, and severity (Franklin et al. 1987, Burrascano et al. 2013). Specific definitions of primary or natural forest structure have been created for various temperate forest types and regions (Burrascano et al. 2013). There is a substantial variability among the definitions (Wells et al. 1998, Turner 2010, Burrascano et al. 2013). Such a finding is not too surprising considering the structural characteristics of various forest types. For example, Norway spruce forests are structurally different from European beech-dominated forests even though they can be geographically located close to one another (Nagel and Svoboda, 2008, Zielonka et al. 2010, Svoboda et al. 2012). Similarly, forests with the same or equivalent species composition might be subject to different disturbance regimes in various regions, resulting in diversity in their structure. Disturbance history leaves biological legacies (e.g., deadwood in different forms, sizes and stages of decay, pit and mound topography) with long-term effect on stand structure and its reaction to subsequent disturbance events (Veblen et al. 1994, Svoboda et al. 2012, Sproull et al. 2015). Various types of disturbances result in specific forms of disturbance (biological) legacies, which in turn promote different structural features. It has been repeatedly highlighted that the evaluation and characterization of primary forests should not be based on the structure itself, but rather on processes creating and maintaining the structures (Lindenmayer et al. 2000, Franklin et al. 2002, Burrascano et al. 2013).

Yet, the natural variation in forest dynamics, and consequently biomass, in temperate mountain forests remains poorly understood. In primary montane Norway spruce forests - the dominant high-elevation forest type of the Carpathians - the disturbance regime is typically defined as mixed severity, meaning a wide range of severities is evident in the disturbance regimes (Trotsiuk et al. 2014, Svoboda et al. 2014, Janda et al. 2017, Schurman et al. 2018). Windstorms and bark beetles are the major natural disturbance agents, and disturbances typically return at relatively short intervals (years to decades) and cause tree mortality at relatively small scales (< 1 ha), however larger, less frequent events affecting tens to hundreds of hectares have also been documented (Svoboda et al. 2014, Sproull et al. 2015, Čada et al. 2016, Janda et al. 2017). This regime results in substantial heterogeneity of the forests, which is dynamically changing. Such a dynamic, yet more or less stable state generates space and resources for new recruitment while providing enough protection against mechanical damage (e.g., wind, avalanches) and shading to limit growth of understory species competing with new seedlings. Stands developing in this way are more likely to have a high diversity in tree ages and dimensions and spatial structure, which improves its resilience (Aussenac et al. 2017).

2.6 Climate

Increased emissions of greenhouse gases are widely acknowledged as a major cause of recent increases in global mean temperature and changes in the global hydrological cycle (IPCC 2007). Future climatic changes are, even under conservative scenarios, likely to include further increases in global temperatures causing major drought conditions in some regions (IPCC 2007, Christensen et al. 2007, Seager et al. 2007, Allen et al. 2010). Understanding the consequences of these climatic changes on forest ecosystems is a major concern for global change scientists (Bonan 2008, Allen et al. 2010). Increases in the frequency, duration, and/or severity of drought and heat stress induced by climate change might significantly alter the structure, composition, and biogeography of forests (Allen et al. 2010, McDowell et al. 2020). The changes in environmental drivers and disturbance regimes are increasing mortality and forcing forests toward younger stands (McDowell et al. 2020).

Climate change is expected to have both positive (e.g., increases in forest growth from CO_2 fertilization, increases in water use efficiency, and extended growing seasons) and negative impacts (e.g., combined effects of climate change and climate-induced shifts in the dynamics of insects and pathogens resulting in reduced growth, more frequent and severe stress, and increased mortality) on forest ecosystems (Ayres and Lombardero 2000, Scholze et al. 2006, McDowell et al. 2020). Increased background mortality rates (van Mantgem et al. 2009) and widespread death of many tree species in multiple forest types (Raffa et al. 2008) associated with drought and/or high temperatures have been reported. Such findings suggest that the world’s forests are increasingly responding to ongoing warming and drying (Allen et al. 2010, McDowell et al. 2020). The patterns of mortality in response to drought and heat stress range from modest and short-term local increases in background mortality rates to periods of acute, landscape-scale forest decline, which might involve biotic agents like insect outbreaks (Allen et al. 2010). At broad spatial scales, mortality associated with drought has been reported near species geographic or elevational range margins where climatic factors (mostly water stress) are commonly presumed to be limiting (Jump et al. 2009, Allen et al. 2010). Large-scale die-offs are commonly associated with prolonged water deficits during extensive periods of drought in specific forest types, for example temperate coniferous forests (Allen et al. 2010), however a higher impact caused by extremes rather than long-term drought conditions have also been reported (Schurman et al. 2018). Under climate change, large areas of formerly low temperature-limited forests seem to be transitioning towards heightened moisture sensitivity (Babst et al. 2019, Schurman et al. 2019). It has become critical to disentangle the developmental and climatic drivers of tree mortality as changes in background mortality rates and episodic mortality events can occur independently of climate change (Allen et al. 2010, Schurman et al. 2018). Many existing projections of tree mortality, however, are based on models that lack functionally realistic mortality mechanisms (Allen et al. 2010). The predicted increases in frequency and severity of certain disturbance agents pose substantial risks to ecosystem services, including loss of sequestered carbon (Allen et al. 2010, Schurman et al. 2019, McDowell et al. 2020). Tree mortality rates are expected to consistently increase while recruitment and growth response to changing drivers will likely vary on both the spatial and temporal scale, resulting in a net reduction of forest canopy cover and biomass (McDowell et al. 2020).

In temperate montane forests, the focus of this study, drought is suggested to be a major climatic characteristic influencing disturbance parameters and tree mortality. Recent studies in primary mountain Norway spruce forests in the Carpathian mountain-arc detected an increase in disturbance rates with decreasing Palmer Drought Severity Index (Schurman et al. 2018), an increase in moisture sensitivity (Bjorklund et al. 2019, Schurman et al. 2019), and an increase in sensitivity to winter drought (Svobodová et al. 2019).

3. Aims and overview of the dissertation thesis

Understanding the mortality processes in primary forests can provide valuable information for the conservation and suitable management of forest ecosystems. Based on data from almost 700 permanent study plots located across primary spruce and mixed forest landscapes, we aim to enhance our knowledge of the interactions between historical disturbance regimes, current forest structure, and mortality. More specifically, the thesis focuses on the evaluation of annual mortality rates and the composition of mortality agents in the context of stand structure and disturbance history. Mortality is an important aspect of stand dynamics, influencing future stand structure and development. Different disturbance types, representing various mortality agents, result in diverse mortality modes, leaving biological legacies that influence the susceptibility of a stand to future disturbances. The composition of mortality agents is therefore of substantial importance for understanding dynamics in specific forest types. Studies from primary forests provide valuable reference baselines for forest management practices as they represent mostly intact ecosystems, thus our results may serve as a guidance for forest management and conservationists in order to promote heterogeneity, biodiversity and stability. In particular the thesis aims to:

1) Evaluate the mortality rates and composition of mortality agents in the context of stand structure in primary mountain Norway spruce forests. (Chapter 5.1)

2) Evaluate the relationship between disturbance history and current mortality. (Chapter 5.2)

3) Evaluate the overall and species-specific mortality rates and mortality agents' composition in primary European beech-dominated mixed stands. (Chapter 5.3)

4) Analyze the main drivers of basal area variability in primary forests. (Chapter 5.4)

4. Methods

4.1 Study area

The thesis was realized within the REMOTE project (Remote Primary Forests, 2021). The project is a long-term international collaboration based on a network of permanent sample plots in the forests of Central, Eastern and Southeastern Europe. The project is focused on surveying the last remaining tracts of primary forest landscapes in Europe and the long-term study of their dynamics. The forests referred to as primary forests are stands that developed for extensive period of time with little to no direct human intervention, with their structure and composition shaped by natural disturbance regimes (Sabatini et al. 2018). However, the old-growth stage is not a required condition and primary forests might contain early seral stages because of natural disturbances (Svoboda et al. 2014, Sabatini et al. 2018). These disturbances range in scale from single tree mortality up to tens or even hundreds of hectares (Svoboda et al. 2014, Čada et al. 2016).

The studies were conducted in the Carpathian Mountains, which host some of the largest tracts of primary forests in Central and Eastern Europe, and the largest primary Norway spruce forest remnants in temperate Europe (Veen et al. 2010, Knorn et al. 2012). The Carpathian mountain arc spans over 220, 400 km^2 and represents the second largest mountain range in Europe. The mountain range stretches across eight European countries: Romania, Ukraine, Slovakia, Austria, Czech Republic, Poland, Hungary, and Serbia. The study plots cover a geographical gradient exceeding 1000 km. Therefore, the region is ideal for investigating natural disturbance processes over large spatial scales.

The remote location and complicated access protected the forests from direct human activities for a long period. Conversely, forests in lower altitudes with easier access were mostly harvested due to human settlement and agriculture. The deforestation process was asynchronous over the region, however, the main pulse happened approximately between 500 and 1500 AD. The forests located deep within steep valleys or on ridges were often left mostly intact. A relatively continuous mountain forest cover remained in some regions of the Carpathians (mostly Romania and Ukraine) until several decades ago, due to operationally and/or economically ineffective conduct of the harvest. With recent introduction of modern logging technologies, however, many previously unaffected sites were destroyed across the Carpathian region. Primary forests currently represent only a small part of the forest cover in the region. As a result of insufficiently-precise mapping in some areas and limited effectiveness of protection measures, the remaining primary forests are still decreasing in size and becoming more fragmented.

Primary forests in the Carpathians are dominated by Norway spruce at higher elevations, usually from ca. 1, 200 m a.s.l. and higher. Other species include European silver fir (*Abies alba* Mill.), Swiss pine (*Pinus cembra* L.), rowan (*Sorbus aucuparia* L.), and birch (*Betula* spp.). These stands are the main focus of Chapters 5.1, 5.2, 5.4.

European beech-dominated (*Fagus sylvatica* L.) mixed forests are the prevalent primary forest type in lower elevations of the Carpathian Mountains. Other major species present are European silver fir (*Abies alba* Mill.), Norway spruce (*Picea abies* (L.) Karst.), and sycamore maple (*Acer pseudoplatanus* L.). Beech-dominated mixed stands are examined in Chapter 5.3.

4.2 Study site selection and sample plot establishment

The first step of study site selection was done combining previous inventories of primary forest remnants (Hamor et al. 2008, Veen et al. 2010) and maps to identify potential primary forest stands. Identified stands were subsequently surveyed for signs of direct human activity and indicators of naturalness (e.g., coarse woody debris in various stages of decay, pit and mound topography) (Mikoláš et al. 2019). Stands containing evidence of past logging or grazing, as well as stands adjacent to previously grazed areas, the tree line, and extreme sites were excluded (Svoboda et al. 2014, Trotsiuk et al. 2014, Wirth et al. 2009). According to available historical documents, the selected study areas were not subject to systematic logging since at least the early eighteenth century and have been protected for a long period (Svoboda et al. 2014). The included localities cover a wide range of variability in topography (elevation, slope, and aspect), and are therefore considered, to some degree, representative of the landscape-scale heterogeneity found in the region. However, a statistical stratification of the stands across the various geographic parameters was not possible, due to the limited distribution of primary forest fragments (Svoboda et al. 2014).

In each stand a stratified random design was applied for sample plot establishment (Svoboda et al. 2014). In spruce stands a 141.4 x 141.4 m grid was overlaid on each stand, and within each grid cell a 0.1 ha (1,000 m^2) sample plot was established at a restricted random point generated in a GIS and located using GPS. The locations of sample plots center points were restricted to the inner 0.49 ha core area in each 2 ha grid cell. In mixed stands the overlaid grid had 10 ha cells and plots established within each cell were circular with the size of 1000 (in 2014) or 1500 m^2 (2015 onwards). A random point was generated in the 0.5 - 3.4 ha core of each grid cell, and a pair of plots was established 40 m from either side of this point along the contour line, resulting in plot centers separated by 80 m.

4.3 Data collection

A total of 371 spruce plots (over 16,000 originally live trees) and 227 mixed plots (almost 14,000 originally live trees) were used for assessing mortality in primary forests (Chapter 5.1 and 5.3 respectively). For analyzing the relationship between historical canopy area removal and contemporary mortality, 370 spruce plots (over 16,000 trees alive during first sampling) were used (Chapter 5.2). The evaluation of drivers of basal area (BA) variation used data from 472 permanent study plots (Chapter 5.4). The plots were resampled five years after their establishment. Environmental characteristics (elevation, slope, and aspect), composition, and structure were recorded for each study plot. The measurement threshold for individual trees was set to 10 cm diameter at breast height (DBH) in spruce stands and 6 cm DBH in beech-dominated mixed stands. For each tree exceeding the threshold, several parameters were recorded: DBH; social status (suppressed vs. released tree; suppression is considered when more than half of the crown is directly shaded by surrounding trees); canopy layer; whether it was dead or alive; and any signs of substantial mechanical damage (e.g., broken crown). In spruce stands we recorded crown width in two perpendicular directions for five randomly selected trees per plot in order to determine the relationship between DBH and projected tree crown for each stand (Chapter 5.2., 5.4).

During the resampling, mortality agents were assessed for recently dead trees (i.e., those that were alive during the initial sampling). Only the agents that could have played a significant role in the mortality of a given tree were recorded (e.g., stem breakage occurring clearly after tree death was not listed). The categories of mortality agents are based on the methodology used by REMOTE project (Remote Primary Forests, 2021). Seven categories were used: Climatic extremes, competition, fungi, insects, and three modes of physical damage - crown break, stem break and uprooted tree. Climatic extremes were considered when there were multiple recently dead released trees within a plot, with no signs of severe infestation or physical damage, based on the assumption that climate acting as a predisposing or inciting factor (Manion et al. 1991, Allen et al. 2010) should influence a substantial proportion of the stand, not just single trees.

Drought is most likely the main climatic factor acting as mortality agent in the study stands (Schurman et al. 2018, Bjorklund et al. 2019, Schurman et al. 2019, Svobodová et al. 2019). However, our approach cannot disentangle all possible climatic extremes, which include drought, frost, and temperature extremes, therefore the broader category was used. Competition was considered for trees with a "suppressed" social status (more than 50% of the crown directly shaded by other trees). Fungi were listed as mortality agent mostly in association with structural failure, or based on abundant evidence of infestation (e.g., mycelia, conks). Insect infestation was recorded for trees with clear evidence of severe infestation (e.g., presence of entry/exit holes, galleries, red-brown dust at the tree base), and also for trees where such evidence was not found (e.g., due to thick bark at the base) but the infestation was estimated as the most likely agent in the context of the surroundings of the tree. Physical damage (structural failure) is further divided into three categories based on the extent and character of the damage. Crown break mode was used for trees with up to one third of their crown missing, stem break mode then includes trees with even bigger portion missing and breakage usually occurring low on the stem (but still above ground). Uprooted trees group contains trees where the mechanical failure occurred below the surface either due to damage to the root system or by movement of the substrate on which the tree was growing.

To evaluate the role of disturbances on plot-level mortality rates and heterogeneity in basal area, chronologies of inferred canopy disturbance (Frelich and Lorimer 1991) were developed using information on projected tree crown area and initial tree radial growth rates (Chapter 5.2 and 5.4). Crown width was recorded in four cardinal directions for five randomly selected trees on each plot to determine the relationship between DBH and projected crown area at each locality. This relationship allows an estimation of the extent of canopy area disturbed in the past, assuming the present canopy area of trees approximately equals to the extent of canopy area removed during the disturbance the trees were released by. Increment cores were collected from 25 randomly selected released trees per plot in order to identify trees with synchronous recruitment or growth release under canopy gaps. Each increment core was collected 1 m above ground, parallel to the slope contour line.

4.4 Data processing and analysis

4.4.1 Mortality rates

Annual mortality rates were calculated from the overall mortality over the period between the inventories. To better reflect a potential continuous decrease in tree density, we used an equation based on interest rate calculations, which should also better accommodate the potential use of different time intervals for which the annual rate is calculated:

$$\mathrm{m} = 1 - (N_t/N_0)^{1/t}$$

where N_0 is the number of live trees during first sampling, N_t is the number of trees still alive during resampling, and t is the number of years between samplings (Sheil et al. 1995, Sheil and May 1996, Kohyama et al. 2017).

Mortality rates are reported on various scales, using different aggregation schemes. The rates were first calculated on the plot level, and then aggregated to the stand, region, and species levels. We further present “overall” mortality calculated for pooled tree data for given aggregate and “plot-level” characteristics where annual rates for each individual plot within respective group were used (Chapter 5.1 and 5.3).

4.4.2 Canopy area removal

For the purposes of relating current mortality rates to past canopy area removal (a proxy for disturbances), in Chapter 5.2 the trees were transformed to their respective canopy area projection which were derived from a DBH-crown relationship. The mortality rate calculation for the comparison with past canopy area removal also excludes suppressed trees in lower canopy layers because such trees cannot be detected via dendrochronological analysis and would cause bias. Death of such tree creates little to no canopy opening and the event is therefore rarely detectable through the means of applied dendrochronological methods.

For the evaluation of the relationship between past disturbance and current mortality (Chapter 5.2) mean, range (difference between decadal minimum and maximum) and standard deviation (SD) were calculated from inferred decadal canopy area removal data for each tested period using raw reconstructed canopy area data. Mean was preferred to median as the outliers (more severe events) are assumed to be defining for subsequent development of the stand. Range and SD were used as proxies of variability in canopy area removal (disturbance severity) over time. The periods for which the relationship was tested represent the progressively extending timeframes, not a particular decade. To evaluate whether the similar relationship pattern can be detected in past decades, or it is subject to a change, tree-ring-derived decadal canopy area removal data were used as proxies for mortality in target decade and corresponding previous disturbance history. It was only possible to assess this for decades since the 1950s because the preceding disturbance data records for older periods would be inaccurate due to limited data prior to 1800 for a substantial share of the plots.

The chronologies of inferred canopy disturbances were developed by first classifying the non-suppressed trees to one of the two modes of accessing the forest canopy: 1) open canopy recruitment - trees that initiated after a canopy-opening disturbance, indicated by rapid initial growth, and 2) release—trees that established in the shaded understory and reached the canopy via one or more canopy gaps, evidenced by slow initial growth and subsequent abrupt growth release (Frelich and Lorimer, 1991). Absolute increase method was used for growth release detection (Fraver and White 2005). Juvenile growth rates were used to detect trees with open canopy recruitment (Trotsiuk et al. 2014), for details on setting the growth thresholds for distinguishing between open canopy recruitment and initial growth beneath forest canopy, and release event detection calculation, please see Chapter 5.4. Over 11, 000 increment cores were crossdated following the list year method (Yamaguchi 1991). Tree rings were measured with 0.01 mm using a Lintab^{TM} sliding-stage measuring system (Rinntech, Heidelberg, Germany) and TSAP-Win^{TM} software (Rinntech, Heidelberg, Germany) and then crossdated using CDendro software (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). Norway spruce is considered moderately shade tolerant (Tjoelker et al. 2007), especially as a juvenile, and it might require multiple disturbances to access the canopy. Multiple canopy accessions were therefore allowed in the disturbance chronologies. However, since disturbances that lead to canopy recruitment of understory individuals were the focus, crown releases were no longer identified after the tree reached a DBH threshold of 23 cm indicating the tree was already part of the main canopy by the time of the release (Lorimer and Frelich, 1989). A logistic regression was used to determine canopy status as a function of DBH in present tree inventory data (Schurman et al. 2018). Both types of events were converted to chronologies representing the canopy area disturbed over time (Lorimer and Frelich 1989). The approach assumes the sum of the current crown area of trees that recruited into a canopy opening approximates the extent of the canopy opening that enabled their recruitment. Current crown area of each tree was estimated using regression of crown width measurements in relation to DBH at each locality. These crown area estimates were combined with information on the timing of disturbance events to develop a chronology of the inferred canopy area disturbed over time in each plot. For further details on calculations please refer to Chapter 5.4.

4.4.3 Climatic data

For an overview of climatic conditions within the beech-dominated mixed stands, the temperature and precipitation data for our study plots were extracted from E-OBS gridded climate dataset (version 23.1e, Cornes et al. 2018). The daily values were aggregated to annual values for temperature and precipitation variables and “water balance”; a metric of drought was calculated as the difference between precipitation and potential evapotranspiration. The data were then averaged across all plots within each stand for a period since 1960 until 2020. The period from 1991 to 2020 was used as a reference period and standard deviations from the average during this refence period were plotted for each stand (Chapter 5.3).

Mean annual temperatures estimated by averaging over mean annual temperatures for the period 1981–2010 based on the Carpatclim dataset (Antolović et al. 2013) were used for evaluating the drivers of variability in basal area (Chapter 5.4).

4.4.4 Statistical analyses

Statistical analyses were conducted in R software (R Core Team 2021). One-way ANOVA and non-parametric Kruskal-Wallis tests were applied to assess the variability of mortality between regions, localities, stands, and species based on plot-level mortality (Chapter 5.1 and 5.3 respectivelly). Pairwise Wilcoxon rank sum test was used to distinguish which groups differ from each other. Chi-squared test was used for the distribution of mortality agents among size classes and species (Chapter 5.3). Generalized additive models (GAM) with negative binomial errors and a log link function were applied to test the relationship between past canopy area removal and current mortality. Generalized additive mixed model (GAMM) was fitted when checking for the effect of stand as a random effect in plot-level data analysis. The mgcv package (Wood 2017) was used for the models (Chapter 5.2).

Several model structures were tested, each of them using different a priori assumptions about the scales at which individual factors could influence the forest biomass. Multiple explanatory variables were used to describe the disturbance regime of each plot: the date and severity of its most severe disturbance event and the basal area of all dead standing trees, which allows to infer relative differences in tree mortality rates (fixed effect). Longitude, latitude, altitude and northness (fixed effect; a transformation of aspect according to formula: northness = cosine [(aspect in degrees * π)/180)]) represent the geographical gradients. Variables of the higher hierarchical levels were calculated as the mean of values from the lower levels (e.g., stand-level basal area was calculated as the mean of plot-level means of basal area within a given stand). A series of linear mixed-effect models (LME) was conducted to compare the roles of site conditions and natural disturbances in driving spatial variation in forest biomass at three hierarchical scales (plot, stand, landscape). A first LME was used to test hypothesis regarding the drivers of variation in live-tree biomass at the landscape scale. Further, to test the next hypothesis regarding drivers of variation in live-tree biomass at various scales, a second LME was conducted by combining the within-stand and between-stand models. LME models were used to fit a combination of predictor variables (and interaction of date and severity of disturbances) with additional consideration of random spatial effects, which allowed to account for systematic variability in space (Wood 2017). In addition to the fixed effects, the applied LME model contains random stand effects (corresponding to random effects or intercepts on the broad scale) and residuals (reflecting random effects on the fine scale). For more detailed reasoning of the methods and formulae used, please refer to Chapter 5.4. The LME models were conducted using nlme package (Pinheiro et al. 2015).

5. Results

The dissertation thesis consists of two published manuscripts, and two soon-to-be submitted manuscripts. The first part examines mortality rates and composition of mortality agents in primary Norway spruce forests (Chapter 5.1). The second part evalutes the relationship between historical disturbances and current mortality rates (Chapter 5.2). The third part presents the mortality rates and composition of mortality agents in primary European beech-dominated forests (Chapter 5.3), and the fourth part analyzes the main drivers of structural variability in primary forests (Chapter 5.4).

5.1 Contrasting patterns of natural mortality in primary *Picea* forests of the Carpathian Mountains

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Contrasting patterns of natural mortality in primary *Picea* forests of the Carpathian Mountains

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ABSTRACT

Mortality, driven by both climate and disturbance legacies, is a key process shaping forest dynamics. Understanding the mortality patterns in primary forests in the absence of severe disturbances provides information on background natural dynamics of a given forest type under ongoing climate change. This can then be compared to mortality rates in severely-disturbed stands. Using a large number of sample plots along a gradient from low to high disturbance, we examined the mortality rates and composition of mortality agents in primary mountain Norway spruce (*Picea abies* (L.) Karst.) forests on different spatial scales. We evaluated the mortality rates and causes of mortality in 28 stands across a large geographical gradient spanning over 1000 km. We resampled (five-year period) 371 plots (16,287 living trees) in primary Norway spruce forests along the Carpathian mountain chain. The estimated overall annual mortality rate was within the previously reported range of background (ambient) mortality, however, stand-level and plot-level mortality rates varied substantially. Over 18% of plots displayed more than 2% annual mortality and 6% of plots even exceeded 10% per year. Stands in the Western Carpathians showed the highest variability in the mortality rate, with 30% of the stands in this region showing annual mortality rates over 5%. At the plot level, mixed-severity disturbances increased variability of mortality rates within most localities. Overall mortality was evenly distributed among size classes up to 50 cm diameter at breast height (DBH). However, the distributions differ for individual mortality agents. Mortality modes were classified into six categories (broken crown, broken stem, uprooted, competition, bark beetle/fungi, climatic extremes). Bark beetle (*Ips typographus* L.) infestation was the most frequent mortality agent in all stands, whereas the influence of competition as a mortality agent varied substantially. Mortality from abiotically-caused physical damage was similar to that from competition, yet the distribution among modes of physical damage (uprooted, crown, or stem breakage) varied. The lack of clear evidence of mortality agents in some locations implies that many tree deaths are caused by a combination of contributing factors. The results suggest the role of bark beetle as a mortality agent does not equate to severe mortality at large scales. Prevalence of different size classes affected by individual mortality agents underline the high complexity of the mortality process in primary forests.

1. Introduction

Tree mortality and its causes are important for understanding forest dynamics (Franklin et al., 1987; Das et al., 2016) because they strongly influence future stand development (Bircher et al., 2015), and play a key role in predicting forest structural and compositional changes in response to global change (Bonan, 2008; Adams et al., 2010; Allen et al., 2010; Dietze and Matthes, 2014). Tree mortality is critical to model carbon residence time, yet it represents one of the highest uncertainties in large-scale models of vegetation dynamics (Friend et al.,

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2014; Bugmann et al., 2019). However, for many forest regions it remains crucial to quantify the contribution of different mortality agents in the context of disturbances and stand density to link tree, stand, landscape, and global processes (Franklin et al., 1987).

Our understanding of tree mortality processes is incomplete because of the problem that tree mortality can rarely be observed and attributed to unequivocal causes (Adame et al., 2010; Das et al., 2016; Vanoni et al., 2016). Many studies have examined forests with consistently low annual mortality rates (Stephenson and van Mantgem, 2005; Das et al., 2016). In such forest ecosystems, even slight changes to the background mortality rates, as low as 0.5 to 2% per year (Stephenson and van Mantgem, 2005), could potentially have larger impacts than a severe disturbance event (van Mantgem et al., 2009). Another group of mortality studies has focused on stands strongly affected by drought and/or insect outbreaks with high mortality rates (Bréda et al., 2006; Sala et al., 2010; McDowell et al., 2011; Anderegg et al., 2015; Sproull et al., 2015, 2016). With predicted increases in the scale and severity of drought and insect outbreak events under climate change (Seidl et al., 2007; Lindner et al., 2010; Jonsson et al., 2012; Vanoni et al., 2016; Seidl and Rammer, 2017; Seidl et al., 2017), such studies are increasingly relevant. Taken together, these different mortality regimes form a continuum from regular (non-catastrophic) to irregular (catastrophic) mortality (Monserud, 1976; Hawkes, 2000). Adding data about demographics and causes of mortality in a forest system experiencing a gradient from low to high mortality is an obvious next step in the field of forest mortality research.

Many individual-based forest models generalize mortality into groups, distinguishing between “vigor-related” mortality and “ambient” (or “background”) mortality. For vigor-related mortality, an inverse relationship between tree growth and mortality probability is assumed (Shugart, 1984; Bugmann, 2001; Bircher et al., 2015), which suggests that trees limited in growth, for whatever reason, are more likely to die. Ambient mortality is generally not related to growth factors. Abiotic factors such as wind, fire, or lightning, are commonly considered to be the factors that underlie the ambient mortality. However, other intrinsic biotic factors may also contribute to mortality (Das et al., 2016). Many individual-based models, however, have been developed for even-aged production forests that often consider only one generation of trees, which makes them inappropriate for forests with complex, uneven-aged structures, typical for many primary forests (Bircher et al., 2015).

Categorizing the factors of mortality based on their role in the mortality process provides a more complex scheme. This concept uses three groups of factors: predisposing, inciting, and contributing (Manion, 1991). Predisposing factors affect stands over the long term, such as climate or competition (Allen et al., 2010). Inciting factors operate in the short term with highly variable intensities; this group includes drought and frost, as well as more or less random events of stem breakage, windthrow, and insect or pathogen attack (Anderegg et al., 2015). The largest contributing factors are primarily insects and fungi; they are often part of the process leading to tree death, but their presence alone might not induce it, and they can have uncertain effects (Allen et al., 2010). Different processes leading to mortality result in different mortality modes (Larson and Franklin, 2010; Holzwarth et al., 2013); for example, competition or drought usually result in dead standing trees, whereas abiotic factors such as wind leave trees uprooted or snapped. It is commonly assumed that the role of mortality drivers is species specific (Holzwarth et al., 2013; Vanoni et al., 2016) and depends on stand conditions (Das et al., 2016). Thus, examining the distribution of different mortality modes among size classes would provide additional information regarding the relationship between mortality and stand structure.

Norway spruce (*Picea abies* (L.) Karst.) stands are a dominant forest type across temperate mountain regions of Europe. Most recent studies of Norway spruce stands have focused on areas affected by insect outbreak or to evaluate the vulnerability of a given stand to a potential severe disturbance event (Dutilleul et al., 2000; Wermelinger, 2004; Seidl et al., 2007; Jakuš et al., 2011; Kautz et al., 2013; Mezei et al., 2014; Seidl et al., 2015; Sproull et al., 2016). Spruce bark beetle (*Ips typographus* L.) and windstorms are the most important disturbance agents in European Norway spruce stands because they influence stand structure on multiple temporal and spatial scales (Grodzki et al., 2004; Jonášová and Prach, 2004; Krumm et al., 2011; Panayotov et al., 2011). However, less intensive but continuously operating agents of mortality also need to be considered. For example, the effect of bark beetle outbreaks is magnified by the presence of spruce monocultures in many European regions, many of which were previously dominated by broadleaf stands (Grodzki et al., 2004; Raffa et al., 2008). Bark beetle outbreaks have had a strong impact on natural or near-natural spruce forests (Svoboda et al., 2010; Wild et al., 2014; Sproull et al., 2015), but the role of bark beetle populations when they are not at outbreak levels and how they relate to tree mortality is less clear. Bark beetles usually colonize trees that have recently been uprooted, weakened by drought, or broken (Schroeder and Lindelow, 2002; Křístek and Urban, 2013; Nelson et al., 2014; Seidl et al., 2015; Sproull et al., 2015; Sproull et al., 2016). Distinguishing which of the contributing factors was the actual cause of death is often problematic (Allen et al., 2010; Das et al., 2016). Even the additional information on the year of tree death derived from dendrochronological data is not always reliable as trees often show abrupt growth decreases several years or decades prior to death (Vanoni et al., 2016).

While mortality modes can only point out proximate causes of tree death (Larson and Franklin, 2010; Holzwarth et al., 2013), and will therefore provide less accurate information than assessing the cause of mortality of each tree shortly after its death (Das et al., 2016), they still allow us to evaluate the main mortality factors. Because composition of mortality agents is an important driver of stand structure, evaluating the relative frequency of different mortality agents on the stand and landscape levels can further improve our understanding of primary mountain Norway spruce forest dynamics.

To better understand mortality processes of these forests, we had three main objectives: i) to quantify annual rates of mortality in primary Norway spruce stands along the Carpathian Mountains during a five-year resampling interval; ii) to evaluate the distribution of mortality among tree size classes; and iii) to evaluate the distribution of the main factors causing mortality in primary Norway spruce stands. Due to the extent of the dataset both geographically and structurally, our results complement longer-term studies covering a much narrower spectrum of stand conditions in primary mountain Norway spruce forests, and they thus help us understand the variability and dynamics in this forest type.

2. Materials and methods

2.1. Study area

The Carpathian Mountains contain the largest tracts of primary forests in Central and Eastern Europe (Veen et al., 2010; Knorn et al., 2012), and the largest remnants of primary Norway spruce forests in temperate Europe. They are therefore ideal for investigating natural disturbance processes over large spatial scales. Forests within the study area are referred to as ‘primary forests’ (Sabatini et al., 2018). Because stands developed under their natural disturbance regimes and there is little or no evidence of past human impacts, the old-growth stage of development is not a required condition (Sabatini et al., 2018; Svoboda et al., 2014), and we can expect a wide range of disturbance severities and frequencies in these stands. Our study contains data from 28 stands that we divided into three geographic regions (Western, Eastern, and Southern Carpathians). The Eastern region was further split into two localities because the distance between the two groups of stands in this region is quite far (Fig. 1, Table 1). The study combines datasets previously analyzed with a focus on regional disturbance regimes (Trotsiuk

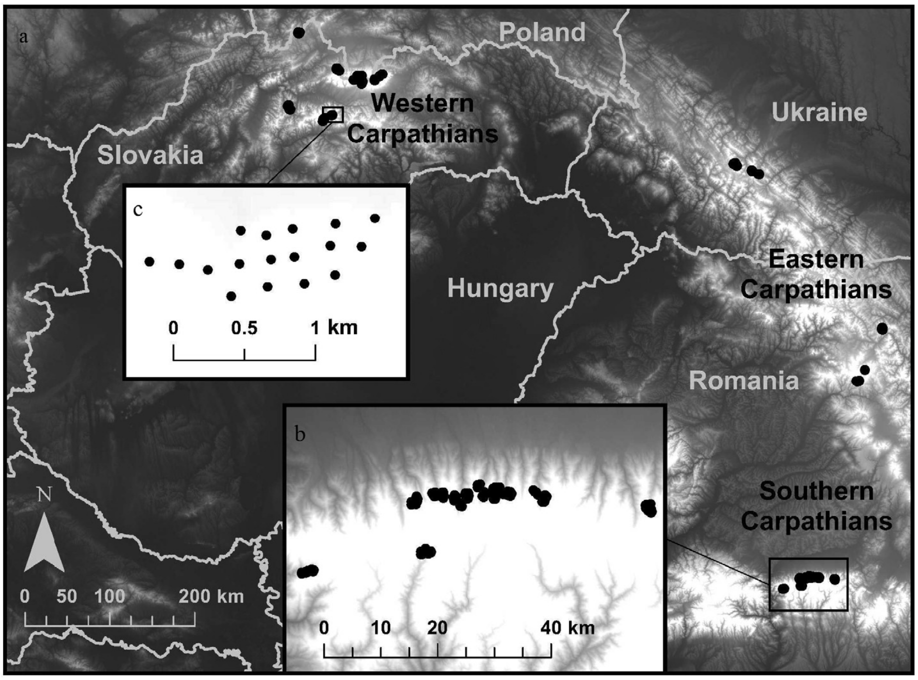

Fig. 1. Hierarchical distribution of permanent study plots (black dots) at landscape (a), regional (b) and stand scales (c). The landscape is divided into three regions in the Carpathian mountain range (Western Carpathians, Eastern Carpathians and Southern Carpathians. The Eastern Carpathian region is further subdivided into two localities (Ukraine and Northern Romania).

Table 1
Annual mortality rates and summary statistics of Norway spruce-dominated temperate forests of the Carpathian Mountains. Statistics are based on a five-year remeasurement period for each stand.

				Annual mortality rate					
Region	Locality	Stand [Abbreviation]	Plots pooled %	Mean %	Max %	Min %	Median %	SD	Plots
Western			3.43	6.12	100.00	0	0.81	14.79	160
	Slovakia		3.43	6.12	100.00	0	0.81	14.79	160
		Bielovodska dolina [BEL]	12.69	16.58	57.83	0	3.28	20.21	11
		Bystra [BYS]	1.77	2.78	20.38	0	0.94	5.13	14
		Dumbier [DUM]	1.84	2.01	16.74	0	0.66	3.87	17
		Hlina [HLI]	5.65	8.30	29.72	0	3.99	9.77	13
		Janosikova Kolkaren [JAK]	0.97	1.29	11.81	0	0.00	2.67	25
		Javorova [JAV]	9.01	22.52	100.00	0	2.66	32.87	8
		Koprova dolina [KOP]	1.12	2.18	24.46	0	0.00	6.47	13
		Zadne Medodoly [MED]	0.69	1.90	7.79	0	1.21	2.49	7
		Osobita [OSO]	4.86	9.44	53.29	0	1.19	15.16	14
		Pilsko [PIL]	1.58	2.85	25.42	0	0.69	6.86	12
		Smrekovica [SMR]	7.18	16.06	100.00	0	0.00	28.46	11
		Ticha dolina [TIC]	1.36	1.25	5.89	0	0.46	1.69	15
Eastern			0.89	0.91	9.81	0	0.56	1.26	118
	Ukraine		0.71	0.73	9.81	0	0.38	1.31	68
		Gropha 1 [GR1]	1.75	1.68	9.81	0	1.33	2.31	16
		Gropha 2 [GR2]	0.83	0.77	2.59	0	0.55	0.84	13
		Gropha 3 [GR3]	0.38	0.36	1.15	0	0.36	0.32	12
		Syvulya 1 [SY1]	0.33	0.31	1.86	0	0.00	0.52	13
		Syvulya 2 [SY2]	0.34	0.32	0.93	0	0.16	0.38	14
	Northern Romania		1.23	1.16	4.56	0	0.98	1.15	50
		Calimani [CAL]	0.95	0.92	3.81	0	0.61	1.19	20
		Giumalau [GIU]	1.39	1.32	4.56	0	1.17	1.09	30
Southern			1.04	1.03	13.82	0	0.62	1.70	93
	Southern Romania		1.04	1.03	13.82	0	0.62	1.70	93
		Sambata [FA1]	0.73	0.65	1.80	0	0.62	0.60	12
		Ucisoara [FA2]	0.87	0.79	1.84	0	0.82	0.63	12
		Vistea Mare [FA3]	1.04	0.93	1.68	0	1.14	0.58	5
		Ucea Mare [FA4]	0.37	0.27	1.76	0	0.00	0.50	12
		Arpasul [FA5]	1.22	1.37	2.67	0.27	1.35	0.94	5
		Doamnei [FA6]	0.69	0.80	5.61	0	0.14	1.56	12
		Boia Mica [FA8]	1.07	0.96	5.06	0	0.62	1.40	11
		Capra [FA9]	1.36	1.35	4.53	0	1.05	1.27	12
		Belia [FA10]	2.07	2.26	13.82	0.53	1.25	3.54	12
ALL			1.88	3.19	100.00	0	0.63	10.10	371

et al., 2014; Svoboda et al., 2014; Janda et al., 2017). Primary forests in the Carpathians are dominated by Norway spruce at higher elevations, usually from ca. 1200 m a.s.l. and higher. Other admixed species include European silver fir (*Abies alba* Mill.), Swiss pine (*Pinus cembra* L.), rowan (*Sorbus aucuparia* L.), and birch (*Betula* spp.).

2.2. Study site selection

Study site selection was initiated using a previous inventory of primary forest remnants (Hamor et al., 2008; Veen et al., 2010) and maps to identify potential Norway spruce stands. Selected stands were then surveyed for indicators of naturalness (e.g., coarse woody debris in various stages of decay, pit-and-mound topography) and direct signs of human activity. We excluded stands that contained evidence of past logging or grazing, and any stands adjacent to formerly grazed areas, tree line, and extreme sites (Svoboda et al., 2014; Trotsiuk et al., 2014; Wirth et al., 2009). We conducted extensive research in all available historical sources of land use information in these areas. According to historical documents, the selected study areas were not logged in the eighteenth and nineteenth centuries and have been protected since then (Svoboda et al., 2014). All the localities include a broad range of variability in terms of elevation, slope, and aspect, thus, to some degree, they represent the landscape-scale heterogeneity found in the study region. However, a statistical stratification of stands across the various geographic positions was not possible because of the limited distribution of primary forest fragments (Svoboda et al., 2014). All the study plots are included in the extensive primary forest dataset of the REMOTE project (Remote Primary Forest, 2019).

2.3. Sample plots

Sample plots in each stand were established using a stratified random design (Svoboda et al., 2014). We overlaid a 141.4 × 141.4 m grid on each stand, and within each grid cell, a circular sample plot (1000 m^2) was established at a restricted random position (generated in a GIS) using GPS. Plot centers were restricted to the inner 0.49 ha core in each 2-ha cell. The plots were resampled after five years from 2016 to 2018 based on the initial sampling year (see also Svoboda et al., 2014; Trotsiuk et al., 2014). At each sample plot we labeled all trees $\geq$10 cm diameter at breast height (DBH) and recorded their DBH, and whether they were alive or dead, or showed any signs of visible damage (e.g., broken crown).

2.4. Trees

For recently dead trees (i.e., those that were alive during the initial sampling), we recorded mortality mode (recent bark beetle infestation; apparent result of competition; crown break; stem break; uprooted; climatic extremes). Only the agents that could have played significant role in the mortality of a given tree were included (e.g. stem breakage occurring clearly after tree death is not counted). Bark beetle mortality mode included both trees with clear evidence of infestation (as evident by the presence of entry/exit holes, galleries, red-brown dust at the tree base) and trees for which we could only assess that the mortality was a result of bark beetle infestation, likely coupled with fungi. Competition was considered to be the mortality agent for trees with a “suppressed” social status (more than 50% of the crown was directly shaded by other trees) without any other evident signs of mortality agents. Crown break category was used for trees with less than one third of their crown missing, and the stem break group includes trees with even larger portions missing. Climatic extremes were considered when there were multiple recently dead trees with no signs of severe infestation or physical damage among released trees within a plot.

Since evidence for multiple mortality agents can be recorded for a single tree, we developed a system for determining a single mortality mode. In the cases where evidence for multiple agents exists, we tried to determine the agent most responsible for a shift from (limited) growth to actual tree death. All the physical damage categories (crown break, stem break and uprooted) were considered only if the tree was clearly damaged while alive (e.g. pointed splinters created by the breakage) and the damage was not recorded during the first measurement. In these cases, this mode overruled any other potential agents (e.g. suppression or bark beetle infestation). For suppressed trees that were also infested by bark beetles, competition was considered to be the main agent. The infestation in these cases typically just speeds up the decline, or it even occurs after tree death (Das et al., 2016). Identification of the ‘climatic extremes’ mode was perhaps the most complicated as it is very difficult to determine in the field. Based on the concept of drought, frost and similar climatic conditions as inciting factors (Manion, 1991) which would have affected a majority of the stand, climatic extremes were applied only if there were multiple released trees without signs of other mortality agents per plot.

2.5. Data processing

Annual mortality rate was calculated from the overall mortality observed over the five-year sampling period. To better reflect potential continuous decrease in tree density, annual rate was not calculated as total mortality divided by number of years between observations, but rather we used an equation based on interest rate calculations, which should also better accommodate the potential use of different time intervals for which the annual rate is calculated:

$$m = 1 - (N_t/N_0)^{1/t}$$

where N_0 is the number of live trees during first sampling, N_t is the number of trees still alive during resampling, and t is the number of years between samplings (Sheil et al., 1995; Sheil and May, 1996).

We reported mortality rate on various scales, using different aggregation schemes. We first calculated the mortality rates at the plot level, then aggregated to the stand, locality and region levels. We further present “overall” mortality calculated for pooled tree data for given aggregate and “plot-level” characteristics where annual rates for each individual plot within respective group were used.

2.6. Data analysis

One-way ANOVA was used to assess the variability of mortality between regions, localities, and stands based on plot level mortality. Statistical analyses were conducted in R 3.3.2 software (R Foundation for Statistical Computing, Vienna, AT).

3. Results

3.1. Mortality rate

A total of 16,287 trees were remeasured five years after plot establishment; we tallied 1444 trees that died during that period. Overall mortality was 1.88% per year. The mean annual plot-level mortality rate across the entire study area was 3.19% (sd = 10.10%). Overall, the annual mortality rate was substantially higher in the Western Carpathians (3.43% for pooled tree data for the region, plot-level mean 6.12%, sd = 14.79%) than in other regions. The lowest mortality was detected in the Ukrainian part of the Eastern Carpathians (0.71% for pooled tree data for the locality, plot-level mean 0.73%, sd = 1.31%). Plot-level annual mortality ranged from 0 to 100% in Western, from 0 to 9.81% in Eastern, and from 0 to 13.82% in the Southern Carpathians, indicating rather high variability (Table 1). The majority of our plots (82%) had annual mortality rates below 2% (we detected no mortality on 131 (35%) plots); of the 18% (68 plots) of our plots that exceeded this threshold, there were 24 plots with an annual mortality higher than 10%. Those plots had recently been affected by windthrows and/or bark beetle. There was significant variability in plot-level annual

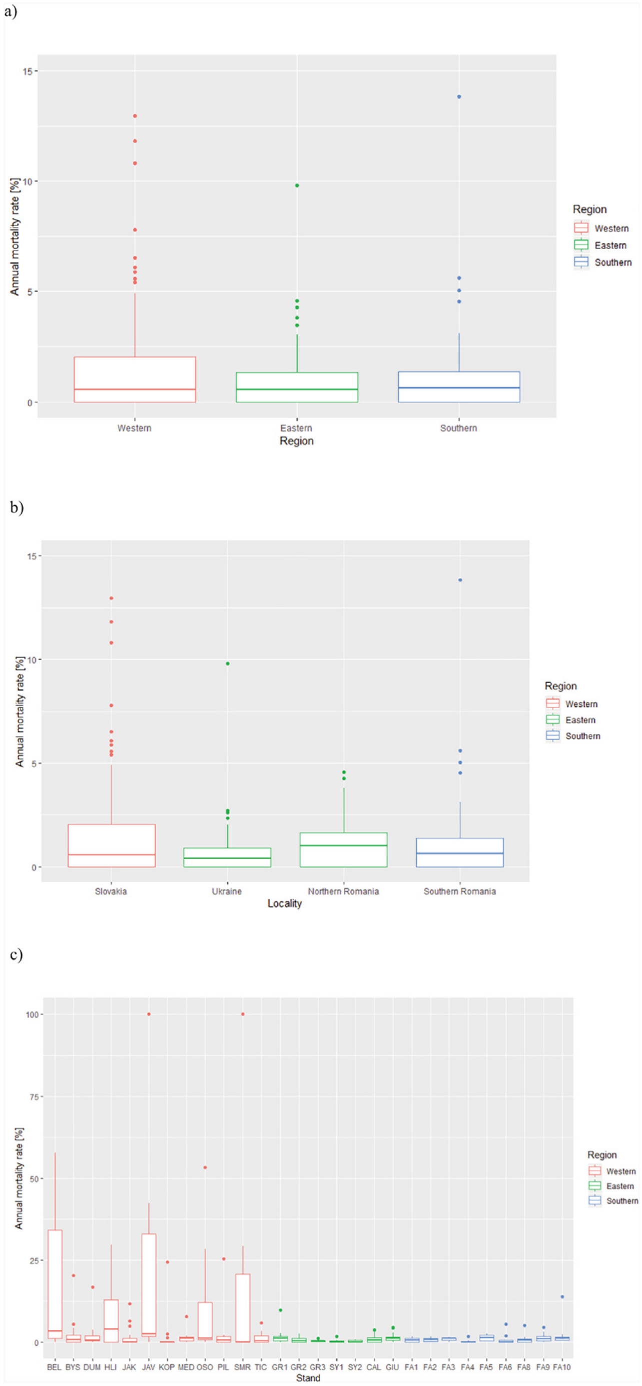

Fig. 2. Observed annual mortality rates for regions, localities, and individual stands based on plot-level data. Percentage calculated based on number of stems. Each box represents the range from first to third quartile and median for a given group of plots. Individual dots show outliers further than 1.5 times the interquartile distance from the first (third) quartile. Graphs a) and b) are capped at 15% annual mortality which covers all plots in Eastern and Southern Carpathians and leaves out 21 plots with high mortality in Western Carpathian region.

mortality rates between regions (p-value < 0.001; F-value = 12.57; 2 degrees of freedom), localities (p-value < 0.001; F-value = 8.375; 3 degrees of freedom), and stands (p-value < 0.001; F-value = 3.946; 27 degrees of freedom; Fig. 2). This variability seems to be mostly driven by recently severely disturbed stands in Western Carpathians and generally very low mortality rates in Ukrainian part of Eastern Carpathians.

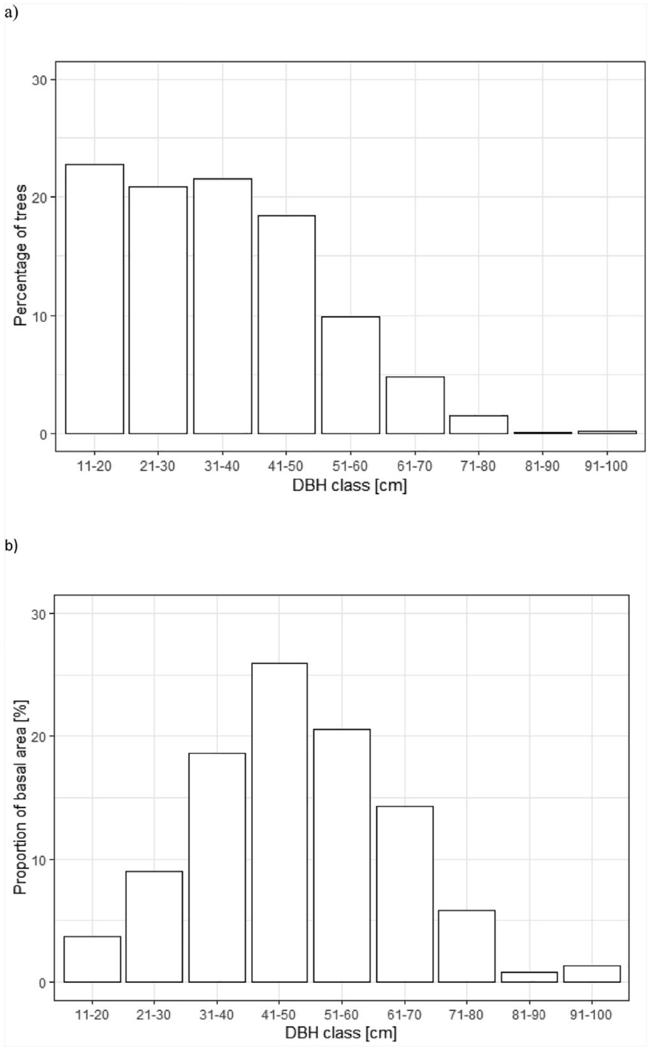

Fig. 3. Distribution of mortality among 10 cm diameter classes. Proportion of trees (a) and basal area (b) of recently dead trees.

3.2. *Size class distribution of mortality*

The proportion of dead trees across diameter classes was balanced, with a continuous decrease for diameter classes greater than 40 cm (Fig. 3). However, at the stand level there was substantial variability. In terms of basal area, the distribution was unimodal around the 41–50 cm class (Fig. 3). The shape of the diameter distribution curve was influenced by the agent of mortality, as particular mortality modes occur more commonly in certain diameter ranges (Fig. 4).

3.3. *Mortality agents*

Contribution of each mortality mode to total mortality suggests that competition was a very important driver of mortality in many stands. The most frequent agent, however, was bark beetle infestations. The portion of trees killed by abiotic factors (mostly wind) cannot be overlooked either; when all three physical damage modes are summed, they account for as much mortality as competition does (Fig. 5). Composition of different forms of physical damage varied among stands and regions. More than one mortality agent was detected on 36% of plots with any recently dead trees (different forms of physical damage are counted as the same agent here).

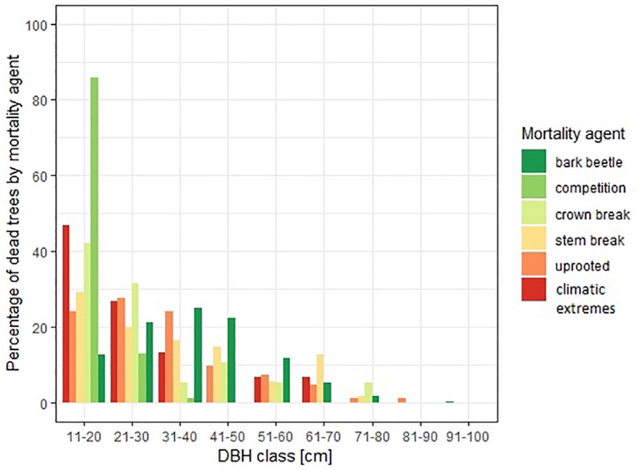

Fig. 4. Mortality agent percentages by diameter class. Bark beetle mode – trees with clear evidence of severe infestation, as well as those where informed estimates were used when lacking other signs; competition mode – no visible physical damage, at least 50% crown was directly shaded; crown break – up to one third of crown was missing; stem break – more than one third of crown was missing; uprooted – by wind or by other falling tree; climatic extremes – multiple trees per plot, no signs of severe infestation or physical damage detected for given trees. The figure is not reflecting relative frequencies of individual agents only their distribution among size classes.

4. Discussion

4.1. *Mortality rate*

The observed overall annual mortality rate was within the range of background mortality reported in studies lacking recent high severity, large-scale disturbances (Stephenson and van Mantgem, 2005; van Mantgem et al., 2009; Das et al., 2016). However, at the stand level, the mortality rates varied substantially. It is important to note that background mortality is not only a result of competition, but also lower intensity (in terms of scale or severity) disturbances (Turner, 1987; Fraver et al., 2009). Only 18% of plots exceeded the 2% annual mortality rate, which could be, in most cases, attributed to dense stand conditions and self-thinning process (Castagneri et al., 2010; Svoboda et al., 2010) and/or combination of windthrows and bark beetle infestation, which were largely responsible for the mortality on 24 plots (6.5%) with an annual mortality rate greater than 10%. Our results match the concept of mixed-severity disturbances – with highly variable severity over larger areas (Panayotov et al., 2011; Trotsiuk et al., 2014; Schurman et al., 2018) in the form of the most typical combination of windthrows and bark beetle infestation. As a characteristic feature of a mixed-severity regime, some of the mortality captured within our observation period is likely related to individual disturbance events that caused intermediate severity damage (Woods, 2004). Records of multiple mortality agents in most stands also suggest mixed-severity regime.

Analysis of variance shows there was a significant difference in the variability of plot-level mortality between stands, localities, and regions. This was clearly driven by recently disturbed plots in the Western Carpathian region, and likely also the generally low mortality in the Ukrainian part of the Eastern Carpathians. These patterns suggest a mixed-severity disturbance regime for these forest stands with higher variability at finer scales. The results indicate substantial heterogeneity on different scales. Local disturbances are considered the main driver of structural variability on a fine scale, while climatic factors are likely to play a key role on a coarse scale (Janda et al., 2019). The increased variability in the observed mortality rates in the most disturbed Western Carpathian region is in contrast to the generally lower, but evenly distributed mortality in Northern Romania, which resulted in a higher plot-level median in Northern Romania. Simple means or medians may therefore not properly capture stand mortality. However, considering the relatively short observation period a single infrequent disturbance event could have influenced the results. The variability in stand structure at the time of plot establishment along with the size of the dataset and the extensive area sampled, allow us to assume the observed patterns are representative of a longer time-frame, although it is necessary to take into account the possible bias caused by stochastic disturbance events which can also lead to a shift in composition of mortality agents. In any case, structural stand parameters, disturbance history (Schurman et al., 2018) and local topography (Senf and Seidl, 2017) are likely key factors. Several studies of mortality rates in other mountain Norway spruce stands in the Carpathians have observed current higher mortality rates compared to the rates we observed (e.g., Sproull et al., 2015; Sproull et al., 2016). However, these studies focused on stands during a period of bark beetle outbreaks. Mortality rates observed prior to the recent outbreak period (e.g., Sproull et al., 2015) were more similar to the levels we observed. For the stands that experienced more severe disturbances, stand-level mortality was comparable to stands affected by bark beetle outbreaks of a lower severity that were not stand replacing (Sproull et al., 2016).

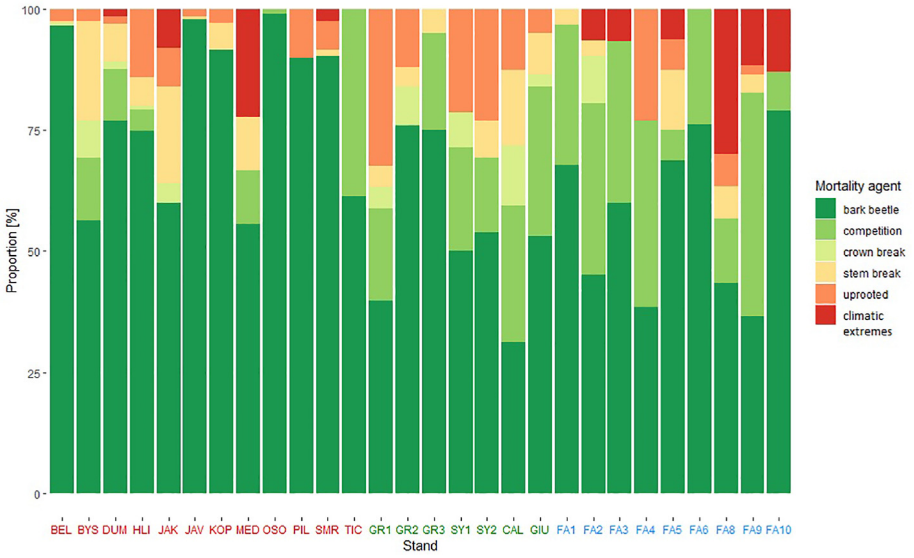

Fig. 5. Contribution of different mortality modes to overall mortality. The mortality mode categories and their descriptions are the same as for Fig. 4. Color of the stand name reflects the region (red for Western, green for Eastern, and blue for Southern Carpathians). The figure reflects contributions of mortality agents among trees over the 10 cm DBH threshold. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.2. Size class distribution of mortality

The diameter class distribution of recently dead trees varied substantially for individual stands. At larger scales, the distribution shows even mortality among DBH classes up to 40 cm followed by continuous decrease for larger classes. This result is not consistent with the common U-shaped curve. This may, to a certain extent, be due to our sampling DBH threshold that omitted the smallest trees, which are expected to have the highest mortality. Another explanation can be seen in species- and site-specific dynamics, as different distributions of mortality have previously been reported for some species (e.g. *Fraxinus excelsior* L.) (Holzwarth et al., 2013). The composition of different mortality agents in each stand may be a key consideration, as certain mortality modes are more common in particular size classes. For example, younger stands with a more pronounced effect of competition show a different mortality distribution among size classes than older stands with lower tree density indicating the importance of forest spatial structure (Das et al., 2008). A similar relationship was previously also observed for *Fagus sylvatica* L., although the overall size class distribution of mortality was different (Holzwarth et al., 2013). Our results also suggest that mortality related to bark beetle might not be restricted to trees greater than 30 cm DBH, which is generally assumed for stands in non-outbreak periods in these forests. However, trees with DBH 41–50 cm accounted for the highest proportion of basal area of recently dead trees, which is related to the combined relatively high BA per tree and high densities in this size class. Relatively short time-frame could have influenced the results because certain lower frequency disturbance events for which we can expect higher impact on larger size classes might not occur during the given observation period (Hurst et al., 2011). Such bias should be, to some extent, mitigated by high number of sample plots spread across large area.

4.3. Mortality agents

Our results demonstrate that competition was a very important driver of mortality in stands that have not been affected by a high severity, large-scale disturbance in the recent past, although it varied substantially among localities. This was evident by the portion of trees assigned to this mortality mode, as well as the higher mortality among suppressed or lower layer trees, as suggested by the distribution of recently dead trees among DBH classes. The contribution of competition is expected to be higher if the sampling threshold is reduced, as indicated by the prevalence of this mortality mode in the smallest size class recorded here.

Bark beetle infestation was the most frequently recorded mortality agent across all stands (75% of all mortality), regardless of the overall mortality rate. Trees, for which bark beetle was recorded as mortality agent, were often clustered on certain plots, which is consistent with the behavior of this insect (Wermelinger, 2004). Distribution of trees most likely killed by bark beetle was unimodal, centered on the 31–40 cm DBH class, as observed in other stands impacted by bark beetle. However, small trees infested by bark beetle were found also in stands recently unaffected by outbreak event. It is important to note that bark beetle as a mortality agent is often not a sole agent leading to death of a given tree. The infestation can just finish the ongoing decline of otherwise weakened tree (e.g. by physical damage or competition) – contributing factor; or make the tree more susceptible to another agent (e.g. fungi) – inciting factor (Manion, 1991). The role of bark beetle infestation, however, is important and should be considered in all cases.

Trees damaged by abiotic factors (crushed, broken, or uprooted) accounted for 11% of all mortality (ranging from 0 to 41% for individual stands). The distribution of trees with crown or stem breakage was decreasing towards higher DBH classes, likely driven by smaller trees facing higher risk of being severely damaged by another falling tree (Woods, 2004; Das et al., 2008; Holzwarth et al., 2013). In line with this concept, the contribution of physical damage as a mortality agent can be expected to increase if the DBH threshold is lowered. The extent of this increase, especially in comparison with a similar change in the contribution of competition, can provide further improvement of our understanding of dynamics in this type of forest stand. While the abiotic factors played an important role in most stands, the contribution of their different effects varied substantially. Given that, abiotic factors are likely more connected to regional conditions and are somewhat random within the region. Stand structure and time since last severe disturbance are likely factors that influence abiotic-related mortality, and of course the role of local topography can be crucial (Senf and Seidl, 2017). Given that abiotic factors were rather important, our results suggest the idea that they are overrepresented at the expense of intrinsic causes in many mortality models (Das et al., 2016) might not always be true. Despite the ratio between abiotic and intrinsic causes in a model, higher severity disturbance events (e.g., windthrow or bark beetle outbreak) can shift it in one direction or another (Allen et al., 2010; Sproull et al., 2015).

A major impact of climatic extremes was only recorded for a limited number of trees. However, this may be attributed to our methodology and the generally difficult identification of trees affected by such impacts when another mortality agent is present. Climatic extremes can operate as inciting (with or without subsequent agent) or contributing factors (Manion, 1991). We were only able to attribute extreme climatic conditions as an inciting factor when no other visible (subsequent) agent was present. The role of climatic extremes may therefore be underestimated in our results, especially considering global climatic trends. It is likely that the major climatic extreme related to mortality in our stands is drought, as suggested also by an observed increase in disturbance rates with decreasing Palmer Drought Severity Index (Schurman et al., 2018), an increase in moisture sensitivity (Bjorklund et al., 2019; Schurman et al., 2019), and an increase in sensitivity to winter drought (Svobodová et al., 2019) in Norway spruce stands in the Carpathians. However, our approach cannot disentangle all possible climatic extremes, which include drought, frost, and temperature extremes, such that we pooled them into the broad “climatic extremes” category.

The presence of multiple mortality agents on more than one third of the plots with any mortality over the previous five years further emphasizes the complexity of mortality processes and simultaneous effects of different agents in primary forests. Uncertainties in identifying the cause of mortality for some trees, especially large fast-growing trees, have been previously reported (Das et al., 2016). Besides determining between combinations of factors and complicated differentiation of primary and secondary (after tree death) occurrences of insects or fungi, accurate evaluation of signs in parts of trees that are difficult to view (e.g., high in the crown) should also be considered (Das et al., 2016). In the upper canopy layer, it is frequently difficult to evaluate the mortality agents in released trees because we often lacked clearly visible evidence of what caused the tree death. The presence of trees recently killed by bark beetle but where clear evidence of mortality agent was lacking or where other contributing factors were suspected, coupled with abundance of such trees mostly among large canopy layer trees correspond with the common behavior of *Ips typographus* L. This beetle predominantly attacks, but is not limited to, trees suffering from another stress factor already, barring outbreak stages of beetle population dynamics. Large, older trees are preferred in these cases (Schroeder and Lindelow, 2002; Křístek and Urban, 2013; Nelson et al., 2014; Seidl et al., 2015; Sproull et al., 2015; Sproull et al., 2016). While the abundance of bark beetle-related mortality is clearly higher in larger size classes, based on our observations, it is possible the predisposition or vulnerability of a given tree to infestation is more important than the size itself. Such predisposition can be of different origin (e.g. drought stress, physical damage, competition).

5. Conclusion

Our findings suggest that the mortality rates in primary mountain Norway spruce forests are comparable to the published range of background mortality. However, the variability was rather wide across the Carpathians, especially in the Western Carpathians, where we observed high mortality rates. Our results also indicate bark beetle infestation was the most frequent mortality agent even in low mortality periods. Higher proportions of bark beetle-related mortality, however, did not always have a severe impact at larger scales, although short-term inventory data might not provide sufficient information to precisely define the mortality processes at different scales; coupling these findings with dendrochronological data could provide better insight. Our study plots will also provide a baseline to evaluate any future beetle outbreaks or whether our findings are simply part of an inherent dynamic in these forest ecosystems. At this point, our results suggest that bark beetle, even in low overall mortality phases, strongly influences mountainous primary Norway spruce forest stands.

Declaration of Competing Interest

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

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5.2 Past disturbances influence current *Picea abies* mortality in primary Carpathian forests

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Past Disturbances Influence Current *Picea abies* Mortality in Primary Carpathian Forests

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Highlights

Mortality rate is in a significant inverse relationship with past canopy area removal.

Disturbances during the past 120 years have the strongest effect on current mortality.

The relationship is more pronounced at the stand level and differs among subregions.

The variation in past canopy area removal is equally important as its mean value.

The length of the period with the strongest effect on mortality rate is changing.

Abstract

Shifting rates of tree mortality is a global-change syndrome influencing forests across the world. However, determining whether environmental changes are altering mortality rates is complicated by the fact that tree mortality inherently changes through time as forests develop following natural disturbances. Unfortunately, forest inventories rarely include the data required to assess how disturbance history shapes current mortality. Even fewer studies have assessed whether spatial scale is relevant to inferring such relationships. We estimated tree mortality in a network of forest inventory plots for which disturbance histories have been previously reconstructed from dendrochronological data. We examined the relationship of past disturbance and current mortality in primary mountain Norway spruce (*Picea abies* (L.) Karst.) forests on different spatial scales and among geographically distinct subregions throughout the Carpathian Mountains. The reconstructed extent of past overstory canopy loss was used as a proxy for associated disturbance severity. The 370 inventory plots (over 16,000 originally living trees) are nested within 28 stands throughout the Carpathian Mountain arc, which allowed us to conduct our analysis at multiple scales. Recent mortality was highest in the historically least disturbed plots. The strongest relationships between the parameters of historical canopy area removal and current mortality were observed at the stand level for the 120-year period immediately preceding the inventory-based observation of current mortality. Results varied among subregions, likely due to local topography or the occurrence of rare higher-severity disturbances. The stronger results at the stand level, as compared with plot level analyses, coupled with the absence of significant results for some subregions, indicate an important role of scale when evaluating the relationship of disturbance history and current tree mortality. Our results suggest not only intensity, but also variability in time are disturbance regime parameters shaping contemporary forest demography. A significant relationship between preceding canopy area removal and mortality rate was detected for past decades, however, the length of the period with the strongest effect on mortality rate is changing, with the relationship to mortality in the target decade shifting. If it is shortening in response to the increase in disturbance frequency and severity with ongoing climate change, or if it is simply changing as a consequence of forest development after disturbances, remains uncertain. Our results highlight the crucial role of past disturbances, as well as their legacies, on contemporary mortality rates.

1. Introduction

Tree mortality is important for understanding forest dynamics, because it substantially influences future development of the stand and its structure (Franklin et al. 1987, Bircher et al. 2015, Das et al. 2016), and is a key variable for assessing forest structural and compositional changes in response to global change (Bonan 2008, Adams et al. 2010, Allen et al. 2010, Dietze and Matthes 2014). Even a slight change in annual mortality rates might have a major impact on further forest growth due to compounding effects (van Mantgem et al. 2009). Mortality processes are highly variable, ranging from low background mortality rates (e.g., Stephenson and van Mantgem 2005, Das et al. 2016) all the way to the severely disturbed stands (e.g., Bréda et al. 2006, Sala et al. 2010, McDowell et al. 2011, Anderegg et al. 2015, Sproull et al. 2015, 2016).

Investigating the continuum from regular (non-catastrophic) to irregular (catastrophic) mortality (Monserud 1976, Hawkes 2000) is essential for improving our understanding of the consequences of global change for forest development (Synek et al. 2020, Nagel et al. 2021). Mortality can be greatly variable through space and time (Sproull et al. 2016, Synek et al. 2020), which might be linked among other factors to the mortality agents. The consequences of different processes ultimately leading to tree mortality are various mortality modes (Larson and Franklin 2010, Holzwarth et al. 2013, Nagel et al. 2021). These different modes create different biological legacies and have therefore different impacts on structure and further development of the stand (Das et al. 2008, Schurman et al. 2018, Esquivel-Muelbert et al. 2020). The combination of mortality agents and their respective contribution is dependent on species composition, stand structure and local topography (Das et al. 2008, Senf and Seidl 2018).

The prevalent mortality agents in primary Norway spruce (*Picea abies* (L.) Karst.) stands are windthrows and spruce bark beetle (*Ips typographus* L.) infestation (Grodzki et al. 2004, Jonášová and Prach 2004, Krumm et al. 2011, Panayotov et al. 2011). It has been reported recently that these events generate substantial variability in mortality over the affected area (Sproull et al. 2015, 2016) and that bark beetle infestations are the most frequent mortality agents even in stands unaffected by recent higher severity disturbance and showing low overall mortality rates (Synek et al. 2020). Inciting factors (Manion 1991), drought in particular, might play progressively more important role as suggested by several recent studies focusing on primary forests in the Carpathian region (Schurman et al. 2018, 2019, Bjorklund et al. 2019, Svobodová et al. 2019).

Disturbances significantly influence forest dynamics (Turner 2010, Čada et al. 2016). Through altering resource availability and opportunities for recruitment, they affect forest structure and composition (Denslow 1995, Oliver and Larson 1996, Canham et al. 2001) and are recognized as a major cause of tree mortality (Turner 1987, Seidl et al. 2007, Fraver et al. 2009, Sproull et al. 2015, 2016 Das et al. 2016). The concept of a "historical range of variability" (Keane et al. 2009) defines the limits of past stand dynamics to which dependent forest species have adapted to over extensive periods of time, and from which they are likely to benefit in the future (Drapeau et al. 2016, Mikoláš et al. 2017, Betts et al. 2019). Variation in disturbance area, frequency, and severity play an essential role in shaping forest structural and compositional heterogeneity at the landscape scale (Fraver et al., 2009, Donato et al., 2012). While climate is the main driver on large scales, local disturbances are likely the most influential factor on a fine scale (Janda et al. 2019). Understanding disturbance parameters becomes crucial to disentangle the effects of environmental changes and developmental drivers of temporally variable mortality rates (Lindner et al. 2010, Jonsson et al. 2012, Vanoni et al. 2016, Kulakowski et al., 2017; Seidl and Rammer 2017, Seidl et al. 2017).

Although a major impact of recent high-severity disturbances on Norway spruce stands (Schurman et al. 2018, Čada et al. 2020) has been repeatedly reported from various areas of their natural range (Čada et al. 2016, Lausch et al. 2011, Svoboda et al. 2012, Mezei et al. 2014, Sproull et al. 2015, 2016), moderate-severity and moderate-scale disturbances are prevalent (Čada et al. 2020). The particular importance of intermediate-severity events in forests predominantly driven by wind or insects (Fraver et al. 2009) emphasizes the relevance of the spectrum of disturbances (Angelstam and Kuuluvainen 2004) between the traditional fine-scale gap dynamics (Seymour et al. 2002) and stand replacing disturbances (Kuuluvainen and Aakala 2011).

The close and intertwining connection of disturbance and mortality processes is apparent; however, it is not yet fully understood on different spatial and temporal scales. There are studies that linked disturbance history with contemporary forest structure (e.g., Zenner 2005, D'Amato et al. 2008, Janda et al. 2017) or current structure with observed mortality (Clyatt et al. 2016). However, we still lack a mechanistic understanding of links between historical disturbance dynamics and contemporary mortality processes. This study combines mortality data based on a repeated inventory of primary forest stands with 200-year long disturbance chronologies based on an extensive collection of increment cores. Primary mountain spruce stands in the Carpathian Mountains are subject to the full range of disturbances from low to high severity, however, the synchronicity of these events on stand or landscape scale is often limited (Svoboda et al. 2014, Trotsiuk et al. 2014). Our main study objective is to uncover quantitative relationships between reconstructed historical forest canopy loss, a proxy for past disturbance severity, and contemporary tree mortality rates in primary mountain Norway spruce forests. For that purpose we have set three main questions: I) is there a clear relationship between past canopy area (CA) removal and current tree mortality?; II) Does the scale matter, in terms of both resolution (individual sample size) and extent of the region sampled?; and III) Is the relationship pattern between preceding canopy area removal and mortality rate detectable in the past, or is it changing possibly in relation to ongoing global changes as suggested by many recent studies?

2. Methods

2.1. Study area

The largest tracts of primary forests in Central and Eastern Europe including the largest remnants of primary Norway spruce forests in temperate Europe can be found in the Carpathian Mountains (Veen et al. 2010; Knorn et al. 2012). Therefore, the region is ideal for investigating natural disturbance processes over large spatial scales. Forests we focus on are referred to as 'primary forests' (Sabatini 2018). These stands developed under their natural disturbance regimes and there is little to no evidence of past human impacts, the old-growth stage of development, however, is not considered a required condition because of the presence of natural disturbances (Sabatini 2018, Svoboda et al. 2014). We can expect a wide range of disturbance severities and frequencies in these stands as well as there are variable contemporary mortality patterns (Schurman et al. 2019, Čada et al. 2020, Synek et al. 2020). Our study contains data from 28 stands that we divided into three geographic regions (Western, Eastern, and Southern Carpathians). The Eastern region was further split into two subregions for finer scale analyses because the two groups of stands sampled in this region are quite far from each other (**Fig.1**). The dataset, previously also used for assessing current mortality rates in primary Norway spruce forests (Synek et al. 2020), consists of several datasets originally used with a focus on regional disturbance regimes (e.g., Trotsiuk et al. 2014, Svoboda et al. 2014, Janda et al. 2017). All the study plots are part of the extensive primary forest dataset of the REMOTE project (Remote Primary Forest, 2020). Norway spruce dominates primary forests in the Carpathians above ca. 1,200 m a.s.l. Additional minor species include European silver fir (*Abies alba* Mill.), Swiss pine (*Pinus cembra* L.), rowan (*Sorbus aucuparia* L.), and birch (*Betula* spp.).

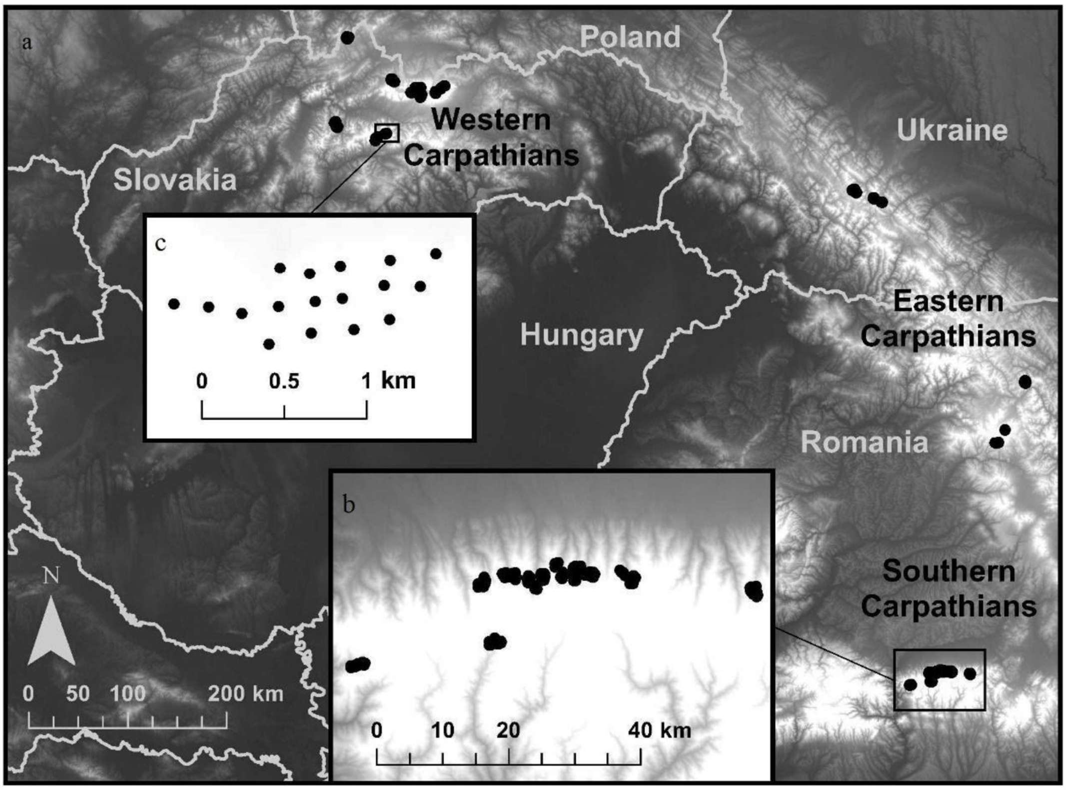

Fig. 1. Hierarchical distribution of permanent study plots (black dots) at landscape (a), regional (b) and stand scales (c). The landscape is divided into three regions in the Carpathian mountain range (Western Carpathians, Eastern Carpathians and Southern Carpathians. The Eastern Carpathian region is further subdivided into two localities (Ukraine and Northern Romania).

2.2. Study site selection

The preliminary step of study site selection was undertaken through the combination of previous inventories of primary forest remnants (Hamor et al. 2008; Veen et al. 2010) and maps, to identify potential Norway spruce stands. The selected stands were then surveyed for direct signs of human activity and indicators of naturalness (e.g., coarse woody debris in various stages of decay, pit-and-mound topography). Stands that contained evidence of past logging or grazing, and any stands adjacent to formerly grazed areas, the tree line, and extreme sites were excluded

(Wirth et al. 2009, Svoboda et al. 2014, Trotsiuk et al. 2014) Extensive research was conducted using all available historical materials dealing with land use information in these areas. According to available historical sources, the selected study areas were not affected by systematic logging in the eighteenth and nineteenth centuries, and have been protected since then (Svoboda et al. 2014).

All included localities cover a broad range of variability in terms of elevation, slope, and aspect, thus, to some degree, they represent the landscape-scale heterogeneity found in this region. A statistical stratification of stands across the various geographic positions was not possible, however, due to the limited distribution of primary forest fragments (Svoboda et al. 2014).

2.3. Sample plots

A stratified random design (Svoboda et al. 2014) was used to locate plots in each stand. We overlaid a 141.4 x 141.4 m grid on each stand, and within each grid cell, a circular sample plot (1,000 m^2) was established at a restricted random position (generated in a GIS) using GPS. Plot center points were restricted to the inner 0.49 ha core in each 2-ha grid cell. A total of 370 plots distributed among 28 stands in four subregions of the Carpathian chain were used for the analysis. The plots were resampled from 2016 to 2018, five years after their respective initial sampling year (see also Svoboda et al. 2014, Trotsiuk et al. 2014, Janda et al. 2017). At each sample plot all trees $\geq$10 cm diameter at breast height (DBH) were labeled and their DBH, alive or dead status, and any signs of visible damage (e.g., crown break) were recorded. We recorded crown width in two perpendicular directions for five randomly selected trees per plot in order to determine the relationship between DBH and projected tree crown for each stand.

2.4. Inventory-based current mortality calculation

Annual mortality rate was calculated from the overall aggregate mortality observed over the period between inventories. We used a function based on interest rate calculations to quantify tree mortality. This form better captures monotonically decreasing patterns and is robust to non-constant census intervals (defined by t):

$$m = 1 - (N_t/N_0)^{1/t}$$

where m is annual mortality rate, N_0 is the number of live trees during first sampling, N_t is the number of trees still alive during resampling, and t is the number of years between samplings (Sheil et al. 1995, Sheil and May 1996, Kohyama et al. 2017). For this study, canopy area projection for each tree was derived, using DBH-crown relationship for given plots and/or stands, and the sum of canopy area projections was used instead of number of stems for each census.

Current mortality rate calculations for the comparison with past canopy area removal reconstruction exclude lower layer suppressed trees, because the contribution of such trees to the canopy area is limited and they cannot be detected via dendrochronological analysis and would therefore cause a bias. The death of a suppressed tree creates little to no actual canopy opening and the event is therefore rarely detectable by the means of our dendrochronological methods.

2.5. Canopy area removal reconstruction

We related the calculated mortality rate (m) to historical decadal mortality based on dendrochronological analysis. Tree ring data were obtained from cores collected during the survey plot establishment. Disturbance chronologies were based on two types of events detectable from tree ring series (Frelich and Lorimer 1991): open canopy recruitment (rapid early growth) and release events (abrupt, sustained acceleration of growth). Absolute increase method was used for growth release detection (Fraver and White 2005). Juvenile growth rates were used to detect trees with open canopy recruitment (Trotsiuk et al. 2014). Disturbance events detected were converted to percentage of canopy removed to avoid a sampling-depth bias towards recent years. For details on calculations and disturbance regimes for given stands, please see Svoboda et al. (2014), Trotsiuk et al. (2014), Janda et al. (2017, 2019), Schurman et al. (2019), and Čada et al. (2020).

2.6. Data analysis

Mean, range (difference between decadal minimum and maximum) and standard deviation (SD) were calculated from decadal disturbance history data for each period using raw reconstructed canopy area data. Other parameters like minimum, maximum, and median were considered. However, minimum does not provide sufficient data variability to fit subsequent analyses due to the abundance of periods with no canopy area removal. Maximum and median can be seen as other interpretations of the same characteristic as range or standard deviation. Mean was preferred to median as the outliers (more severe events) are assumed to be crucial for subsequent development of the stand. Range and SD were used as proxies of variability in canopy area removal (disturbance severity) through time. Periods represent the progressively extending timeframes, not a single decade at a certain point in time.

General additive models with negative binomial errors and log link functions were used to evaluate relationships between past canopy area removal and current mortality rates. Analyses were conducted at both plot and stand scales. In addition, generalized additive mixed models (GAMM) were used at the plot-level to account for a hierarchical field sampling scheme using stand as a random effect. All calculations and statistical analyses were conducted in R 4.0.4 software (R Core Team 2021) using the mgcv package (Wood 2017).

To verify that the observed relationship between historical canopy area removal and current mortality and the pattern of the relationship with changing length of the considered preceding period were consistent throughout time, we attempted to reconstruct the relationship for several previous decades. Since exact mortality data were not available, they were approximated by canopy area removed which was inferred from tree-ring data. These mortality rate estimates were used with their respective reconstructed previous canopy area removal data in the same models used for current mortality rates. We could only assess this for periods since the 1950s representing the "contemporary mortality" in the models because preceding canopy area removal records for even older periods would be either short or inaccurate due to limited data prior to 1800 for a substantial share of plots.

3. Results

For plot-level data covering the extensive gradient of the Carpathians, the current mortality, based on repeated inventory, was in a significant inverse relationship with historical decadal canopy area removal (based on tree ring data). This relationship was detected for different parameters of past decadal canopy area removal – Mean, Range, and Standard deviation (**Fig.2**).

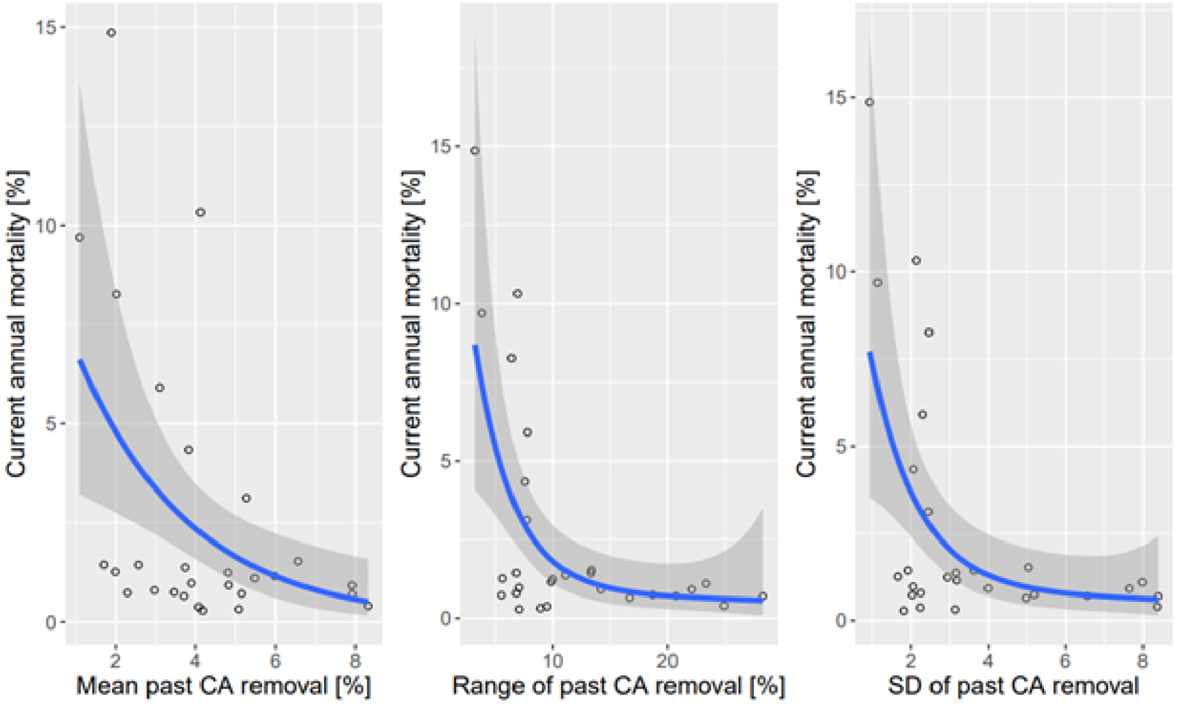

Fig. 2. Plot-level relationship between current annual mortality rate and past canopy area (CA) removal during the last 120 years before the plot establishment. Results based on mean, range and standard deviation (SD) of decadal values during the period are shown. The circles represent observed data, blue curves reflect the predicted values. Confidence intervals (95%) are shaded. This period is presented because it shows the strongest relationship with current mortality. The plots were very similar for all periods with significant relationship detected. Period lengths up to 210 years were tested.

The results differed substantially with changing length of period of past canopy area removal, with the results for all three main characteristics following a similar trend along this gradient on both plot- and stand-level. The strength of the relationship culminated for the period of 130 years for plot-level, and 120 years on the stand-level and in both cases abruptly decreased with further extension of the tested period (**Fig. 3, Fig. 4**). There are, however, major differences between individual subregions (**Table 1**). Local variability is likely a reason for the occurrence of a smaller second peak on a stand-level (see **Fig. 4**).

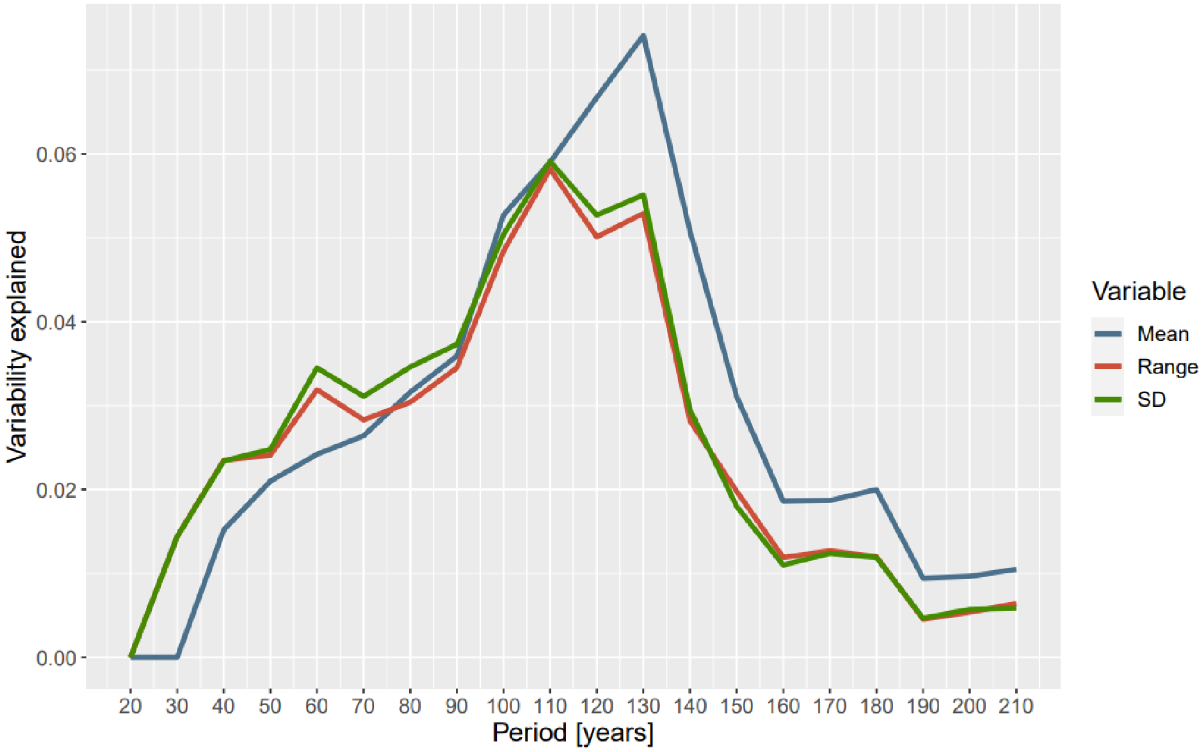

Fig. 3. The amount of plot-level variability in current mortality explained by past canopy area removal for periods of different length. Past canopy area removed was derived from dendrochronological reconstruction. Generalized additive models (GAM) were used and associated R^2 values were plotted. Results based on mean, range and standard deviation (SD) of decadal values during each period are shown.

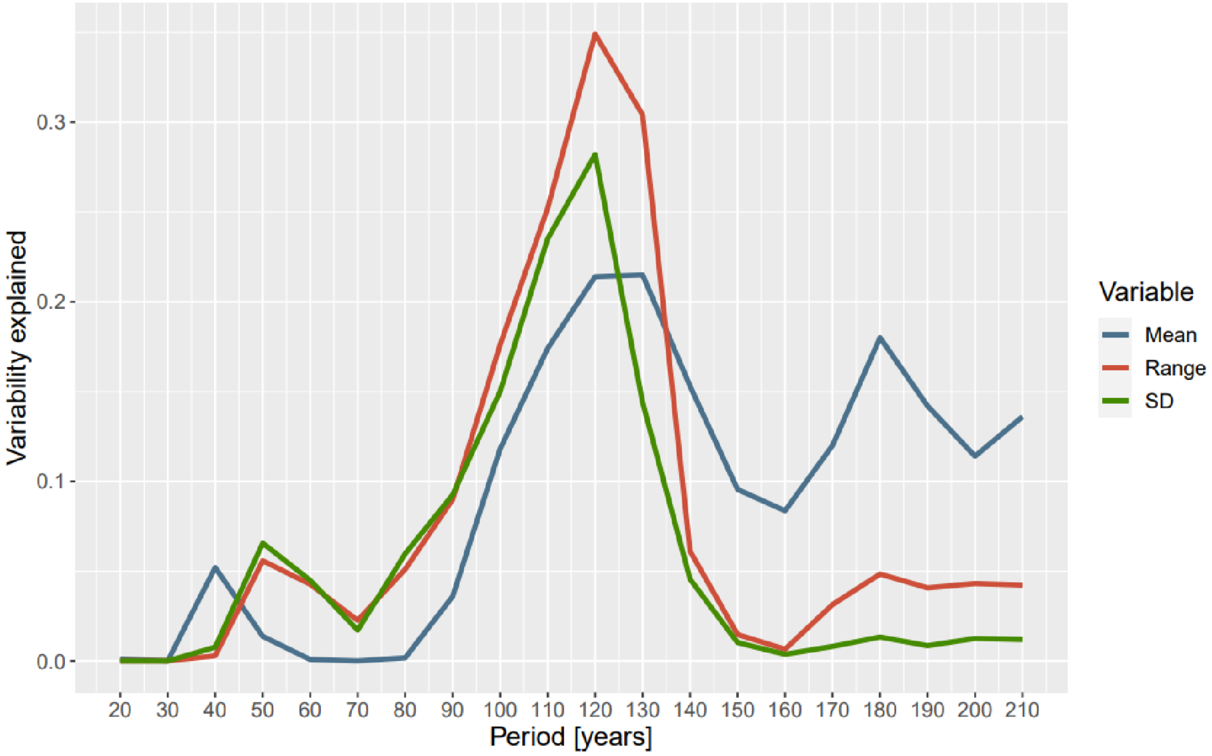

Fig. 4. The amount of stand-level variability in current mortality explained by past canopy area removal for periods of different length. Past canopy area removed was derived from dendrochronological reconstruction. Generalized additive models (GAM) were used and associated R^2 values were plotted. Results based on mean, range and standard deviation (SD) of decadal values during each period are shown.

Table 1. Relationship between current mortality and past canopy area removal. P-values and amount of variability explained for the period, with strongest relationship detected on plot- and stand-level for the whole dataset, and on plot-level for individual subregions.

		Mean		Range		Standard deviation	
Region	Period (years)	p-value	R-squared	p-value	R-squared	p-value	R-squared
Slovakia (Western Carpathians)	130	<0.0001	0.1100	0.0005	0.0870	0.0002	0.0943
Ukraine (Eastern Carpathians)			No significant relationship detected				
Northern Romania (Eastern Carpathians)			No significant relationship detected				
Southern Romania (Southern Carpathians)	160	0.0237	0.0714	0.0186	0.0681	0.0235	0.0643
All	130	<0.0001	0.0741	<0.0001	0.0529	<0.0001	0.0551
Stand level All	120	0.0010	0.2150	<0.0001	0.3490	0.0002	0.2820

The amount of variability explained on plot-level was low and the statistical significance can be attributed to the large dataset, however, the corresponding results on stand-level showing substantially higher values of explained variability support the relevance of the relationship. When stand is added as a random effect to the plot-level model to account for spatial hierarchy of the plots, the amount of explained variance (R^2) reaches similar values as for the stand-level analysis (0.238 for the period with strongest relationship at plot scales).

Application of the same models on canopy area removal (a proxy for mortality) in the past several decades and their respective preceding disturbance histories suggests the relationship between mortality and past canopy area removal is not constant through time. While there are significant results for certain periods, and the amount of explained variability is considerable in some cases, even at plot-scales, the results do not follow the same pattern observed for the most recent period (**Fig. 5**). It is possible the pattern would show a similar shape if older data were available, however, even then the period with the strongest relationship would be several decades longer than it is for contemporary data.

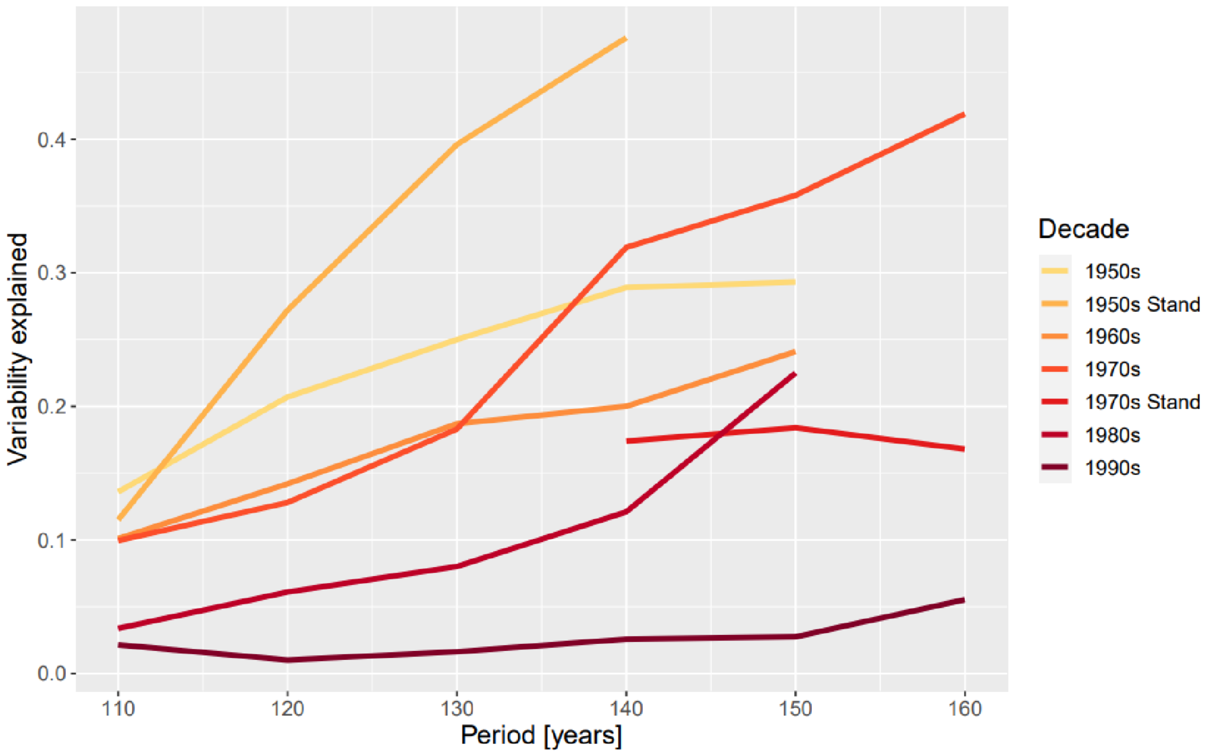

Fig. 5. Amount of variability in canopy area removed for 1950s through 1990s explained by the mean of preceding decadal canopy area removal on the plot- and stand-level. Period refers to a number of years for which the canopy area removal is considered; decade reflects the date (decade) for which the relationship between estimated mortality rate (approximated as canopy area loss) and preceding canopy area removal was tested. Only relationships with significant correlations are shown. Older periods were not analyzed the same way due to limited canopy area removal data prior to 1800 for a considerable share of plots.

4. Discussion

The study was conducted over a wide geographic gradient and examined plots and stands with variable trajectories of past canopy area removal (disturbance history). The majority of the study stands are predominantly shaped by a mixed-severity disturbance regime with rare occurrences of high-severity disturbances (e.g., Trotsiuk et al. 2014, Meigs et al. 2017, Čada et al. 2020). Current empirically observed mortality on a plot-level in primary spruce stands in the studied region ranges from 0 to 100% (Synek et al. 2020). The biasing potential of a relatively short re-census interval (used for mortality rate calculations) was offset by a spatially extensive inventory that spanned broad environmental gradients and stand conditions.

Significant relationships between past canopy removal and modern mortality rates support results from other studies that disturbance history critically influences future stand development (e.g., Panayotov et al. 2011, Janda et al. 2019). The results coupled with studies dealing with relationship between disturbance history and current stand structure (e.g., Janda et al. 2017) or stand structure and mortality (e.g., Clyatt et al. 2016) indicate that all three aspects (disturbances, mortality, stand structure) are representative of different phases of the same repeating process. The inverse nature of the relationship could be simplified as generally, younger stands experience lower mortality rates. However, this explanation does not cover the whole situation in uneven-aged stands with the rare occurrence of stand replacing events. Older, undisturbed stands become increasingly vulnerable to high-severity events (Pickett and White 1985, Schurman et al. 2018). However, our results show that more frequent, less severe, gap-forming processes are more important drivers of modern mortality dynamics. Such a dynamic yet more-or-less stable state generates space and resources for new recruitment while providing enough protection against mechanical damage (e.g., wind, avalanches), and shading to limit growth of understory species competing with new seedlings. Stands developing in this way are more likely to have high diversity in tree ages and dimensions as well as general spatial structure, which improves overall forest resiliency (Aussenac et al. 2017). The changing strength of the relationship with increasing length of the period of past stand development reaching its peak at 120 and 130 years for stand- and plot-level respectively, indicates a major influence of infrequent higher-severity disturbances. Expected average return intervals of such events should be considered in this context (Čada et al. 2020). The length of the period with the strongest effect slightly exceeds the mean time required for complete decay of large logs (Holeksa et al. 2008). Such prolongation might be attributed to a substantial number of trees which die standing due to insect infestation with their subsequent fall being lagged; assuming the decay rate is slower for standing deadwood. If these assumptions are correct the period length would fit nicely for insect and wind driven forest type (Grodzki et al. 2004, Krumm et al. 2011, Panayotov et al. 2011) where deadwood represents important disturbance legacy (Hunziker and Brang 2005, Zielonka 2006). The period with strongest relationship could be also related to average tree longevity (Čada et al. 2020) and would therefore be species-specific. However, we were unable to test that due to the nature of largely-monospecific mountain spruce stands.

The amount of variability explained by a single parameter of past canopy area removal on the plot-level is low. However, our results show, particularly at stand scales, that various measures of past disturbance significantly predict current rates of tree mortality. The results allow us to hypothesize that not only the average amount of past canopy area removal is important for future stand dynamics. A measure of variability of past canopy removal is equally or even more relevant on a stand-level. This finding indicates the need for both variables to be included in order to make the complex stand dynamics models more precise since tree mortality represents one of the highest sources of uncertainty in large-scale vegetation dynamics models (Bugmann et al. 2019). A significant relationship with a similar pattern was also detected when all plots with no current mortality were excluded, suggesting low to no mortality periods to be a distinctive part of the stand development just like more severe disturbances.

On a finer scale the same pattern observed for the whole gradient can be detected for some subregions only (Table 1). The generally observed pattern can be best seen in the most recently disturbed Western Carpathians (Synek et al. 2020), which might indicate the limited possibility to detect the relationship in stands that are currently experiencing low overall mortality rates with low variability among plots. Significant relationships were detected for most subregions, but they differ in strength and length of the period with the closest relationship. This variance can be attributed to differences in local topography (Senf and Seidl 2018) or effects of high-severity stochastic events in certain localities (Čada et al. 2020). These rare events can disrupt our ability to detect the relationship on a time-scale that we were working with due to their specific legacies. However, their impacts are still only temporary and are part of the long-term dynamics. The general pattern does not change with changing size of the individual samples (plot vs. stand), however, broader-scale data provide stronger results (more variability is explained by the model). This finding can be explained by relatively small areas of plots which can easily be not affected by some lower severity events or quite contrary be substantially influenced by a small-scale random event, blurring slightly the shape of the canopy area removal curves. Another possible explanation can be seen in the smaller effect of random single tree or small gap events on a broader scale (Janda et al. 2019), resulting in a more pronounced effect of more severe, larger scale events which are likely to have synchronized effects across the stand (Janda et al. 2017). The difference in period lengths with the strongest relationships on both plot- and stand-levels may be explained by the effects of progressively spreading disturbances, such as insect outbreaks. In such cases, some individual plots would be substantially affected earlier than the stand as a whole, consistent with our results – the period on the plot-level was longer, meaning it started earlier. Based on observations of progressively expanding bark beetle outbreaks (e.g., Sproull et al. 2015, 2016) and the fact that bark beetle infestation was reported as the most frequent cause of tree mortality in Norway spruce stands in this region, even in stands with low overall mortality (Synek et al. 2020), this explanation seems to be reasonable. Prevalent mortality agents likely influence the observed pattern, which is therefore assumed to be species-specific (Holzwarth 2013, Vanoni et al. 2016) and related to stand conditions (Das et al. 2016). To verify that the nature and strength of detected associations between disturbances and current mortality are temporally consistent, we reconstructed these linkages for several decades that preceded the field-based re-census interval. Canopy area removal based on dendrochronological data was used instead of empirically observed mortality. Significant relationships were found in most cases, however, the period with the strongest relationship is not consistent with the pattern observed for current field data. The amount of variability explained is still increasing with the extended length of the observation period several decades past the period length showing the strongest relationship with most recent mortality. Limited canopy area removal data for some stands prior to 1800 make it impossible to accurately follow the relationship further into the past and we are therefore unable to find the exact period with the strongest relationship. We therefore argue that the critical disturbance period driving current morality dynamics is decreasing in length. This can be attributed to increased frequency of disturbances under the ongoing global changes (Seidl et al. 2014, Schurman et al. 2018) or increased susceptibility of the stands to disturbances again as a result of climatic changes (Čada et al. 2016). However, it is uncertain if the change is indeed a result of environmental changes forcing forests towards younger stands (McDowell et al. 2020) or a consequence of changing conditions of the stand following its development after disturbances. On a landscape scale (subregions), the period with the strongest relationship corresponding in length with those found for past decades was detected in the Southern Carpathians. The prolonged period could be related to lower human impacts and reduced levels of forest fragmentation as a result of a lack of access in remote locations. There is a possible bias caused by recent large-scale disturbance in some of our study stands which might override the role of past development for the affected stands for a period of time. Disturbance events occurring shortly before the first sampling of the plots might not be fully detectable by the means of our dendrochronological methods. It is also important to consider that canopy area removal based on tree ring data is not an exact measure of tree mortality, although it is a very good proxy for that purpose. Some events causing release of surrounding trees are not caused by actual tree deaths but only by substantial damage to canopy from which the affected trees might recover. However, we argue that the associated potential biasing effect is limited in spruce stands compared to stands composed of tree species with high resprouting ability (Roženbergar et al. 2020).

The influence of past stand development on contemporary mortality also further supports the concept of emulating natural disturbances in managed stands. Using the historical range of variability in canopy area removal or disturbances in general (e.g., by emulating natural disturbances) to guide forest management can help sustain forest ecosystem structures, composition, and functions (Seymour et al. 2002, Long 2009, Kulakowski et al. 2017). Natural disturbance characteristics can provide guidelines to important management decisions, such as harvest rotation periods, extent, and intensity, that can be linked to natural disturbance frequency, patch size, and severity, respectively (Seymour et al. 2002, Keane et al. 2009), which might in turn lead to improved stability of target stands. However, these primary forest stands, which are allowing us to improve our understanding of forest dynamics, are facing great human-induced risk which has accelerated in recent years. Based not only on the results of this study it would be wise to preserve this unique landscape.

5. Conclusion

The results indicate quantification of mortality is an important aspect of the disturbance-stand structure relationship which should not be neglected. Our results indicate primary Norway spruce stands with higher average canopy area removed per decade in the last 120 years are now experiencing lower annual mortality. A measure of variability in canopy area removal among individual decades during the observed period seems to be equally important as the average canopy area removed. However, the pattern was not found for all subregions. A much higher portion of variability in current mortality can be explained by past canopy area removal on stand level. The pattern appears to be changing over time as the same pattern was not detected for past periods. However, it is still uncertain if the change is related to global change and is working towards shortening the period with the strongest effect on observed mortality, indicating accelerated stand dynamics, or it is a consequence of changes in forest stands following development after disturbances. These observed relationships help us to understand ongoing processes and provide suggestions for ecological modelling and forest management. Parameters of canopy area removal, or disturbance characteristics in general, could help improve future models of stand development. Linking past disturbance characteristics with parameters of management operations might help improve stability of managed stands.

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5.3 Diverse patterns of mortality in primary beech-dominated mixed forests of the Carpathians

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Diverse patterns of mortality in primary beech-dominated mixed forests of the Carpathians

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Highlights

- Overall mortality rates are low despite indications of drought
- Mortality patterns differ among subregions
- Composition of mortality agents is species-specific
- Competition and abiotically caused physical damage are the main mortality agents
- Insects are the most frequent mortality agent for *Picea abies* (L.) Karst.

Abstract

Tree mortality, driven by disturbance legacies and climate, represents a crucial process shaping forest dynamics and influencing forest structure. Exploring the mortality patterns in primary forests during periods without severe disturbances provides information on natural background dynamics of the particular forest type under ongoing climate change. These observations can then be compared to mortality rates in other forest types sharing the region or stand conditions. Using an extensive set of sample plots, we examined the mortality rates and composition of mortality agents in primary European beech-dominated (*Fagus sylvatica* L.) mixed forests on different spatial scales. We resampled (five-year period) 227 plots (13,915 living trees) within 16 stands in primary European beech-dominated mixed forests spanning a large geographical gradient along the Carpathian Mountains. The estimated overall annual mortality rate was well within the previously published range of background mortality. Stand- and plot-level mortality rates varied, although, not as much as has been reported from other forest types in the same region. Overall mortality was 0.89% per year. Species-specific annual mortality rate was 0.76% for *Abies alba* Mill, 0.88% for *Fagus sylvatica*, and 1.1% for *Picea abies* L. (Karst.). Annual mortality rates below 2% were detected on 90.3% of plots; 5% per year were exceeded only for conifers on 5% of plots. Plot-level mortality varied; lower rates were observed in the Western Carpathians compared to other regions and significant differences were found in species-specific mortality between coniferous species and *Fagus sylvatica*. At the plot level, mixed-severity disturbances increased variability of mortality rates within most localities. Most recently dead trees were found in the smallest diameter classes and the counts were continuously decreasing towards bigger size classes. However, individual mortality agents have different distributions across the size classes, highlighting the complexity of the mortality process in primary forests. Despite climatic extremes as a major mortality agent were recorded in a limited number of cases, most study stands are experiencing drought conditions. While competition and various forms of abiotically caused physical damage (crown break, stem break, uprooted) were major mortality agents for *Fagus sylvatica* and *Abies alba*, insect infestation was the most frequent mortality agent for *Picea abies*. The frequency of insect-related mortality among *Picea abies* trees even in stands with low overall mortality and relatively low abundance of the species suggests the crucial role of insects in the dynamics of particular tree species and emphasizes the importance of structural and compositional heterogeneity.

1. Introduction

Tree mortality and its causes play major role for understanding forest dynamics (Franklin et al. 1987, Das et al. 2016) because they strongly influence future stand development (Bircher et al. 2015) and are a key in predicting forest structural and compositional changes in response to global change (Bonan 2008, Adams et al. 2010, Allen et al. 2010, Turner 2010, Dietze and Matthes 2014, Thom et al. 2017). Tree mortality is critical for modeling carbon residence time, yet it represents one of the highest sources of uncertainty in large-scale models of vegetation dynamics (Friend et al. 2014, Bugmann et al. 2019). Thus, robustly quantifying the contribution of different mortality agents in the context of disturbances and stand conditions remains crucial to link tree, stand, landscape, and global processes (Franklin et al. 1987).

Our understanding of tree mortality processes is incomplete, as associated causal mechanisms are difficult to determine with high certainty from observational data alone (Adame et al. 2010, Das et al. 2016, Vanoni et al. 2016). Multiple recent studies have focused on forests severely affected by drought and/or insect outbreaks that generate extensive mortality (e.g., Anderegg et al. 2015, Sproull et al. 2015, 2016). In contrast, other forest systems are characterized by processes that generate low background mortality rates, as low as 0.5 to 2% per year (e.g., Stephenson and van Mantgem 2005). However, even in these forests, the aggregate effects of low mortality summed over long timeframes are substantial, and may exceed the impacts of individual catastrophic events (van Mantgem et al. 2009). These different mortality regimes form a continuum from regular (non-catastrophic) to irregular (catastrophic) mortality (Monserud 1976, Hawkes 2000). At broad regional scales that span wide environmental gradients, montane forests are subject to a wide spectrum of mortality agents and modes, ranging from occurrences of background tree mortality to high-severity disturbance-driven events that generate extensive tree mortality (e.g., Synek et al. 2020, Nagel et al. 2021).

Older individual-based forest models often generalize mortality into two major groups distinguishing between “vigor-related” mortality and “background” (“ambient”) mortality. For vigor-related mortality, an inverse relationship between tree growth and mortality probability is assumed (Shugart 1984, Bugmann 2001, Bircher et al. 2015), suggesting that trees limited in growth, for whatever cause, are more likely to die. Ambient mortality is mostly attributed to random factors, generally not related to growth. Abiotic factors such as wind, fire, or lightning, are commonly considered to be the fundamental drivers of ambient mortality. It has been suggested that other biotic factors contributing to mortality are not sufficiently assessed in some models (Das et al. 2016). Disturbance-related tree mortality should be considered in long-term forest dynamics regardless of mortality rates and developmental stages (Turner 2010).

Many individual-based models, however, have been developed for even-aged production forests and often consider only one generation of trees, which makes them inaccurate for forests with complex, uneven-aged structures, typical for many primary forests. In this context, a need for inventory-based mortality functions, especially in mixed-species forests under changing climatic conditions, emerges (Bircher et al. 2015).

More complex scheme can be created when mortality agents are sorted based on their role in the mortality process. According to this concept mortality agents can be categorized as predisposing, inciting, and contributing factors (Manion 1991). Factors, or agents, affecting stands over the long term are classified as predisposing factors (Allen et al. 2010). Inciting factors act in the short term with highly variable intensities; drought and frost, random physical damage (e.g., windthrow), and insect or pathogen attack are included in this group (Anderegg et al. 2015). The main contributing factors are insects and fungi; these agents are often part of the process ultimately leading to tree death, but their presence alone might not induce it, and their effects might vary (Allen et al. 2010). Different processes resulting in tree mortality create different mortality modes (Larson and Franklin 2010, Holzwarth et al. 2013); for example, abiotic factors such as wind leave trees uprooted or snapped while competition or drought result in dead standing trees. Various mortality modes lead to specific legacies which consequently affect future stand structure and susceptibility to disturbances (Johnstone et al. 2016, Schurman et al. 2018). The role of mortality agents is assumed to be species-specific (Holzwarth 2013, Vanoni et al. 2016) and influenced by stand conditions (Das et al. 2016). Examining the distribution of different mortality modes among size classes should, therefore, provide further insight into the relationship between mortality and stand structure.

Mortality modes can point out only proximate causes of tree death (Larson and Franklin 2010, Holzwarth et al. 2013), and therefore provide less accurate information than assessing the cause of mortality of each tree shortly after its death (Das et al. 2016). It is often problematic to decide which of the contributing factors was the actual cause of death (Allen et al. 2010, Das et al. 2016). The additional information on the year of tree death which can be extracted from dendrochronological series is also reliable only to some extent as trees often show abrupt growth decreases several years or even decades prior to death (Vanoni et al. 2016). Despite these limits, mortality modes still allow us to evaluate the main mortality agents. Since the composition of mortality agents is an important driver of stand structure, also evaluating the relative frequency of different mortality agents on both landscape and species levels can further improve our understanding of primary forest dynamics and provide insight on how the disturbance regime can interact with ongoing climate change (Turner 2010, McDowell et al. 2020).

Many recent studies have highlighted the predicted increases in the scale and severity of drought and insect outbreak events induced by climate change (Seidl et al. 2007, Jonsson et al. 2012, Vanoni et al. 2016, Seidl and Rammer 2017, Seidl et al. 2017). Combining empirical mortality data with demographics and causes of mortality and collecting extensive datasets from various forest types provides a robust analytical approach that will improve our understanding of causal mechanisms and the consequences of climate change on tree mortality.

European beech-dominated (*Fagus sylvatica* L.) mixed primary forests are the prevalent primary forest type in the lower elevations of the Carpathian Mountains. Despite the role of windstorms and insects not being as pronounced in mixed forests as it is in Norway spruce (Picea abies (L.)

Karst.) forests in the same region, abiotic factors (wind and snow mostly) are expected to be important drivers of mortality (Nagel et al. 2016). The relative frequency of bark beetle-related mortality in mixed stands can be high, however, among spruce trees, based on the abundance of this mortality agent even in spruce stands with low overall mortality (Synek et al. 2020). Due to expected less turbulent dynamics of mixed forests (Motta et al. 2011), less intensive but continuously operating agents of mortality, like competition or fungi, are likely to be more frequent.

To better understand mortality processes in primary forests, we had three main objectives: i) to quantify annual rates of mortality in primary beech-dominated mixed forest stands along the Carpathian Mountains during a five-year resampling interval; ii) to evaluate the distribution of mortality among tree size classes; and iii) to evaluate the distribution of the mortality agents in primary beech-dominated mixed forests. Considering the extent of the dataset both geographically and structurally, our results complement longer-term studies observing a much narrower spectrum of stand conditions in primary mixed forests, and studies done in different forest types, and they thus help us understand the dynamics and variability in primary forests.

2. Methods

2.1. Study Area

The Carpathian Mountains contain the largest tracts of primary forests in Central and Eastern Europe (Veen et al. 2010, Knorn et al. 2012, Sabatini et al. 2018, Mikoláš et al. 2019). The area is therefore ideal for investigating natural disturbance processes over large spatial scales. Forests within the study area are referred to as ‘primary forests’ (Sabatini et al. 2018). Because stands developed under their natural disturbance regimes and there is little or no evidence of past human impacts, the old-growth stage of development is not a required condition (Sabatini et al.

2018, Mikoláš et al. 2019). We can expect a wide range of disturbance severities and frequencies in these stands resulting in a broad spectrum of mortality rates on fine scales. Our study contains data from 16 stands that we divided into three geographic regions (Western, Eastern, and Southern Carpathians) (**Fig.1**). Primary forests in the Carpathians at elevations under ca. 1,200 m a.s.l. are dominated by European beech; monodominant spruce forests are typical in the higher elevations. Other species include European silver fir (*Abies alba* Mill.), Norway spruce, sycamore maple (*Acer pseudoplatanus* L.), rowan (*Sorbus aucuparia* L.), and birch (*Betula* spp.). We investigated mortality processes in *Abies alba, Fagus sylvatica*, and *Picea abies*, since only these species were adequately distributed and provided sufficient samples sizes for statistical analyses.

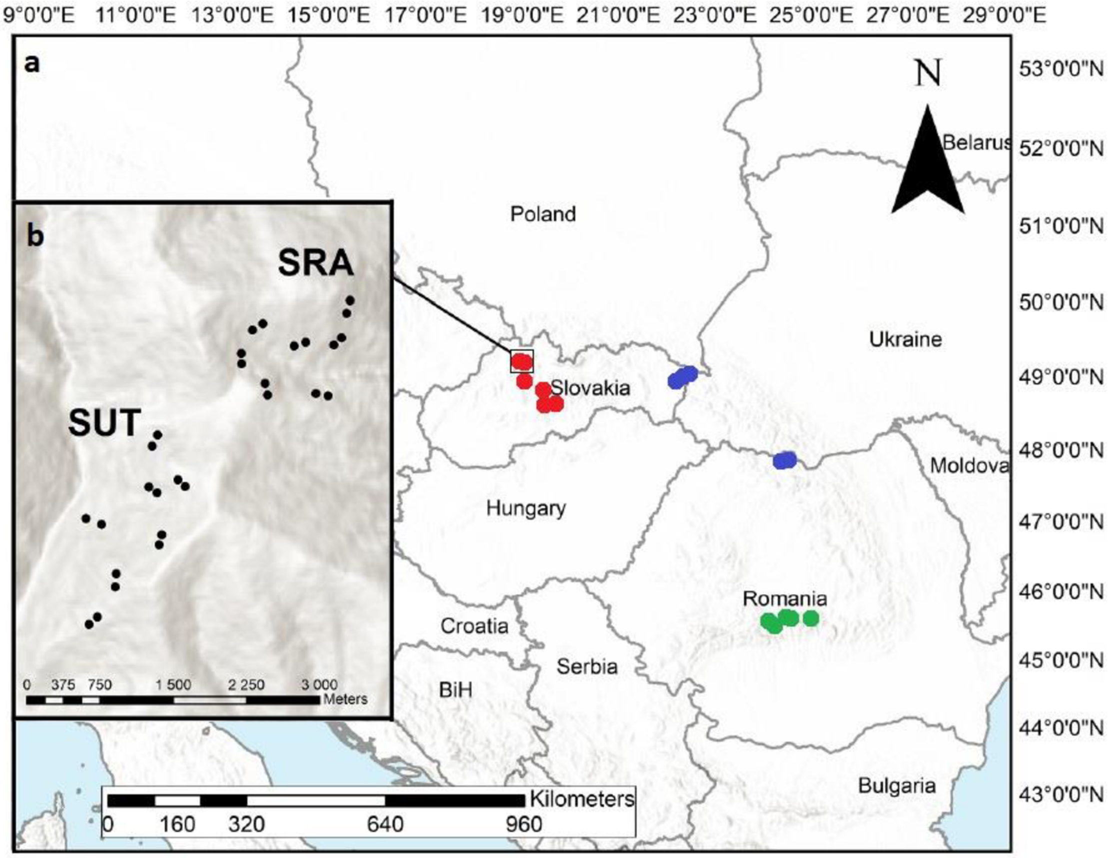


Fig. 1. Hierarchical distribution of study stands at landscape scale (a) and permanent sample plots within stands (b). The study region is composed of the Western, Eastern and Southern Carpathians and these areas were analyzed separately.

2.2. Study Site Selection

Study site selection was initiated using a previous inventory of primary forest remnants and maps to identify potential primary stands. Selected stands were then surveyed for indicators of naturalness (e.g., coarse woody debris in various stages of decay) and direct signs of human activity (Mikoláš et al. 2019). We excluded stands that contained clear evidence of past logging or grazing, and any stands adjacent to formerly grazed areas, and extreme sites. All the localities include a broad range of variability in terms of elevation, slope, and aspect, thus, to some degree, they represent the landscape-scale heterogeneity found in the study region. All the study plots are included in the extensive primary forest dataset of the REMOTE project (Remote Primary Forest, 2021) which is focused on surveying remaining tracts of primary forest landscapes in Europe and long-term study of their dynamics.

2.3. Sample Plots

Sample plots in each stand were established using a stratified random design (Svoboda et al. 2014). We overlaid a 10 ha grid on each stand, and established circular, 1000 (in 2014) or 1500 m^2 plots in each cell. A random point was generated in the 0.5–3.4 ha interior of each grid cell, and a pair of plots was established 40 m from either side of this point along the slope contour, such that plot centers were separated by 80 m. The plots were resampled after five years from 2019 to 2020 based on the initial sampling year. All plots were extended to 1500 m^2 during resampling, however only trees already sampled during first census were used for the analyses. Within each sample plot we labeled all trees ≥6 cm diameter at breast height (DBH) and recorded their species, DBH, social status (released vs. suppressed; suppressed tree should have more than 50% of its canopy directly shaded by other trees) and whether they were alive or dead, or showed any signs of visible damage (e.g., broken crown).

2.4. Tree Mortality Agents

For recently dead trees (i.e., those that were alive during the initial sampling), we recorded mortality agent(s). Seven categories of mortality agents were applied (climatic extremes; apparent result of competition; fungi; insect infestation; and tree forms of physical damage: crown break; stem break; uprooted). Only the agents that could have played significant role in the mortality of a given tree were included (e.g., stem breakage occurring clearly after tree death is not counted). Climatic extremes were considered when there were multiple recently dead trees with no signs of severe infestation or physical damage among released canopy trees within a plot. Competition was determined to be the mortality agent for standing dead suppressed trees occurring in a canopy understory. Crown break category was used for trees with less than one third of their crown missing, and the stem break group includes trees with even larger portions missing.

Since evidence for multiple mortality agents can be recorded for a single tree, and structural damage and infestations might occur after tree death, we developed a system for determining actual mortality agents. In the cases where evidence for multiple agents exists, we tried to determine the agents responsible for a shift from (limited) growth to actual tree death. All the physical damage categories (crown break, stem break and uprooted) were considered only if the tree was clearly damaged while alive (e.g., pointed splinters created by the breakage) and the damage was not recorded during the first measurement. For suppressed trees that were also infested by bark beetles, competition was considered to be the main agent. The infestation in these cases typically just speeds up the decline (Das et al. 2016), however, the insects were still listed as mortality agent. Identification of the 'climatic extremes' mode was perhaps the most complicated as it is very difficult to determine in the field. Based on the concept of drought, frost and similar climatic conditions acting as inciting factors (Manion 1991) which would have affected the majority of the stand, climatic extremes were applied only if there were multiple released (upper canopy layer, small to no part of the crown directly shaded) trees without signs of other mortality agents per plot.

2.5. Data Processing

Annual mortality rate was calculated from the overall mortality observed over the period between inventories. We used a function based on interest rate calculations to quantify tree mortality. This form better captures monotonically decreasing patterns and is robust to non-constant census intervals (defined by t):

$$m = 1 - (N_t / N_0)^{1/t}$$

where m is annual mortality rate, N_0 is the number of live trees during first sampling, N_t is the number of trees still alive during resampling, and t is the number of years between samplings (Sheil et al. 1995, Sheil and May 1996, Kohyama et al. 2017).

We present mortality rate on various scales, using different aggregation schemes. We first evaluated the mortality rates at the plot level, then aggregated to the species, stand, and region levels. We further report mortality rates calculated for pooled tree data for each group and "plot-level" characteristics where annual rates for each individual plot within respective group were used.

For an overview of climatic conditions within our study stands, we extracted temperature and precipitation data for our study plots from E-OBS gridded climate dataset (version 23.1e, Cornes et al. 2018). The daily values were aggregated to annual values for both temperature and precipitation and "water balance"; a metric of drought was calculated as the difference between precipitation and potential evapotranspiration. The data were then averaged across all plots within each stand for a period since 1960 until 2020. The period from 1991 to 2020 was used as a reference period and standard deviations from the average during this refence period were plotted for each stand.

2.6. Data Analysis

Non-parametric Kruskal-Wallis test was used to assess the variability of mortality between regions, stands and species based on plot-level mortality. Pairwise Wilcoxon rank sum tests were applied to distinguish which groups differ from others. Chi-squared test was used for the distribution of mortality agents among size classes and species. Statistical analyses were conducted in R 4.0.4 software (R Core Team 2021).

3. Results

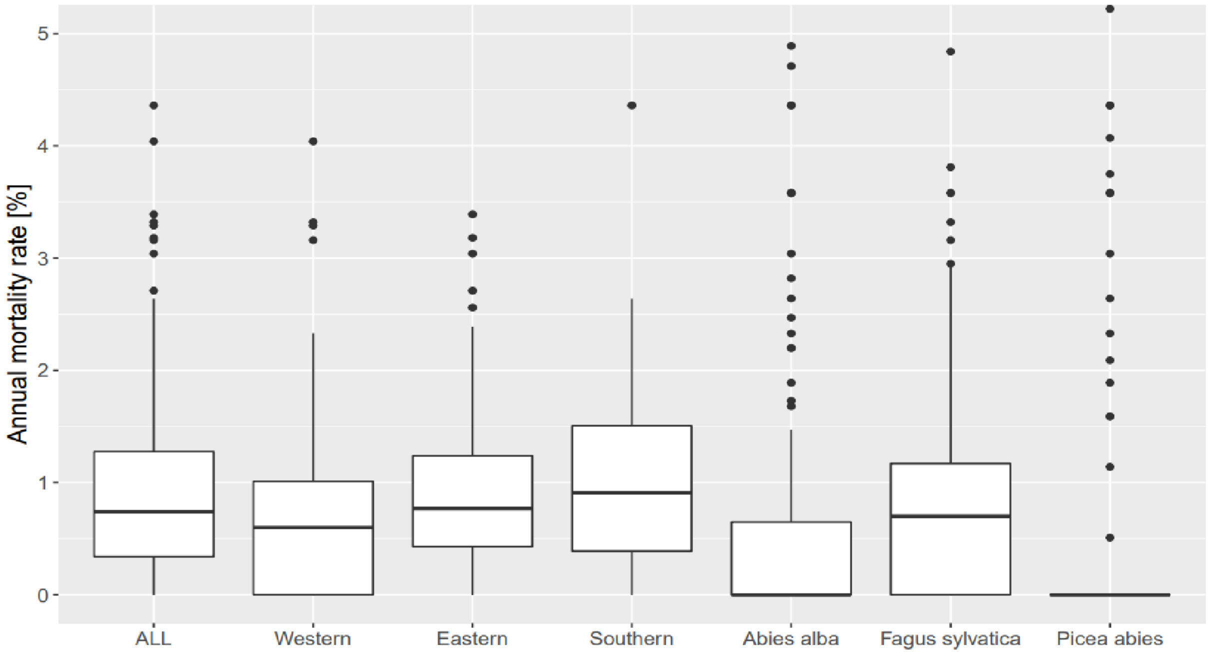
3.1. Mortality Rates

A total of 13,915 trees were remeasured five years after plot establishment; 606 of these trees died during that period. Overall mortality across all species was 0.89% per year. For individual species the overall annual mortality was as follows: 0.76% for *Abies alba*, 0,88% for *Fagus sylvatica*, and 1.10% for *Picea abies*. The mean annual plot-level mortality rate across the entire study area was 0.91% (sd = 0.82%). Plot-level annual mortality ranged from 0 to 4.34%; the ranges were similar for all regions. For individual species, associated mortality rates ranged from 0 to 12.94% for *Abies alba*, 4.84% for *Fagus sylvatica* and 10.59% for *Picea abies* (**Table 1**). We detected annual mortality rates below 2% on a majority of our plots (90.3%). No mortality was detected on 42 (18.5%) plots. Except for species-specific mortality of *Picea abies* on 8 plots and *Abies alba* on 4 plots, no mortality rates exceeding 5% annually were observed. A significant difference in the mortality rates of both coniferous species compared to *Fagus sylvatica* was detected (p-value < 0.0001 in both cases). Plot-level variability in mortality rates differs significantly among regions (p-value = 0.0378). Lower plot-level annual mortality rates were found in Western Carpathian region (mean 0.78%, sd = 0.87% compared to 0.96%, sd = 0.77% and 0.99%, sd = 0.80% for Eastern and Southern region respectively; p-value = 0.042 for each) (**Fig. 2**). Higher local mortality of conifers is the most likely driver behind variability in mortality rates when combination of species and regions is considered. The observed increased recent mortality of *Picea abies* in certain stands (**Fig. 3**) is, however, still substantially lower than what has been reported from pure spruce stands.

			Annual mortality rate [%]					
				Plot-level data				
Species	Region	Plots	Pooled data	Mean	Median	Minimum	Maximum	SD
ALL	All	227	0.89	0.91	0.74	0.00	4.36	0.82
	Western	76	0.74	0.78	0.60	0.00	4.04	0.87
	Eastern	87	0.93	0.96	0.77	0.00	3.39	0.77
	Southern	64	0.99	0.99	0.91	0.00	4.36	0.80
Abies alba	All	152	0.76	0.67	0.00	0.00	12.94	1.63
	Western	59	0.67	0.51	0.00	0.00	12.94	1.97
	Eastern	38	0.95	0.80	0.00	0.00	6.89	1.56
	Southern	55	0.71	0.76	0.00	0.00	4.71	1.22
Fagus sylvatica	All	227	0.88	0.84	0.70	0.00	4.84	0.89
	Western	76	0.67	0.58	0.00	0.00	3.32	0.82
	Eastern	87	0.91	0.93	0.75	0.00	3.58	0.78
	Southern	64	1.07	1.01	0.84	0.00	4.84	1.03
Picea abies	All	103	1.10	1.00	0.00	0.00	10.59	2.22
	Western	55	1.06	1.03	0.00	0.00	9.71	2.34
	Eastern	11	2.38	1.56	0.00	0.00	10.59	3.12
	Southern	37	0.95	0.79	0.00	0.00	5.59	1.57

Table 1. Annual mortality rates and summary statistics of mixed temperate forests of the Carpathian Mountains. Statistics are based on data for five-year remeasurement periods.

a)



b)

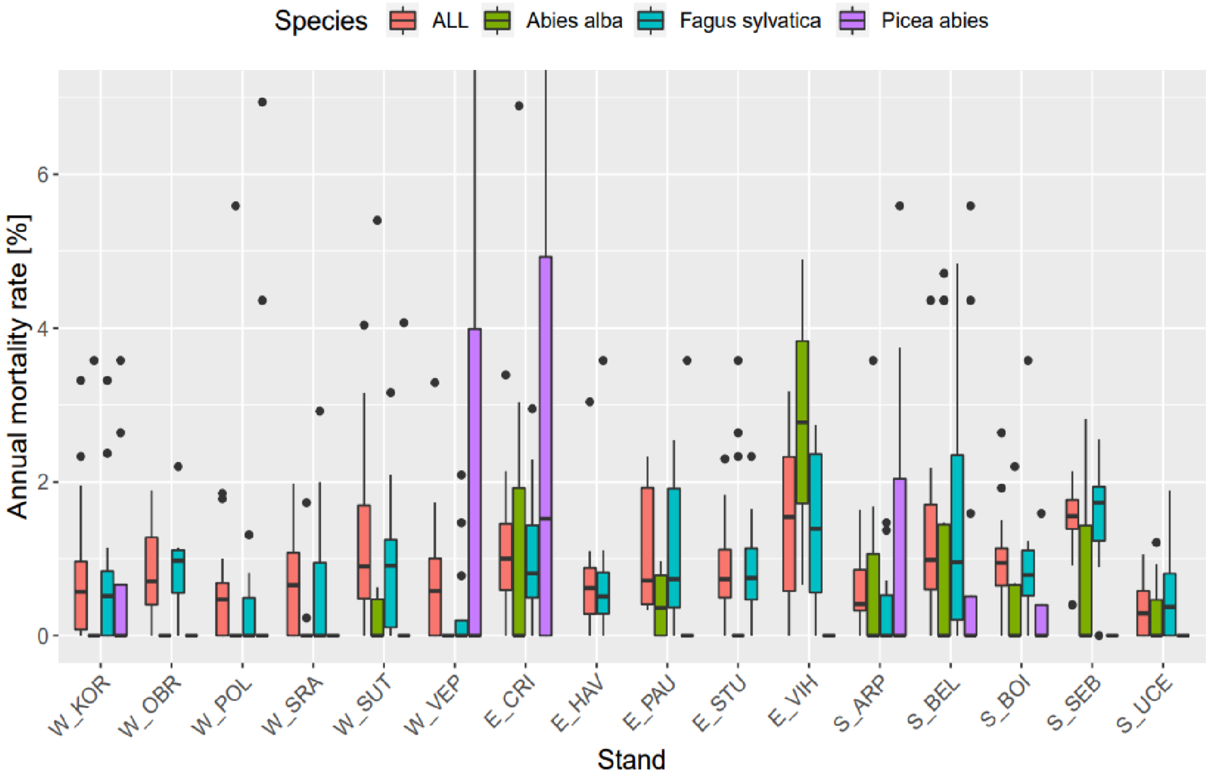
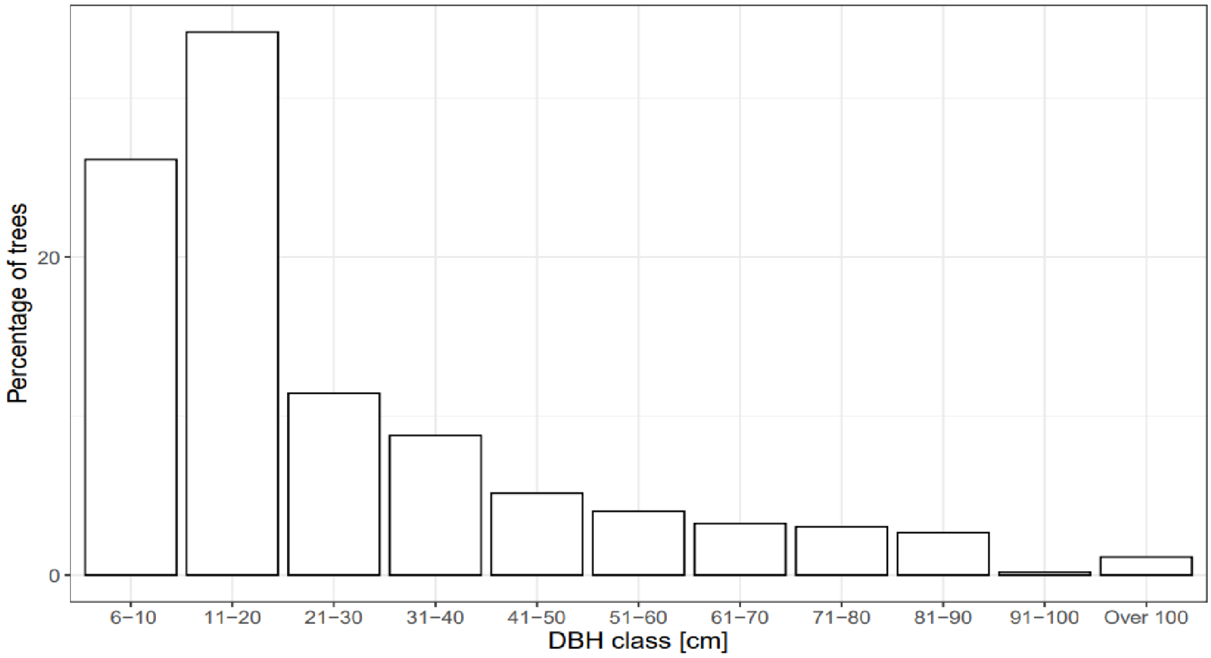


Fig. 2. Annual mortality rates on the plot-level for all data, subregions and for each of the main species (a; capped at 5% annual mortality) and stand level resolution (b; capped at 7% per year). Percentage calculated based on number of stems. Each box represents the range from first to third quartile and median for a given group of plots. Individual dots show outliers further than 1.5 times the interquartile distance from the first (third) quartile. Cases of species-specific plot-level mortality of *Picea abies* and *Abies alba* exceeding the caps are not shown, however the data are included. The region each stand belongs to is denoted by first letter of the stand name.

3.2. Size Class Distribution of Mortality

Most recently dead trees were found in the smallest recorded size classes, up to 20 cm DBH, and the proportions were continuously decreasing towards larger classes. In terms of basal area, most mortality is represented by trees in diameter classes between 50 and 90 cm (**Fig. 3**). The observed pattern is similar for all regions (X-squared = 31.013, df = 20, p-value = 0.05502). Differences were, however, detected among individual species (X-squared = 53.599, df = 20, p-value = $6.631e^{-05}$), which can be linked to the relatively higher abundance of large dead *Picea abies* trees. This shift in distribution compared to other species can be attributed to the influence of mortality agents on size class distribution of mortality. Particular mortality agents are more frequent in certain diameter ranges. Significant differences were detected in distribution of mortality agents among size classes (X-squared = 284.29, df = 60, p-value $< 2.2e^{-16}$). These differences are, as expected, driven by prevalence of competition-related mortality in the smallest size classes, and high proportion of fungi- and insects-related mortality in the large ones (**Fig. 4**).

a)



b)

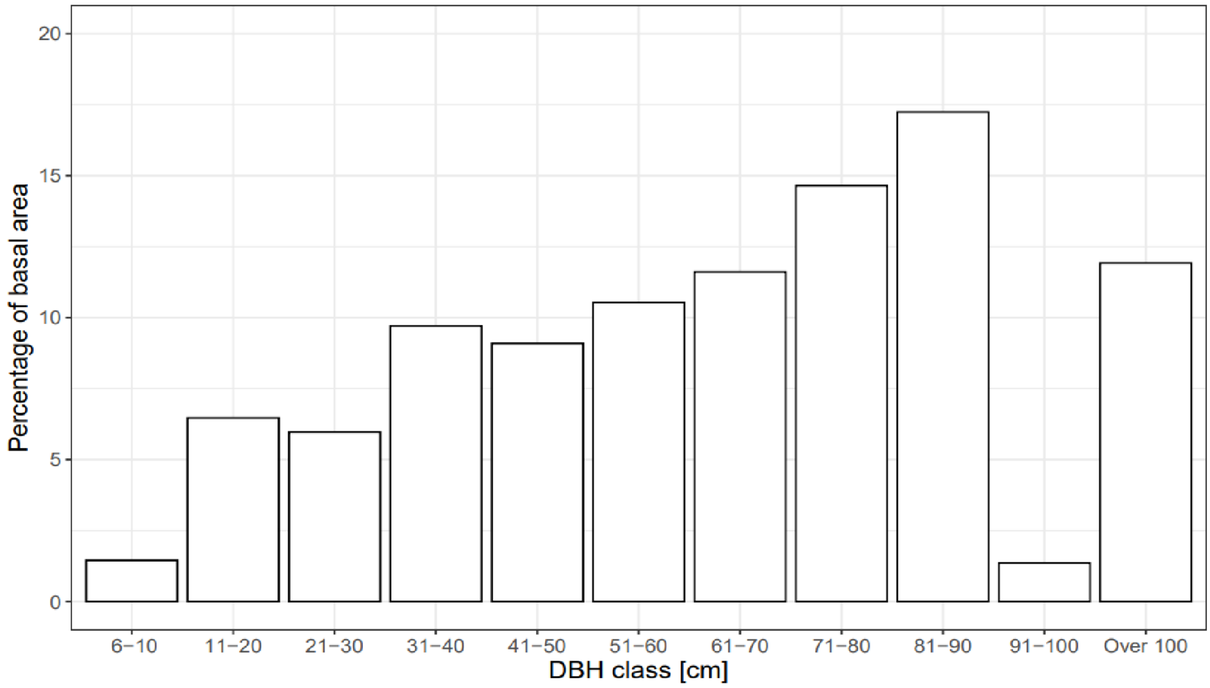


Fig. 3. Distribution of recently dead trees among size classes presented as number of stems (a) and basal area (b).

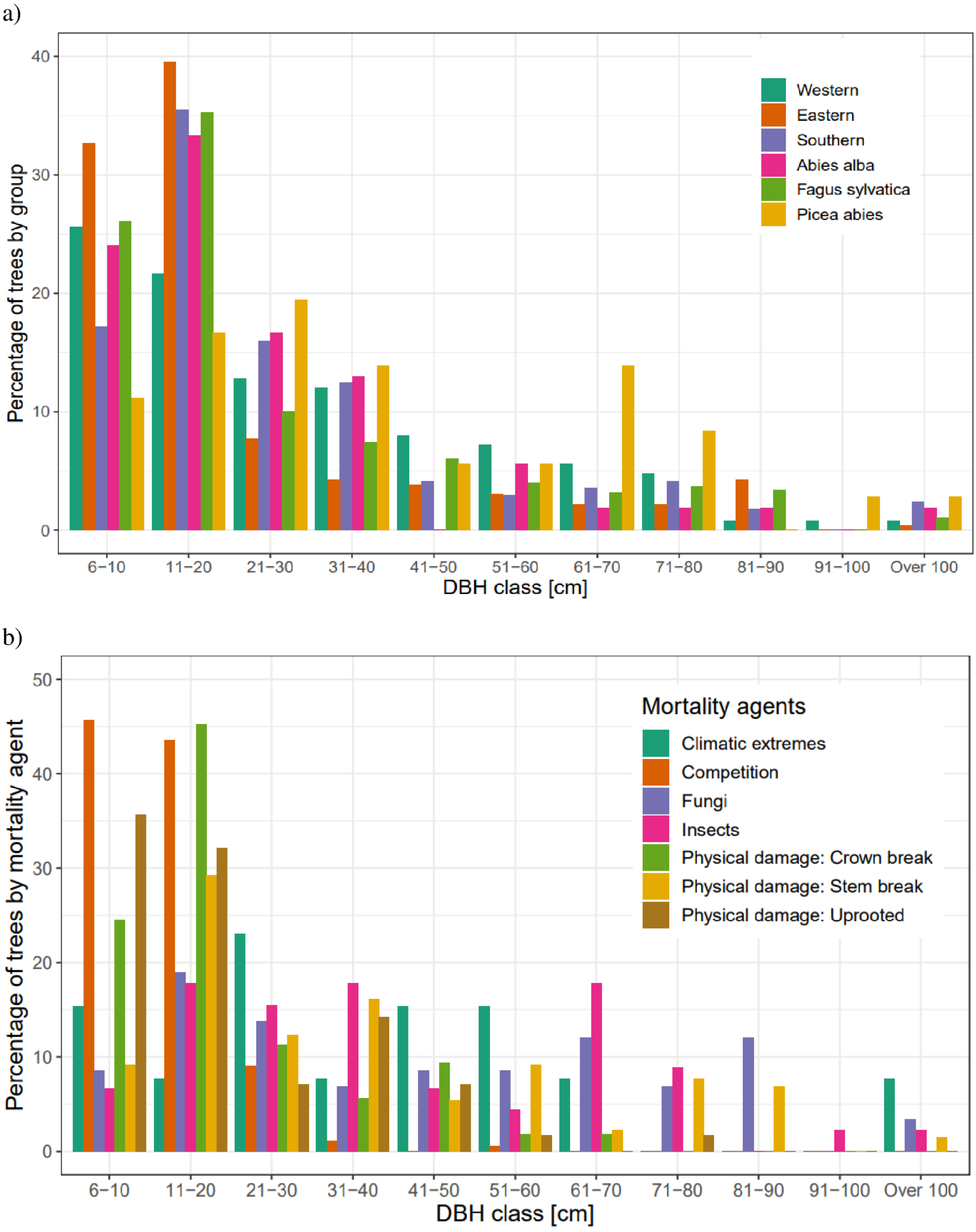


Fig. 4. Distribution of recently dead trees among size classes by subregions and species (a) and by mortality agent (b). Categories of mortality agents used are explained in the Methods section.

The figure is not reflecting relative frequencies of individual agents only their distribution among size classes.

3.3. Mortality Agents

The contribution of each mortality agent to total mortality indicates the major role of competition and physical, abiotically-caused damage in its various forms. When all three physical damage modes are summed, they account for as much mortality as competition does (**Fig. 5**). Relative frequency of various forms of physical damage is consistent across regions but differs among species. Statistically significant differences in the relative frequency of mortality agents were observed among the regions (X-squared = 33.142, df = 12, p-value < 0.001), driven mostly by low proportion of insect related mortality and more frequent records of fungi as a mortality agent in the Eastern Carpathians (likely due to species composition). The relative prevalence of mortality agents for individual species differs significantly (X-squared = 68.038, df = 12, p-value = $7.445e\text{-}^{10}$), mostly due to the dominant role of insect-driven mortality in *Picea abies*.

Climatic data indicate temperatures above the long-term mean in all our study stands, while the relative amount of precipitation varies remarkably. Water balance is, however, below average in the majority of stands, indicating widespread drought conditions (**Appendix S1**). In the Southern Carpathian region the stands with the lowest mortality also showed a mostly positive water balance during the resampling period, while such pattern was not found for other regions.

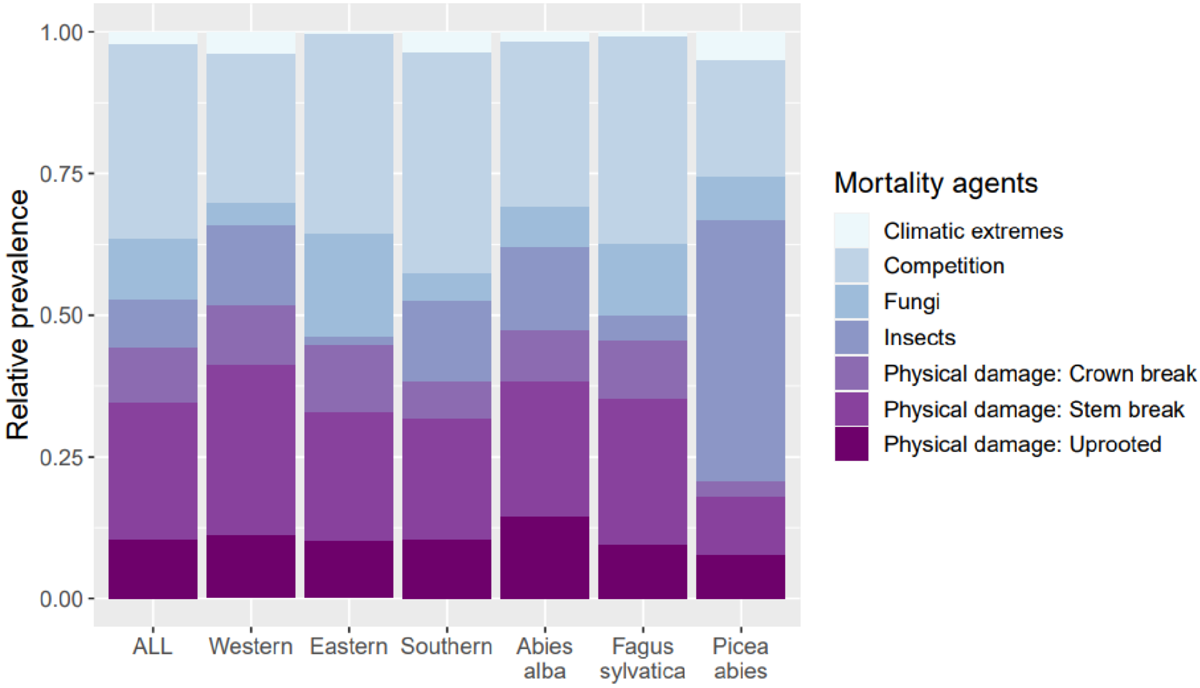


Fig. 5. Composition of mortality agents. Compositions of detected mortality agents for all data, each subregion and each of the main species. Mortality agents are defined in the Methods section. The figure reflects contributions of mortality agents among trees over the 6 cm DBH threshold.

4. Discussion

4.1. Mortality rate

The observed overall annual mortality rate was well within the reported range of background mortality in forests recently unaffected by high-severity, large-scale disturbances (Stephenson and van Mantgem 2005, van Mantgem et al. 2009, Das et al. 2016). However, at the stand level, the mortality rates varied, and the variability is even more evident when individual species are considered. It is necessary to note that background mortality is not only an outcome of competition but also includes lower intensity (in terms of scale or severity) disturbances (Turner 1987, Fraver et al. 2009). Annual mortality rate exceeding 2% was detected on less than 10% of all plots. The locally higher mortality could be, in many cases, attributed to dense stand conditions and self-thinning process (Castagneri et al. 2010, Svoboda et al. 2010), and/or relatively higher mortality of *Picea abies,* often attributed to bark beetle infestation. Mortality of coniferous species, *Picea abies* and *Abies alba*, represents the only cases (12) where a plot-level mortality exceeded 5% annually. Higher mortality detected for *Picea abies* in primary mixed stands is, however, still substantially lower than that detected in spruce-dominated primary forests in the Carpathian region (Sproull et al. 2015, 2016, Synek et al. 2020), or even-aged spruce monocultures across Europe. Like in the higher elevation spruce stands our findings in beech-dominated mixed forests match the concept of mixed-severity disturbances – with severity substantially variable over larger areas (Panayotov et al. 2011, Trotsiuk et al. 2014, Schurman et al. 2018). Some of the mortality recorded within our observation period is likely related to individual disturbance events that caused intermediate-severity damage (Woods 2004) which leaves similar legacies but affects the stand over short, more distinct periods. Records of multiple mortality agents in most stands also suggest mixed-severity regime rather than single major events.

Analysis of variance detected a significant difference in the variability of plot-level mortality between the Western Carpathians and other regions. The expected role of drought conditions was not confirmed as the Southern Carpathians – the region generally less affected by drought - had the highest mortality rates. The variability is likely driven by relatively higher *Picea abies* mortality. The role of species-specific mortality rates has been further highlighted by the significant difference between mortality rates of coniferous species and *Fagus sylvatica.* The results indicate substantial heterogeneity on different scales. Such patterns suggest a mixed-severity disturbance regime for these forest stands with extensive variability on both the regional and fine scale, influenced also by exact species composition in each stand. Local disturbances are considered the major driver of structural variability on a fine scale, while climatic factors are likely the most important characteristic on a coarse scale (Janda et al. 2019). Considering the relatively short observation period, a single infrequent disturbance event, or absence thereof could have influenced the results. However, the variability in stand structure at the time of plot establishment along with the size of the dataset and the extensive area sampled, allow us to assume the observed patterns are representative of a longer timeframe. Although, it is necessary to take into account the possible impact of stochastic disturbance events, which can also lead to a shift in species composition and subsequently the relative prevalence of mortality agents. Structural stand parameters, disturbance history (e.g., Schurman et al. 2018) and local topography (Senf and Seidl 2018) are likely crucial factors underlying the variability in the periods without major disturbance events, and substantially influence the impact of these. Several studies of mortality rates in the Carpathian region lately reported substantially higher mortality rates, but most of these studies were conducted in higher elevation spruce-dominated stands, and often focused on stands during a period of bark beetle outbreaks (e.g., Sproull et al. 2015, Sproull et al. 2016). However, spruce-dominated stands are apparently subject to higher mortality rates even in non-outbreak conditions (Sproull et al. 2015, Synek et al. 2020) and our results suggest this statement remains valid even when spruce trees only are considered in mixed stands.

4.2. Size Class Distribution of Mortality

The diameter class distribution of recently dead trees follows similar pattern for both regions, with considerable variation among stands. Overall, the distribution shows the highest number of recently dead trees in DBH class 11 to 20 cm followed by continuous decrease towards larger classes. Smallest trees are expected to have the highest mortality. However, in this case, the smallest recorded size class shows substantially high mortality, but it is exceeded by the slightly larger class. This may, to a certain extent, be attributed to our sampling DBH threshold that omitted the smallest trees (under 6 cm DBH), although such individuals can be more appropriately included in analysis of regeneration than tree mortality. Another interpretation can be found in species- and site-specific dynamics, as different mortality distributions have previously been reported for other species or forest types (e.g., *Fraxinus excelsior* L., *Picea abies*) (Holzwarth et al. 2013, Synek et al. 2020). The significant difference in size-class distribution of individual species in our study further supports the concept of species-specific patterns. Considering the differences between species and regions we assume the species-specific dynamics might be stronger driver than site conditions, provided the site conditions are appropriate for given species. The composition of different mortality agents for each species and/or stand may be a key consideration, as certain mortality modes are more frequent in particular size classes (Holzwarth et al. 2013). For example, more pronounced effect of competition in younger stands result in a different mortality distribution among size classes than what can be found in older stands with lower tree density, which indicates the importance of forest spatial structure (Das et al. 2008). In terms of basal area, however, the highest proportions of mortality can be found in size classes between 50 and 90 cm DBH. In other words, size classes which are still relatively abundant within the stands, with substantially high basal area per tree. The relatively short timeframe could have influenced the results as certain lower frequency disturbance events with expected higher impact on larger size classes might not occur during the observation period (Hurst et al. 2011). Although such bias should be, to certain extent, limited by high number of sample plots spread over a large area.

4.3. Mortality Agents

Our results demonstrate that competition is a very important driver of mortality in primary beech-dominated mixed stands during periods without high-severity, large-scale disturbances, although the variability among stands should not be neglected. The evident abundance of trees assigned to this mortality mode is further supported by the higher mortality among suppressed or lower layer trees, as suggested by the distribution of recently dead trees among DBH classes. The contribution of competition to total mortality is expected to be highest in the smallest size classes, however, while the portion of competition-related mortality is indeed highest in size classes up to 20 cm DBH, we are unable to confirm the monotonous decrease as the two smallest size classes each represent substantial and similar portion of cases. We can speculate that the most affected class is determined by certain lower and upper thresholds. Such result could be further validated when combined with data about mortality among seedlings and saplings. Competition as a mortality agent was less frequently recorded for *Picea abies* compared to other species and all data. The impact of competition in this case might be blurred by vulnerability of spruce trees to insect infestation when weakened.

Trees damaged by abiotic factors (crown or stem breakage or uprooted) accounted for roughly the same portion of all mortality as competition. Wind-damage is considered main form of disturbance in this type of forest (Splechtna et al. 2005, Nagel and Svoboda 2008). Ice-storms are another significant source of abiotically-caused damage, affecting the stands less frequently, but with high severity (Nagel et al. 2016). The exact composition of the three modes is similar across regions but varies among species suggesting vulnerability to above-ground structural failures is species-specific, likely linked to presence of fungi. Spruce trees exhibited less physical damage-related mortality in general. That can be perhaps attributed to the lower vulnerability of spruce trees to wind damage in relatively denser mixed stands, or just the common combination of less severe physical damage and insect infestation. The distribution of trees with broken crown was decreasing towards higher DBH classes, likely driven by smaller trees facing higher risk of being severely damaged by another falling tree (Woods 2004, Das et al. 2008, Holzwarth et al. 2013). Stem breaks have comparably higher shares spread over the larger size classes, probably because bigger trees, especially in case of broadleaves, must suffer massive damage to the crown to die while stem breakage (loss of most or all photosynthetically active parts) is just as lethal in all sizes. Unlike competition-related mortality, physical damage was found less often in the smallest size class than in the next one. Based on the similarity in relative prevalence of physical damage modes across subregions, abiotic factors in mixed stands are likely reflecting regional or even global conditions and are somewhat random within the region. Stand structure and time since last severe disturbance are factors that can influence abiotic-related mortality on finer scales (Čada et al. 2020, Schurman et al. 2018). The role of local topography (Senf and Seidl 2018) seems to be less pronounced in mixed stands compared to spruce stands in higher elevations. Given that abiotic factors represent a substantial share of mortality cases, our results suggest that the concern they are often overrepresented at the expense of intrinsic causes in mortality models (Das et al. 2016) might not always be relevant. The ratio between abiotic and intrinsic causes, however, can be altered by higher-severity disturbance events (e.g., windthrow or insect outbreak) (Allen et al. 2010, Sproull et al. 2015).

The role of insects as a mortality agent was rather low overall, however, bark beetle infestation was a major mortality agent for *Picea abies*. Considering the abundance of this tree species in our study stands and low mortality rates observed, we surely cannot talk about outbreak conditions. Our results support the findings from spruce stands in the region, reporting bark beetle infestation as a major mortality agent for *Picea abies* even in stands with low mortality and affecting trees in all size classes (Synek et al. 2020). The clustering of insect infested trees on certain plots is consistent with the general behavior of bark beetle (Wermelinger 2004). It is important to note that insects are often only part of the combination of agents inducing death of a given tree. The infestation can act as both contributing factor - just finishing the ongoing decline of the tree weakened by other means (e.g., by physical damage or competition); and inciting factor – making the tree more susceptible to another agent (e.g., fungi) (sensu Manion 1991).

We recorded a major impact of climatic extremes for a limited number of trees only. This may be attributed to our methodology, however, since the identification of such trees is difficult when another mortality agent is present. Climate in general is considered a predisposing mortality factor, whereas acute stress induced by climatic extremes (drought, frost) operates as an inciting factor with or without subsequent agent (sensu Manion 1991). We were only able to attribute extreme climatic conditions as an inciting factor when no other visible (subsequent) agent was present. Climatic data for our study stands indicate drought was affecting a majority of the stands during the period between samplings. Such evidence implies climate could have operated as predisposing factor in many cases of tree mortality, and the role of climatic extremes in our results may therefore be underestimated. Response to climatic change can be highly altered by changes in the disturbance regime in temperate forests (Seidl et al. 2011, Thom et al. 2017) and the impact of the specific climatic drivers can be affected by increasing temperatures (Schurman et al. 2019). Our findings suggest the important effects of shifts in temperatures and precipitation are indeed strongly influenced by other stand conditions (e.g., stand structure, disturbance history) (McDowell et al. 2020), and should be therefore considered in their context. Our approach cannot disentangle all possible climatic extremes, which include drought, frost, and temperature extremes, with reliable accuracy and therefore we pooled them into the broad "climatic extremes" category.

A substantial share of plots with a record of multiple mortality agents during the five-year resampling period further accentuates the complexity of mortality processes and simultaneous effects of different agents in primary forests. Some uncertainty in identification of the exact cause of mortality, especially for large dominant trees, remains. The often complicated determination of combinations of factors, differentiation of primary and secondary agents, and limits of evaluation of signs present in hardly visible and/or accessible parts of trees (e.g., high in the crown) are a major consideration (Das et al. 2016, Synek et al. 2020).

5. Conclusion

Our results indicate the low overall mortality rate in primary beech-dominated stands is well within the published range of background mortality. While the variability in mortality rates is not as high as for other forest types in the Carpathian region, it is still substantial. We have observed differences in mortality rates for individual species. These differences are likely driven by species-specific composition of mortality agents. Competition and abiotically caused physical damage are major mortality agents for *Fagus sylvatica*, while insect infestation is the most frequent mortality agent for *Picea abies*, even in stands with low overall mortality and relatively low abundance of the species. Species-specific relative prevalence of mortality agents is reflected in distribution of mortality along the DBH gradient, because particular mortality agents are more abundant in specific size classes. Our results suggest that high mortality rates observed in the region relate to specific forest types with their characteristic structure and species composition, which highlights the need for structural and compositional heterogeneity not only in primary forests. Despite the overall low mortality rate in mixed forests in the region the frequently observed drought situation in recent years deserves further consideration.

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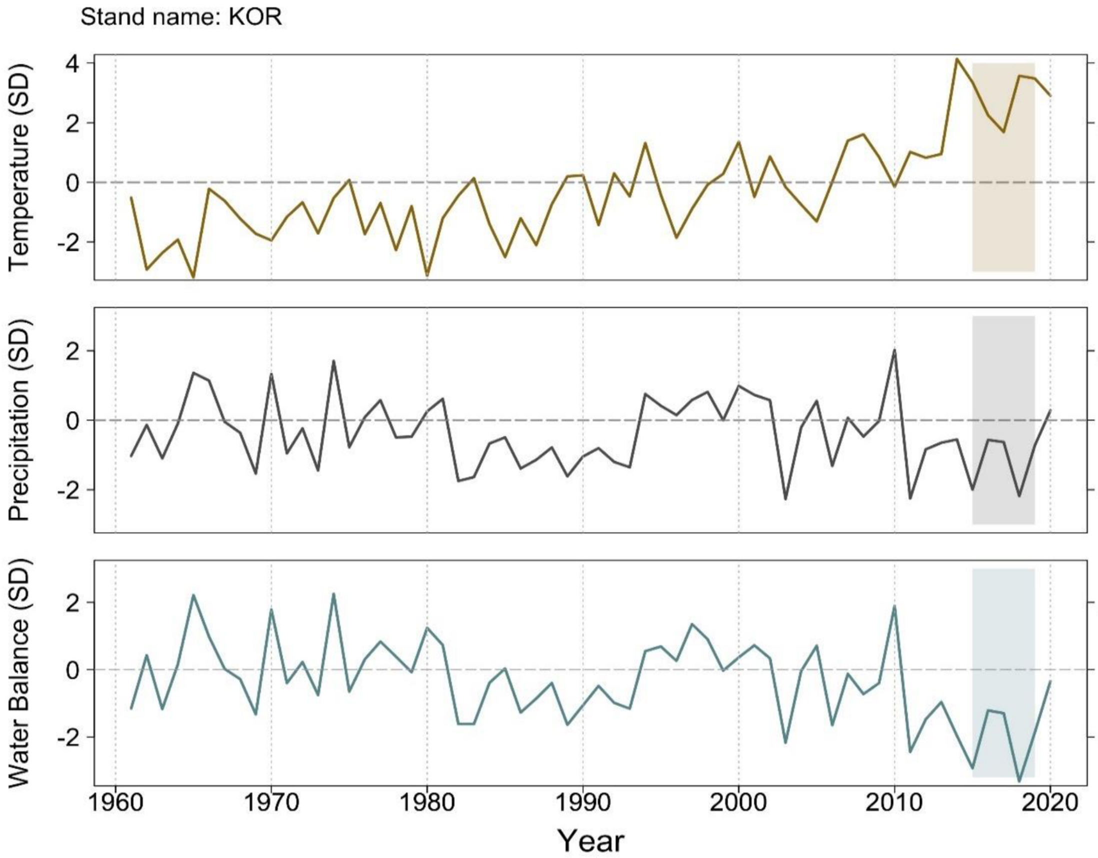
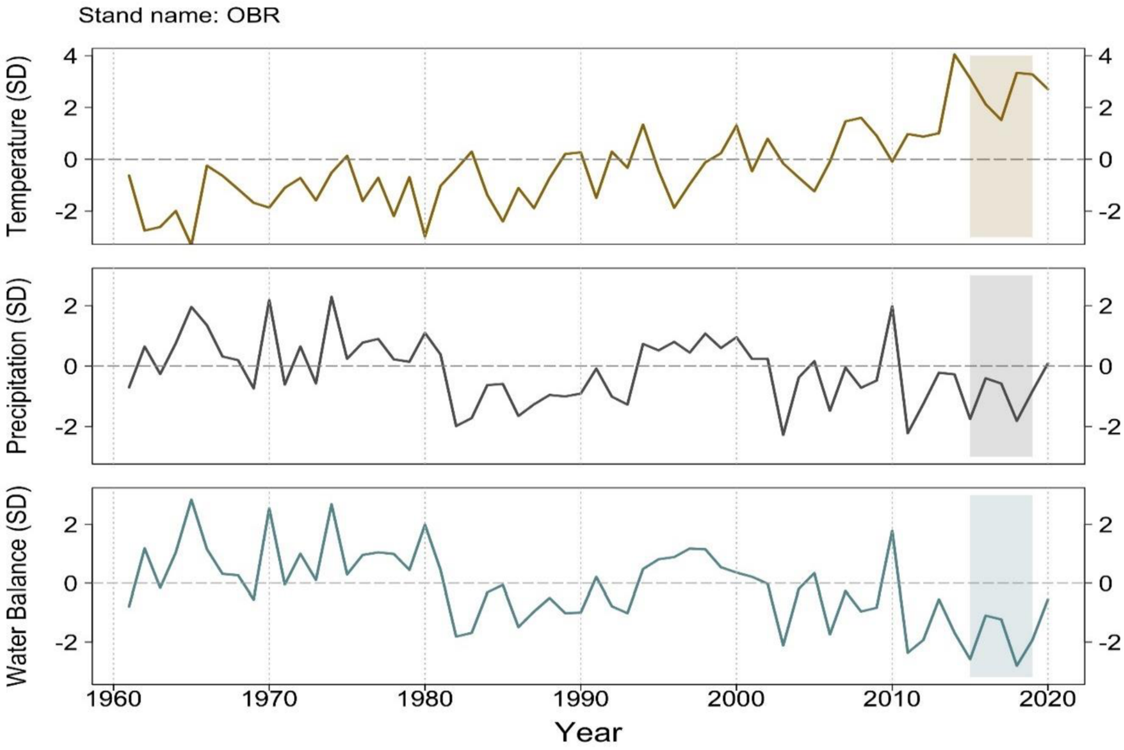
Appendix S1

Climatic conditions within study stands. Standard deviation (SD) of annual average temperature, precipitation and water balance (difference between precipitation and potential evapotranspiration) compared to mean values of the 1991-2010 reference period. The resampling period is shaded. Stands are listed by regions in order Western Carpathians, Eastern Carpathians and Southern Carpathians, within the regions the stands are listed in alphabetical order.

Western Carpathians

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2000
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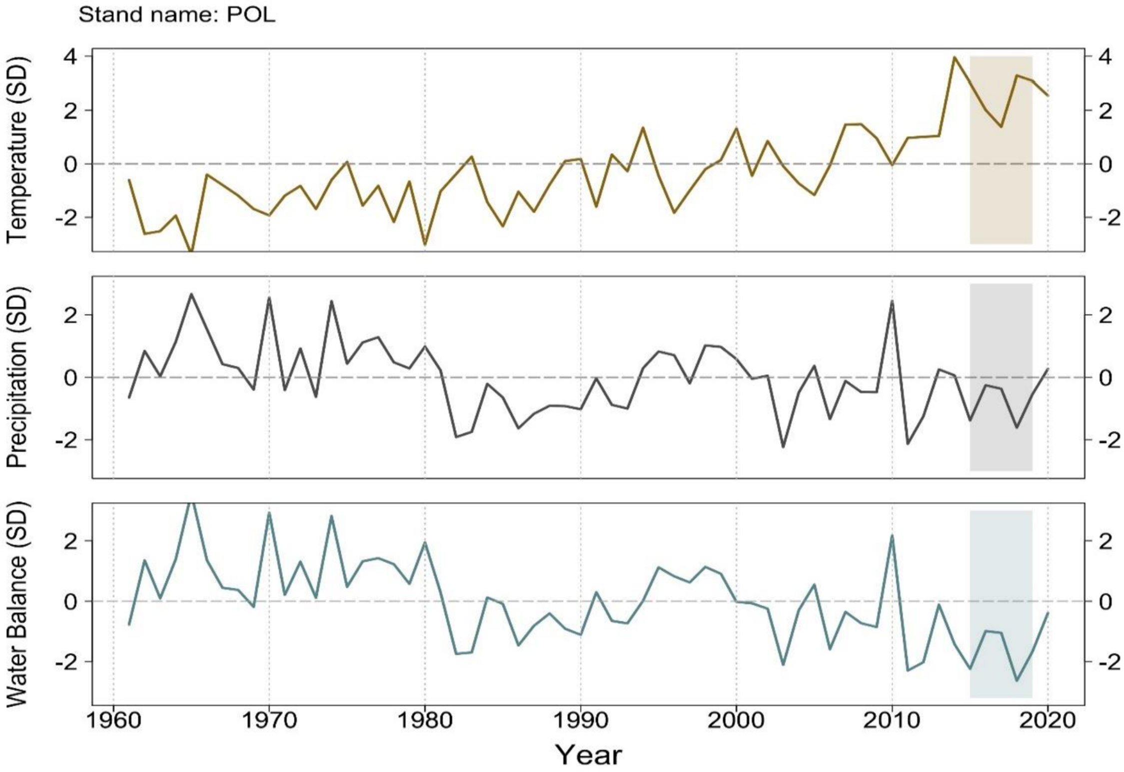
2020
Year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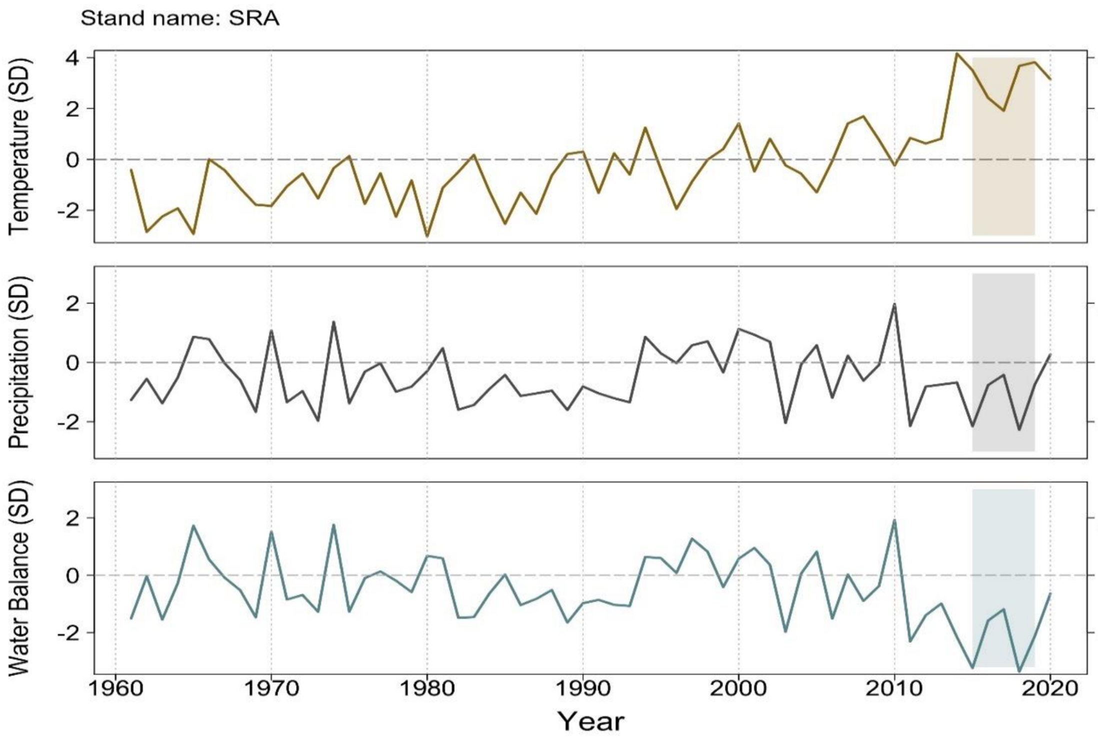
Year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0
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Precipitation (SD)
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Water Balance (SD)
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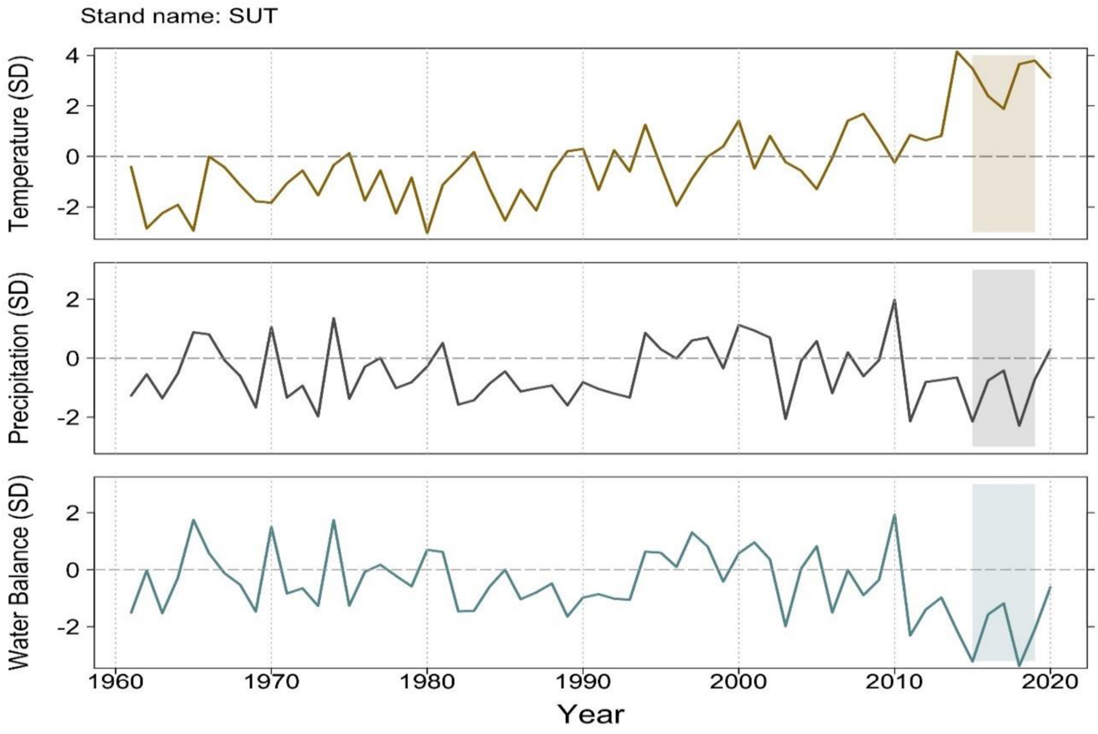
Year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Precipitation (SD)
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Water Balance (SD)
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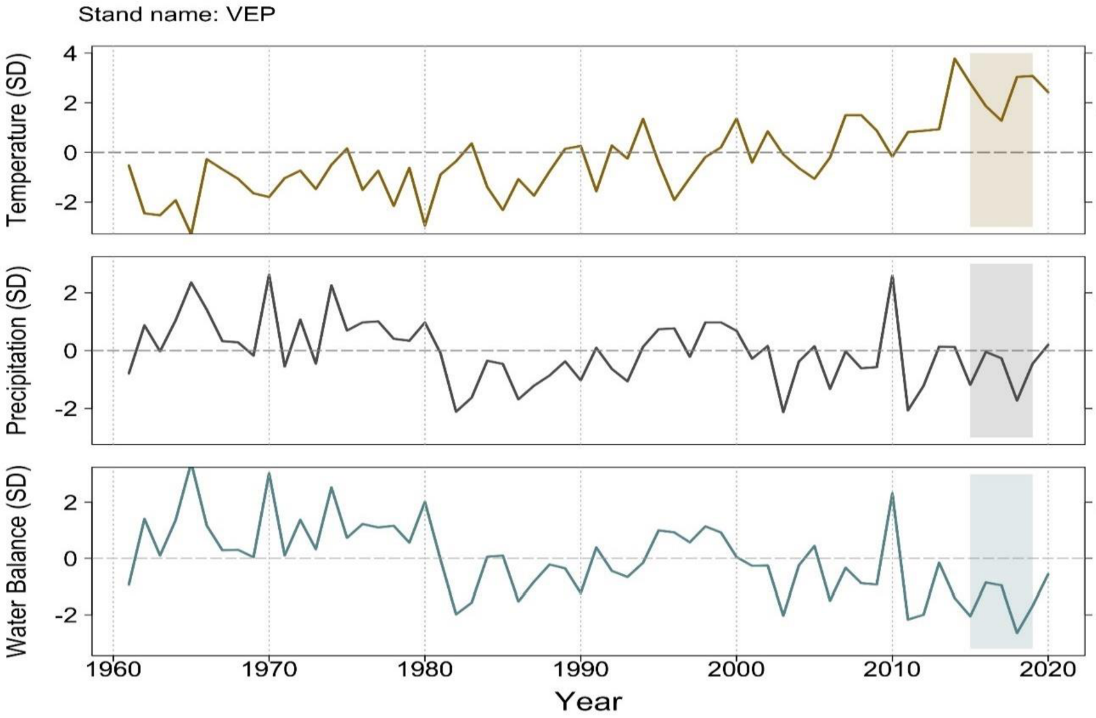
Year



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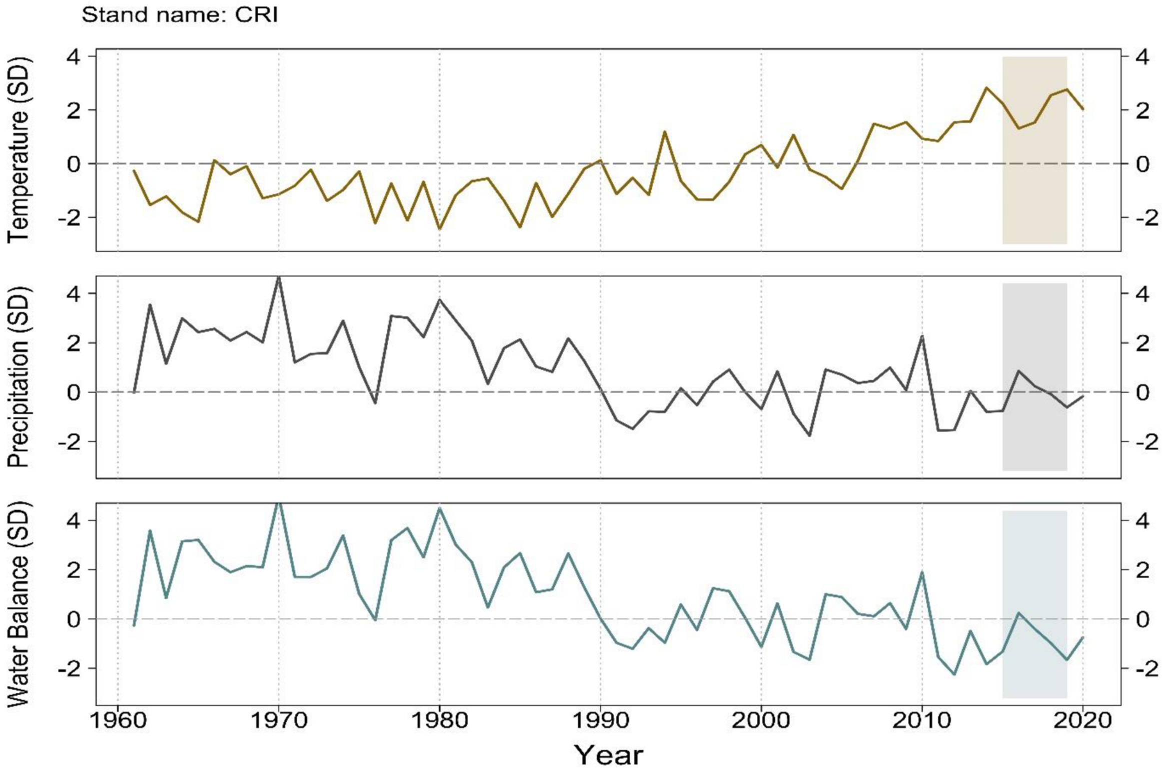

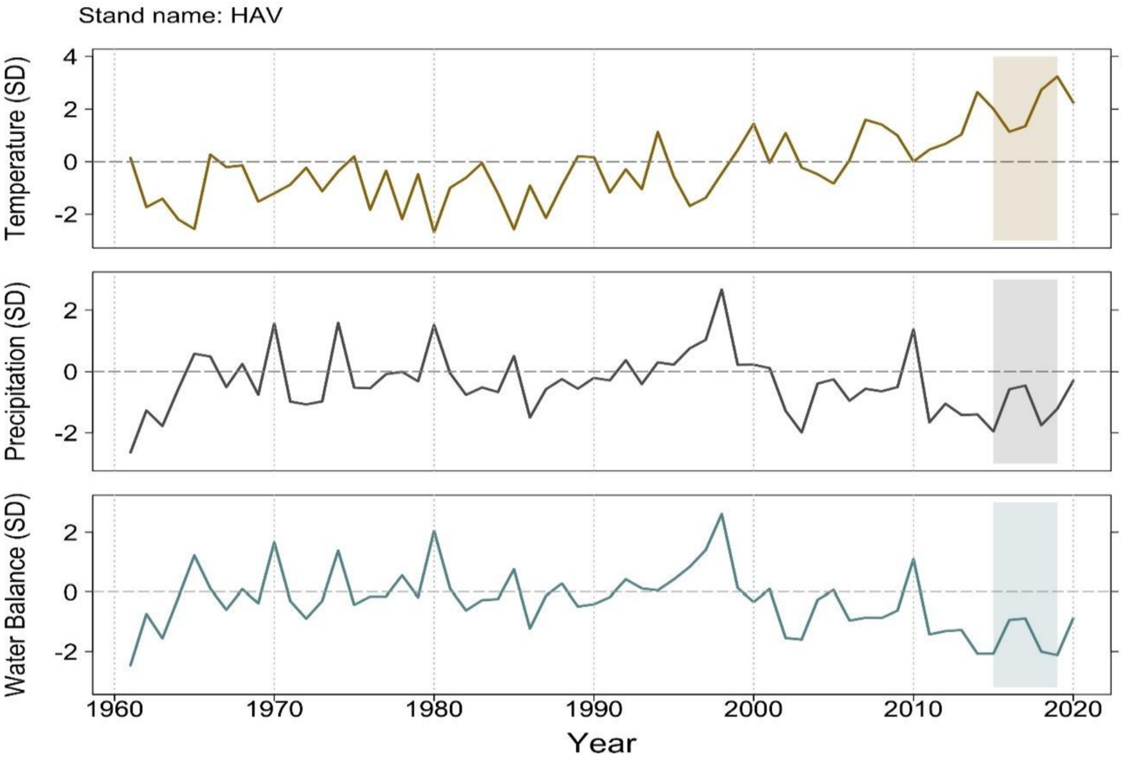
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Water Balance (SD)
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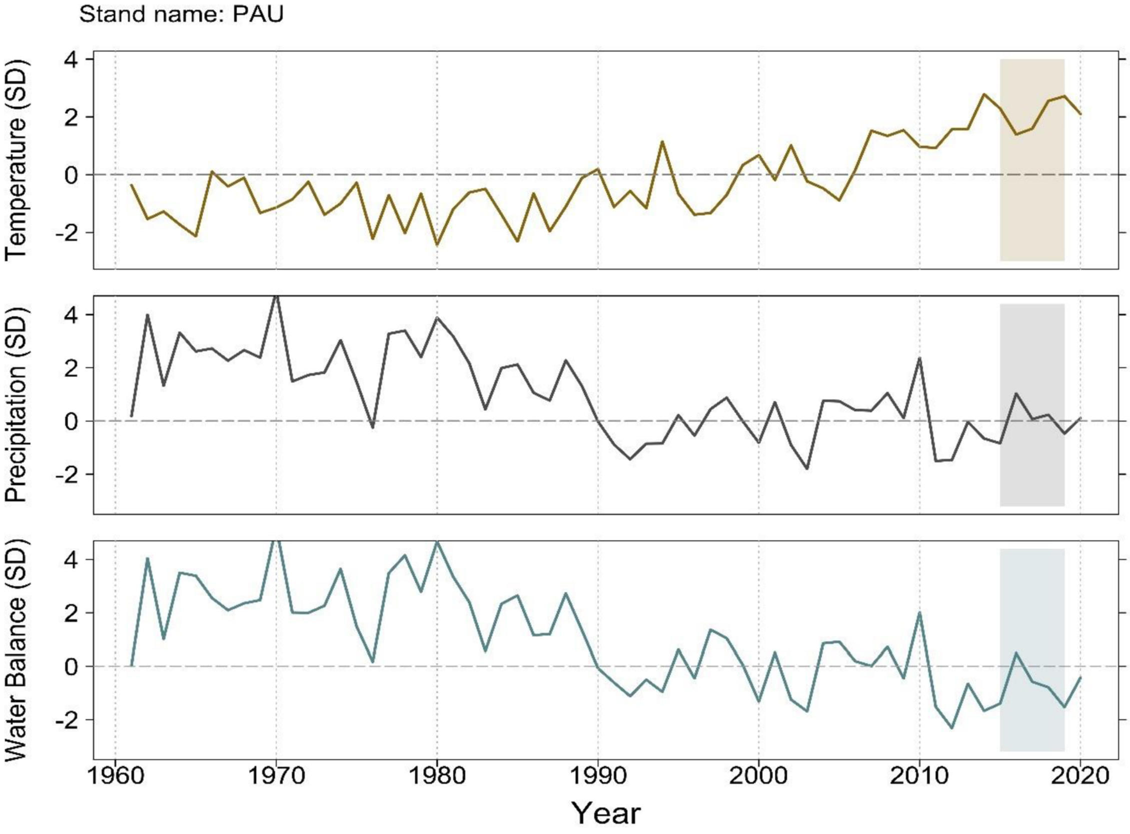
Year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Precipitation (SD)
Water Balance (SD)
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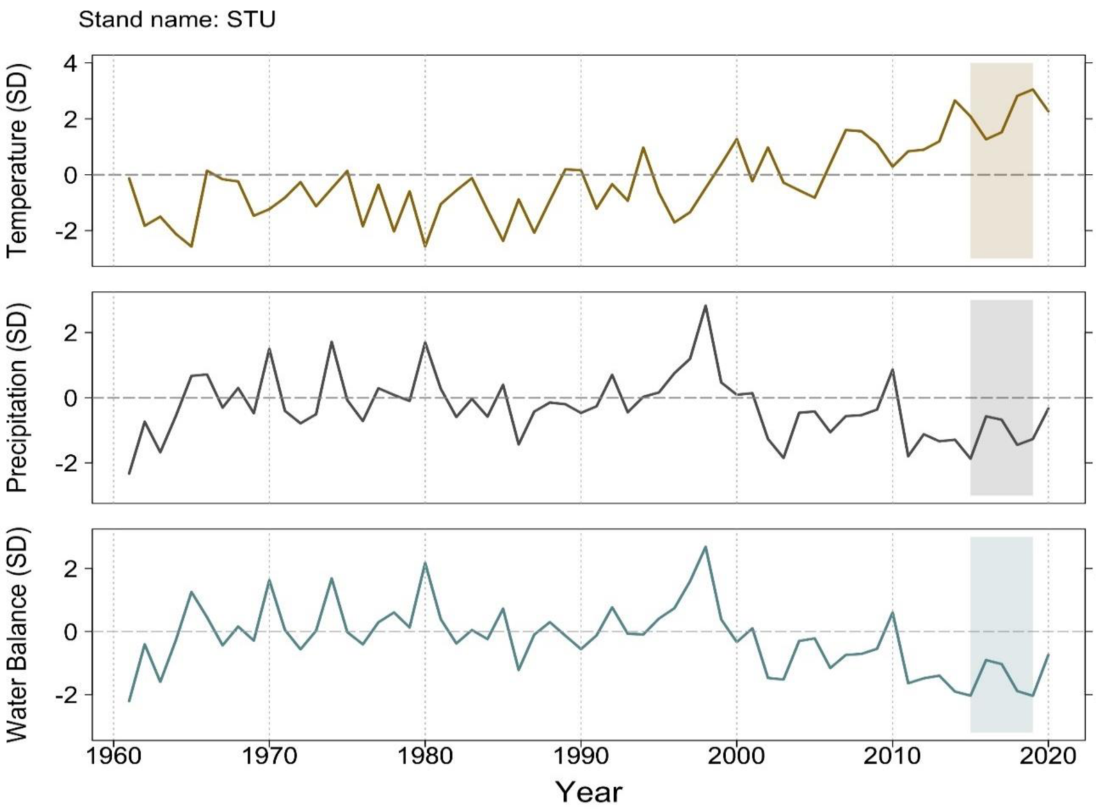
Year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Water Balance (SD)
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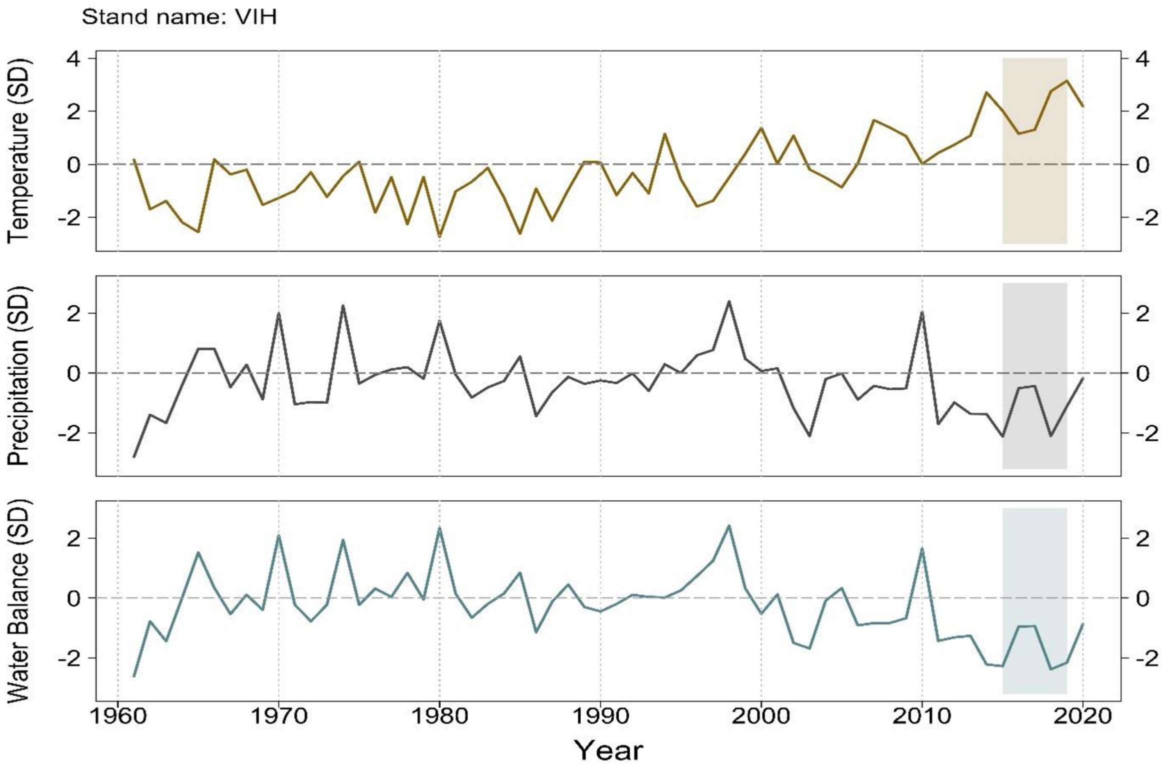
Year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Temperature (SD)
Precipitation (SD)
Water Balance (SD)
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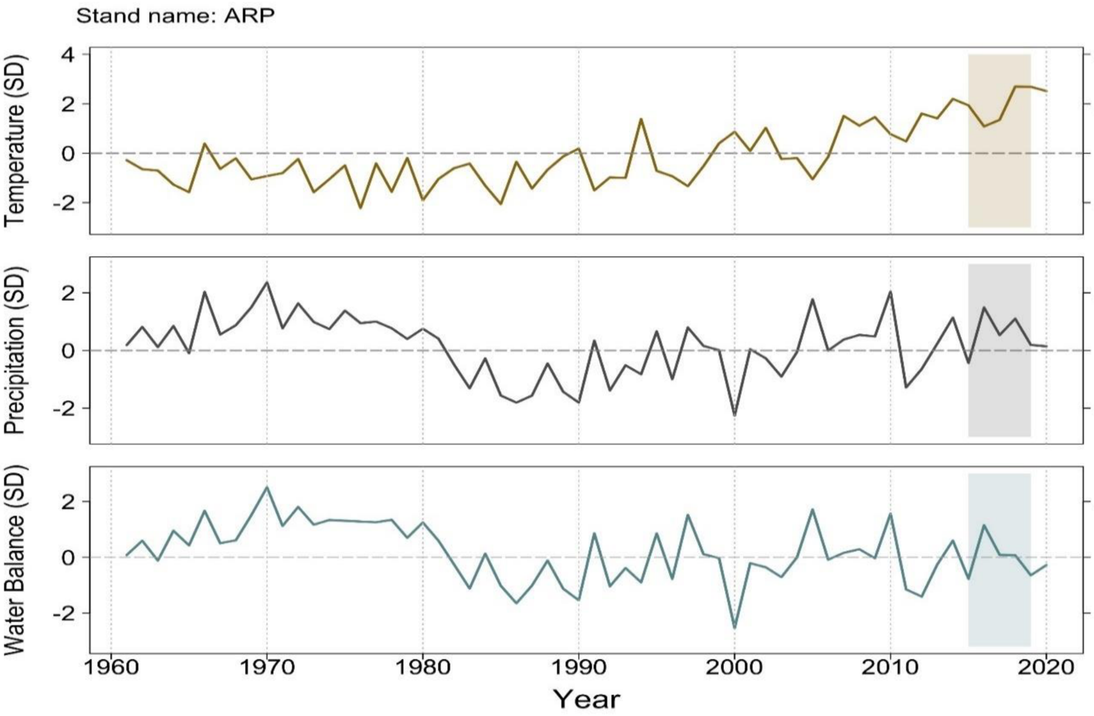
Year

Southern Carpathians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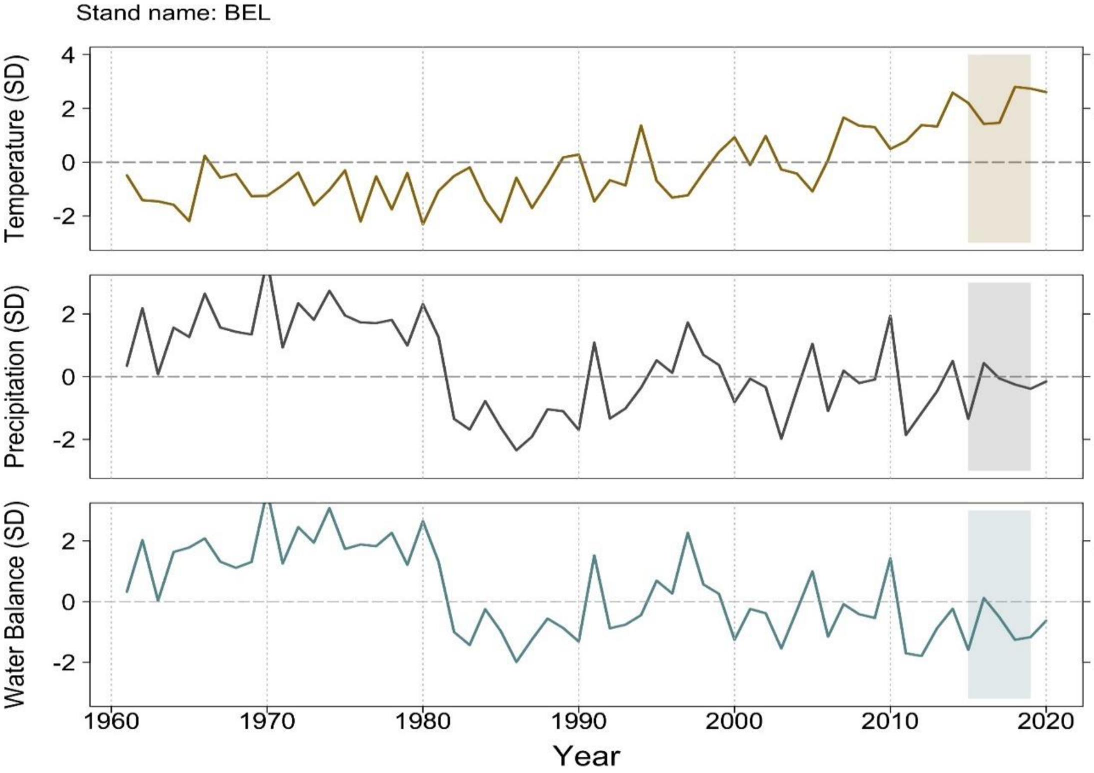
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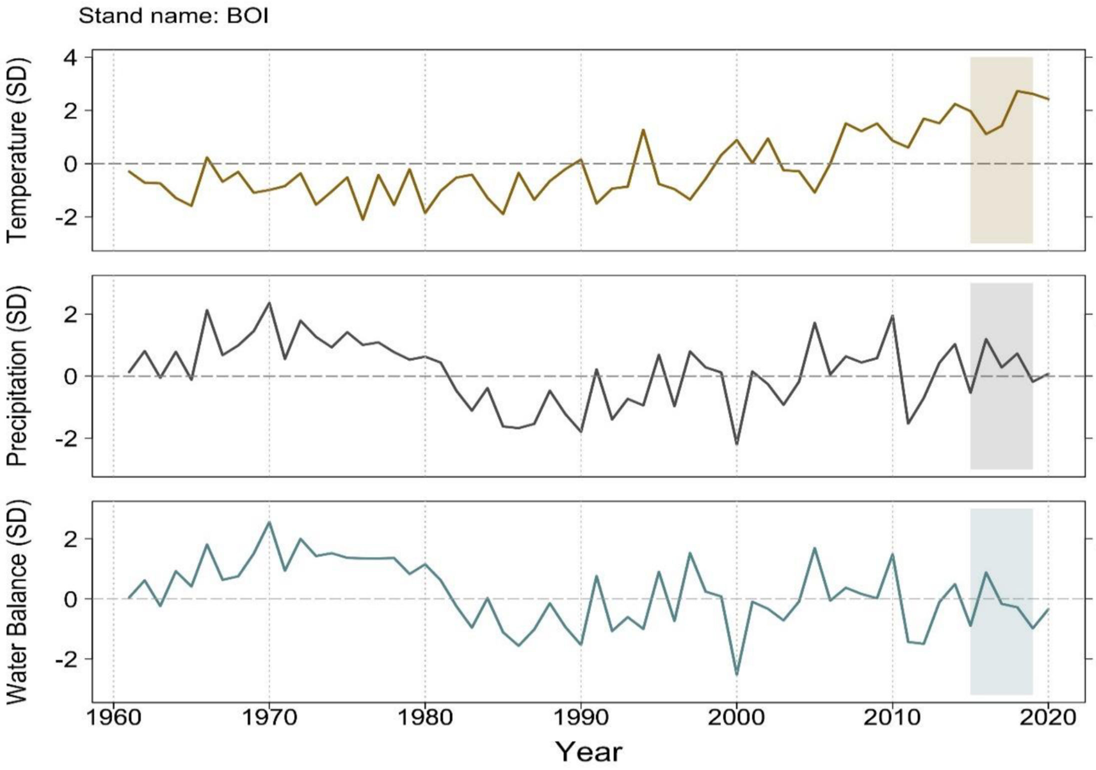
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Water Balance (SD)
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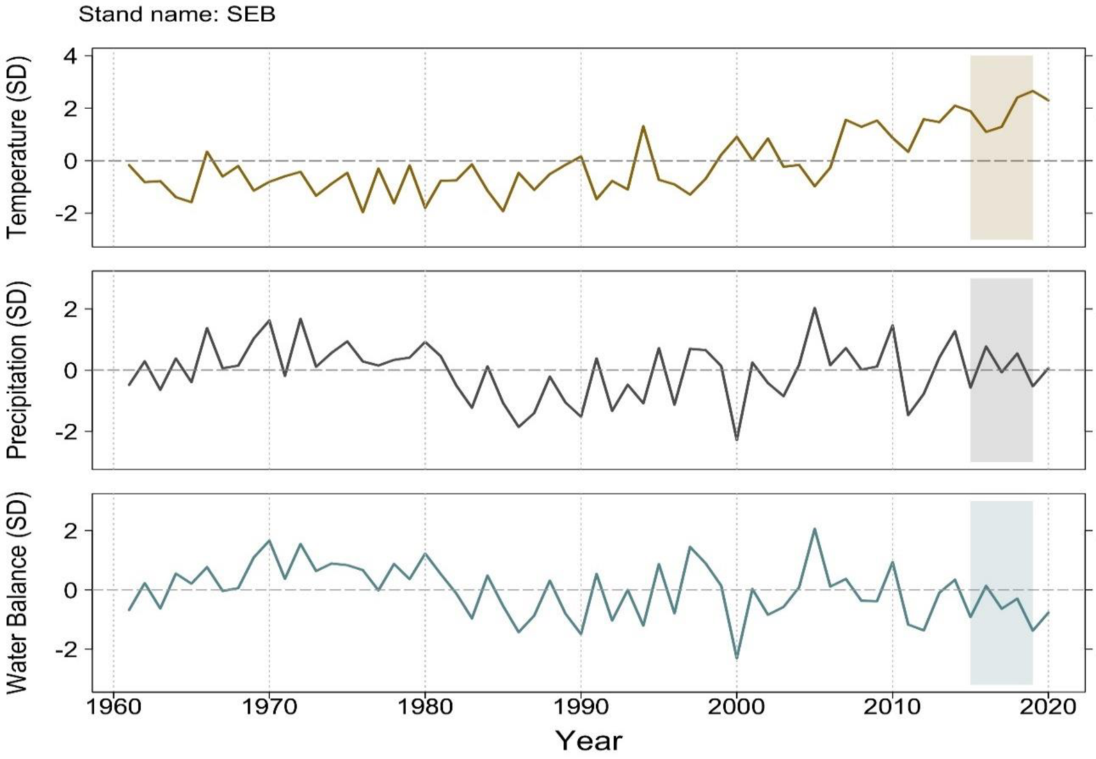
Year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Precipitation (SD)
Water Balance (SD)
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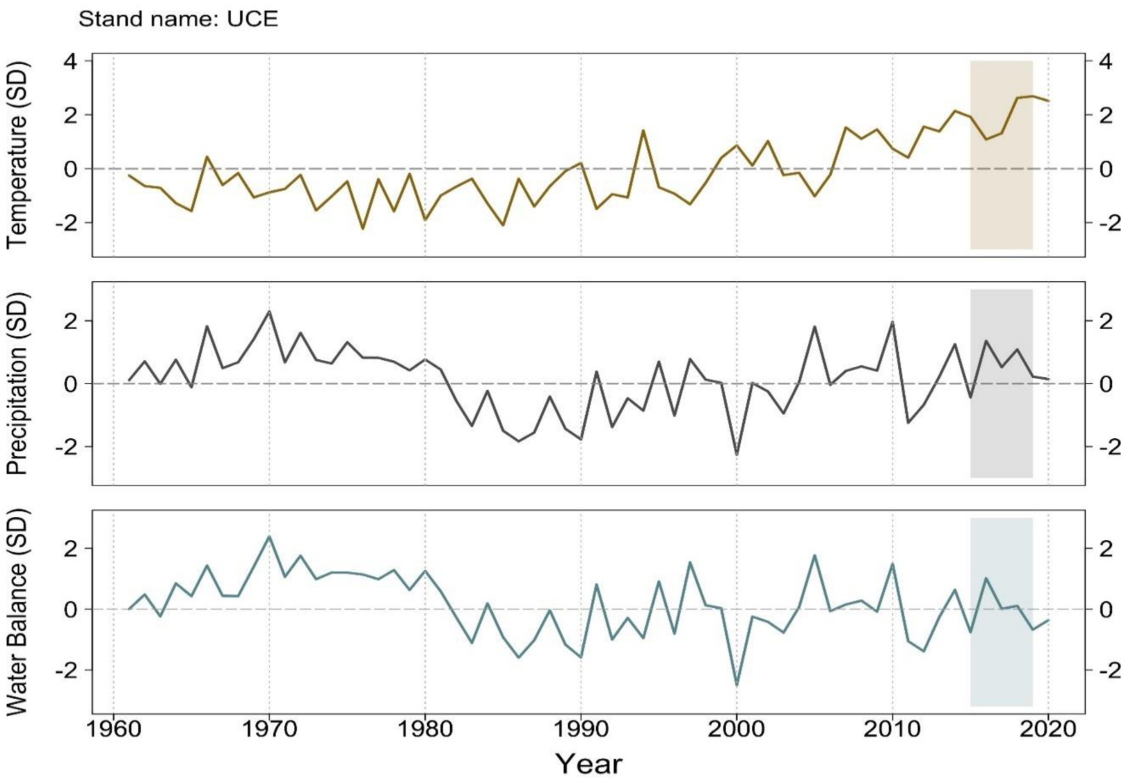
Year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Precipitation (SD)
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Water Balance (SD)
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5.4 Drivers of basal area variation across primary late-successional *Picea abies* forests of the Carpathian Mountains

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Drivers of basal area variation across primary late-successional *Picea abies* forests of the Carpathian Mountains

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ABSTRACT

Disentangling the importance of developmental vs. environmental drivers of variation in forest biomass is key to predicting the future of forest carbon sequestration. At coarse scales, forest biomass is likely to vary along major climatic and physiographic gradients. Natural disturbance occurs along these broad biophysical gradients, and depending on their extent, severity and frequency, could either amplify or dampen spatial heterogeneity in forest biomass. Here we evaluate spatial variation in the basal area of late-successional *Picea abies* (L./Karst.) forests across the Carpathian Mountain Range of central Europe and compare the roles of coarse-scale biophysical gradients and natural disturbances in driving that variation across a hierarchy of scales (landscapes, stands, and plots). We inventoried forest composition and structure, and reconstructed disturbance histories using tree cores collected from 472 plots nested within 30 late-successional stands, spanning the Carpathian Mountains (approximately 4.5 degrees of latitude). We used linear mixed-effects models to compare the effect of disturbance regimes and site conditions on stand basal area at three hierarchical scales. We found that the basal area of late-successional *Picea abies* forests varied across a range of spatial scales, with climatic drivers being most important at coarse scales and natural disturbances acting as the primary driver of forest heterogeneity at fine scales. For instance, the stand-level basal area varied among landscapes, with the highest values (48–68 $m^2\ ha^{-1}$) in the warmer southern Carpathian Mountains, and lower values (37–52 $m^2\ ha^{-1}$ on average) in cooler areas of the eastern and western Carpathians. Finer-scale variation was driven by local disturbances (mainly bark beetle and windstorms) and the legacies of disturbances that occurred more than a century ago. Our findings suggest that warming could increase the basal area of northern sites, but potential increasing disturbances could disrupt these environmental responses.

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1. Introduction

Forests play a key role in the global carbon cycle due to their high carbon storage capacity (Yang et al., 2011, Pan et al., 2013). The amount of carbon stored in forest biomass varies across a range of spatial scales (Hernández-Stefanoni et al., 2011, Schietti et al., 2016), reflecting differences in site conditions, species composition, and disturbance regimes (Frelich, 2002, Chapin et al., 2006). Disentangling the drivers of spatial variation in forest biomass is important for evaluating the future of the forest biomass sink (Pan et al., 2013), especially quantifying the proportions of terrestrial uptake due to developmental increases in forest biomass or responses to environmental change (e.g., Pastor and Post, 1988, Pacala et al., 2001, Seidl et al., 2014).

Forest biomass varies greatly among forest regions, primarily due to climatic effects on growth rates and potential tree size (Keith et al., 2009). On average, forest biomass tends to increase towards the equator, due in part to a longer growing season and greater precipitation; the most important exception to this trend being the extremely high biomass of cool-temperate rainforests (Keeling and Philips, 2007). Studies of forest structure along latitudinal gradients within forest regions can therefore inform our understanding of how present patterns in climate-driven variation may change under a warming climate (De Frenne et al., 2013). Despite clear climate-driven differences in biomass among forest regions, intraregional differences associated with stand age, or the time since a severe disturbance, can be larger than differences along climatic gradients (Pregitzer and Euskirchen, 2004). The relative importance of environmental factors vs. disturbance will depend largely on the dimensions characterizing disturbance regimes, including disturbance frequency and severity.

The Carpathian Mountains of central Europe represent one of the largest forested regions of the continent with relatively large tracts of unmanaged forests (Oszlányi et al., 2004, Sabatini et al., 2018). Yet, the natural variation in forest dynamics, and consequently biomass, across this region remains poorly understood. In natural mountain *Picea abies* forests, the dominant high-elevation forest type of the Carpathian Mountains, the disturbance regime is typically characterized as mixed-severity (a wide range of severities is evident in the disturbance regimes of our studied stands) (Trotsiuk et al., 2014, Janda et al., 2017, Svoboda et al., 2014, Schurman et al., 2018). Windstorms and bark beetles are the primary natural disturbance agents, and disturbances typically recur at relatively short intervals (years to decades) and cause tree mortality at relatively small scales (< 1 ha), although larger events with low frequency of 10 s to 100 s of hectares have also been documented (Svoboda et al., 2014, Janda et al., 2017, Čada et al., 2016).

In the *Picea abies* forests along the Carpathians, disturbances commonly alter forest structure at the scale of 0.1-ha plots (Meigs et al., 2017), with occasional instances of larger scale events synchronizing forest structure and successional dynamics over larger areas (Schurman et al., 2018). Recognition that large-scale disturbance is a major constraint on forest biomass has increased, especially in cases where increased disturbance severity has been linked to managerial practices (Kurz et al., 2008, Seidl et al., 2014). However, the understanding of how scale-dependence of natural disturbances acts as a driver of biomass variation in primary forest landscapes has received little emphasis, largely because opportunities to do so are rare.

Extensive and severe disturbances in recent years have resulted in widespread mortality in spruce forests of the Western part of the Carpathians Mountains (Mezei et al., 2014, Nikolov et al., 2014) and the Bavarian Forest (Kautz et al., 2011). These recent events may reflect two important factors that could be making spruce forests increasingly prone to disturbance. First, climate change is increasing tree stress, especially in times of extended drought (Raffa et al., 2008, Solberg et al., 2004), making the forests more susceptible to spruce beetle outbreaks (Rouault et al., 2006). For instance, radial growth of *Picea abies* trees in unmanaged (i.e., primary) forests is mostly temperature dependent (Primicia et al., 2015), and forests in part of the region have been affected by recent drought (Schurman et al., 2018, Senf and Seidl, 2018). Second, temporally synchronous disturbances in the past promoted uniformity in tree size and forest age structure, which could predispose portions of the landscape to the extensive disturbances that have occurred in recent years (Janda et al., 2017, Schurman et al., 2018).

The scale over which disturbance and environmental gradients drive variation of biomass will have a large effect on the likelihood of accurately detecting the role of each driver. For example, in general, where disturbances are small relative to landscape extent and relatively infrequent, the live aboveground forest biomass is likely to oscillate specifically around a stable mean value (Turner et al., 1993). If disturbance dynamics are stable along broadly distributed environmental gradients, the likelihood of detecting environmental effects increases (Halpin and Lorimer, 2016). On the other hand, if biophysical gradients are steep or if severe disturbances are too frequent for landscape dynamics to stabilize, increasing the spatial extent of the analysis will lead to higher variability of site conditions and topography (Quesada et al., 2012; Zald et al., 2016), potentially precluding stable conditions even at broad spatial scales. Thus, forest biomass dynamics are best understood when spurious anthropogenic effects can be controlled, but these forests are very rare in central Europe. A better understanding of the natural variation in forest biomass within *Picea abies* forests of central Europe and the drivers of that variation may provide insight into likely future development, and a benchmark for measuring future changes.

Our objective was to determine how forest basal area varies across a range of spatial scales, using forest basal area or diameter at breast height, a commonly used parameter for biomass estimation (Wirth et al., 2004; Zianis et al., 2005). Focusing on a monospecific primary *Picea abies* forests (unmanaged forests, where *Picea abies* typically accounts for > 90% of overstory basal area) enabled us to disentangle the roles of biophysical environments and natural disturbances while minimizing the roles of varying species composition and species-specific responses to disturbances. We propose the following hypotheses concerning variation in late-successional forest basal area across hierarchical spatial scales: (a) at coarse scales, variation in forest biomass among landscapes and stands is primarily driven by broad factors linked to the biophysical environment, such as climate and topography; (b) at finer scales (among the plots within each stand), differences in biomass are primarily driven by local disturbances. We propose an alternative hypothesis where disturbance regimes and environmental characteristics operate at both fine and coarse scales, with varying scale dependence specific to each bioclimatic zone considered in this study.

2. Material and methods

2.1. Study area

The study was conducted in primary temperate *Picea abies* forests of the Carpathian Mountain Range of central Europe (Fig. 1, Table 1), spanning portions of Slovakia, Ukraine, and Northern and Southern Romania. Selection of primary forests in these countries was based on the methods described in Sup. X1. We combined datasets that were previously only evaluated at plot and stand scales (Trotsiuk et al., 2014; Svoboda et al., 2014; Janda et al., 2017), where the field sampling procedures are summarized in the project REMOTE (Remote Primary Forest, 2018). From these study areas, 30 late-successional stands (age over 90 years, Table 1) were selected. Only stands without severe recent disturbances were selected from the total number of 34 stands belonging to the project REMOTE.

The Carpathian Mountains are unique among European forest regions because of their well-preserved primary forests (Oszlányi et al., 2004; Sabatini et al., 2018), which we define as forests that have not been directly altered by human management for at least the last century. In most cases, the primary forests have remained unmanaged due to difficulty of access. These unmanaged forests are not necessarily in

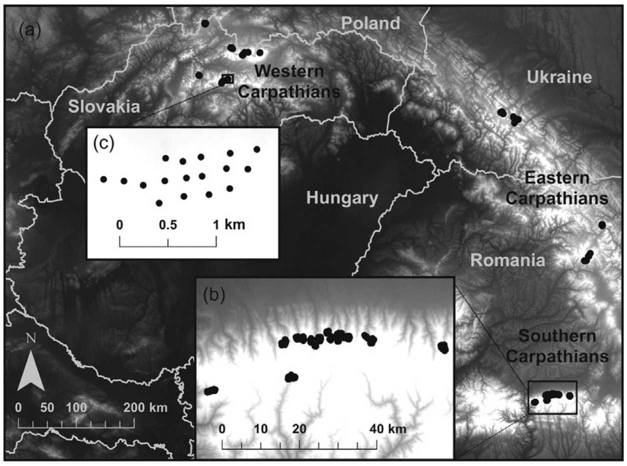

Fig. 1. Hierarchical distribution of permanent study plots (black dots) at landscape (a), between stand (b) and within stand scales (c). The landscape is divided into three landscapes in the Carpathian mountain range (Western Carpathians, Eastern Carpathians and Southern Carpathians; see Table 1).

an advanced developmental phase because some of them may have been affected by recent natural disturbances (primarily by wind and the European spruce bark beetle; *Ips typographus*) that caused tree mortality at scales ranging from individual trees to dozens or even hundreds of hectares (Mueller et al., 2008; Svoboda et al., 2014; Čada et al., 2016).

Natural forests of the Carpathian Mountains are dominated by Norway spruce (*Picea abies*) at upper elevations (above ca. 1200 m) and European beech (*Fagus sylvatica*) at lower elevations. We limited this study to the upper-elevation forests where *Picea abies* typically accounts for > 90% of overstory basal area (Tjoelker et al., 2007). Additional tree species include silver fir (*Abies alba* Mill.), Scots pine (*Pinus sylvestris*), rowan (*Sorbus aucuparia* L.), European beech, and birch (*Betula* spp.).

2.2. Field methods

We used a hierarchical sampling framework to characterize spatial variation in forest basal area across the *Picea abies*-dominated primary forests of the Carpathian Mountains. First, we divided the mountain range into three landscapes—Western, Eastern, and Southern Carpathians—that roughly correspond to major clusters of primary forest stands that we identified in Slovakia, Ukraine, and Romania, respectively (Fig. 1, Table 1). Sampling was conducted in a total of 8 stands in the Northern Carpathians, 10 in the Eastern Carpathians, and 12 in the Southern Carpathians. Within each stand, we established a series of Permanent Sample Plots (PSPs, 1000-m^2 circular plot or 500 m^2 in recently disturbed plots with high stem density) using a stratified random design. The sampling design was determined by laying a grid over each area with cell sizes of either one or two hectares depending on total stand area. Within the interior (0.25 ha or 0.49 ha, respectively) of each cell one PSP was randomly placed. In all, 472 PSPs were sampled, representing an average of 16 plots per stand.

Within each PSP, we measured environmental characteristics (elevation, slope, and aspect) and the composition and structure of live and standing dead trees. For each live tree ≥10 cm diameter at breast height (DBH), we recorded DBH and canopy status (suppressed vs. non-suppressed, depending on whether at least half of the crown area was exposed to full sunlight). For each standing dead tree, we sampled DBH and classified its decay status into one of the following classes: 1 = recently dead with fine twigs and needles present; 2 = recently dead and lacking fine twigs or needles; 3 = only large branches (first and second order) present; 4 = main stem broken, only a few of the largest branches present; and 5 = main stem broken and decayed, total height < 2 m.

In order to understand the contribution of disturbances to plot-level

Table 1
Stand characteristics.

Landscape	Country (Locality)	Stand	No. of plots	Mean elevation (m a.s.l.)	Mean basal area of living trees (m^2/ha)	Mean basal area of dead trees (m^2/ha)	Mean tree density (N/ha)	Mean dbh (cm)	Mean age (year)
Southern Carpathians	Southern Romania	Fagarash 1	12	1496	53.63	9.8	603	32.67	141
		Fagarash 2	12	1426	56.82	5.45	603	34.23	137
		Fagarash 3	12	1460	59.54	6.28	546	34.48	146
		Fagarash 4	12	1458	53.24	6.23	490	35.66	146
		Fagarash 5	14	1450	56.92	7.8	682	31.94	135
		Fagarash 6	12	1516	48.85	7.27	434	36.18	154
		Fagarash 7	12	1477	55.61	6.17	520	36.4	142
		Fagarash 8	11	1465	52.16	4.88	519	32.46	105
		Fagarash 9	12	1574	68.11	5.29	657	34.53	96
		Fagarash 10	12	1505	57.85	4.01	613	32.81	124
Eastern Carpathians	Northern Romania	Calimani 1	20	1590	51.48	6.7	603	31.88	117
		Calimani 2	20	1565	51.03	7.19	591	32.6	110
		Calimani 3	21	1567	51.51	7.01	529	34.5	125
		Giumalau 1	29	1406	41.55	8.19	427	32.19	127
		Giumalau 2	29	1432	46.28	10.42	507	32.81	118
		Giumalau 3	23	1451	47.73	10.93	473	34.11	132
	Ukraine	Grofa 1	19	1379	38.5	8.45	451	31.76	127
		Grofa 2	15	1355	40.66	6.39	423	32.21	155
		Grofa 3	15	1321	45.61	8.26	681	28.57	149
		Syvulya 1	20	1426	42.01	6.38	659	26.68	173
		Syvulya 2	15	1355	41.53	6.28	513	30.15	141
		Syvulya 3	15	1298	40.51	6.85	633	27.21	140
Western Carpathians	Slovakia	Bystra	16	1410	37.12	14.47	376	36.29	126
		Dumbier	17	1495	51.76	10.13	483	37.11	156
		Hlinna	16	1433	46.09	12.34	494	34.57	124
		Javorova	8	1439	43.63	13.11	494	33.49	179
		Osobita	14	1363	47.7	7.01	389	39.21	157
		Pilsko	12	1329	41.4	14.82	273	45.34	168
		Smrekovica	11	1386	42.22	7.57	265	44.11	140
		Ticha	16	1414	40.58	13.67	568	30.24	97

heterogeneity in basal area, we developed chronologies of inferred canopy disturbance (sensu Frelich and Lorimer, 1991) using information on projected tree crown area and initial tree radial growth rates. We recorded crown width in four cardinal directions for five randomly selected trees per plot in order to determine the relationship between DBH and projected tree crown area at each locality (see Table 1). This relationship enables us to estimate the extent of canopy area disturbed in the past under the assumption that the present canopy area of trees is approximately equal to the extent of canopy area removed during the disturbance they were released by (see next section). To identify trees with synchronous recruitment or growth release under canopy gaps, we collected an increment core from 25 trees randomly selected non-suppressed trees ≥10 cm DBH in each 1000-m^2 plot (or 15 trees per plot in the more recently disturbed 500-m^2 plots that were more homogeneous in forest structure and tree ages). Each increment core was collected 1 m above the soil surface.

2.3. Data analysis

To quantify the role of disturbance in driving variability of forest structure, we developed chronologies of inferred canopy disturbances by first classifying the non-suppressed trees as having one of two modes of recruitment to the forest canopy: (1) open canopy recruitment—trees that initiated under relatively open conditions shortly after a canopy-opening disturbance event as indicated by rapid initial growth, or (2) release—trees that established in the shaded understory and recruited to the canopy through one or more canopy gaps, as evidenced by slow initial growth followed by an abrupt growth release (Frelich and Lorimer, 1991). To analyse disturbance events, a total of 11,727 increment cores were crossdated following the list-year method of Yamaguchi (1991). Tree rings were measured to the nearest 0.01 mm using a LintabTM sliding-stage measuring system (Rinntech, Heidelberg, Germany), and the crossdating was verified using COFECHA (Holmes, 1983). For cores that did not intersect the pith, we estimated the number of years to the pith following the geometric method of Duncan (1989).

Trees that had open canopy recruitment were detected by tree juvenile growth rates following Trotsiuk et al. (2014). We set growth thresholds to distinguish seedlings that established under an open canopy from seedlings that were initially suppressed based on growth rates of two groups of saplings that we previously sampled in a subset of the plots used in this study: one group was suppressed beneath the forest canopy and the other was found in canopy openings (Svoboda et al., 2014; Fraver and White, 2005). Thresholds were calculated using logistic regression and the intersection of specificity (an expression of the likelihood of false negatives) and sensitivity (likelihood of false positives) (Hosmer and Lemeshow, 2000). Based on a previous evaluation of juvenile growth rates over the last three centuries, such thresholds have been shown to distinguish between seedlings that recruited beneath a canopy over our entire analysis period (Janda et al., 2014).

For growth release detection, we used the absolute increase method (Fraver and White, 2005). The method identifies pronounced changes in growth rates by first compiling 10-year running means of radial growth for each tree. We then defined growth releases as instances when the difference between successive 10-year means was more than 1.25 standard deviations (approximately 90% of variability) above the mean for the tree. To avoid short-term growth fluctuations, we only included growth releases when the post-release ring widths continued to exceed the pre-event 10-year running mean for at least seven years (Fraver et al., 2009). Because *Picea abies* is moderately shade-tolerant (Tjoelker et al., 2007), especially as a juvenile, multiple disturbances are sometimes required for the trees to reach the canopy. We therefore allowed multiple canopy accessions in the disturbance chronologies. However, because we were explicitly interested in disturbances that lead to canopy recruitment of understory individuals, we did not continue to identify crown release in individuals after they reached a DBH threshold of 23 cm (determined using a logistic regression of canopy status as a function of DBH in present tree inventory data; see Schurman et al., 2018) indicating that the individual had already reached canopy status at the time of release (Lorimer and Frelich, 1989).

The growth releases and gap recruitment events were converted to chronologies representing the canopy area disturbed over time following Lorimer and Frelich (1989). This approach assumes that the sum of the current crown area of trees that recruited into a canopy opening approximates the extent of the canopy opening that enabled their recruitment. We estimated the current crown area of each tree using our regression of crown width measurements as they relate to DBH at each locality (see Table 1). We then combined these crown area estimates with information on the timing of disturbances (growth release dates for initially suppressed seedlings or the timing of establishment for trees showing open-canopy recruitment) to develop a chronology of the inferred canopy area disturbed over time in each plot.

To account for the potential of prolonged tree recruitment in large canopy gaps, we compiled chronologies using a three-decade running sum of canopy area disturbed in each plot. This procedure smooths out high-frequency variation in canopy accession dates when individuals were likely released by the same events and further emphasizes the most severe disturbance events (Svoboda et al., 2014, Janda et al., 2017). After smoothing, we identified the most severe disturbance event per plot (i.e., the event with the largest canopy area disturbed) by dividing the estimated amount of canopy area removed by the present canopy area of the plot. Present canopy area was the sum of all extant living trees as estimated using the same allometric conversion detailed earlier. In plots that were very recently disturbed, we could not infer severity from crown area and modes of recruitment for regenerating seedlings (i.e., gap release vs. open-grown). Thus, we assessed the severity of the recent disturbances using the percentage of estimated canopy area of recently dead trees (decay classes 1–3). If the percentage of canopy area of recently dead trees was higher than the most severe historical event on an individual plot, the recent event was accepted as the most severe disturbance event of the plot.

The drivers of spatial variation in forest structure are theoretically well described, but could play out over different scales in different geographical contexts, ultimately affecting the relative magnitudes of small-scale variability (within-stands) and large scale variability (among broadly distributed stands). We expect forest biomass to differ along climatic gradients, due to expected temperature effects on ecophysiological processes (Primicia et al., 2015). Prior research in the Carpathians suggests that frequent, small- to medium-scale disturbances have contributed substantially to variation within stands (Meigs et al., 2017), while other evidence suggests that climate could synchronize forest structure across large areas (Schurman et al., 2018). Furthermore, other disturbance analyses have found that density-dependent processes (e.g., thinning of post-disturbance cohorts) could promote uniformity in stand structure, provided environmental conditions do not change (Kashian et al., 2005). We therefore tested a number of model structures, that each make different *a priori* assumptions about the scales at which different factors could influence forest biomass.

We used several explanatory variables to describe the disturbance regime of each plot: the date and severity of its most severe disturbance event and the basal area of all dead standing trees, which enables us to infer relative differences in tree mortality rates (fixed effect). Site conditions were represented by geographical gradients described by longitude and latitude combined with altitude and northness (fixed effect). Aspect was transformed into northness according to the formula: northness = cosine [(aspect in degrees * π)/180)]. Mean annual temperature was estimated by averaging over mean annual temperatures for the period 1981–2010 based on the Caraptclim dataset (Antolović et al., 2013). Mean annual temperature was not included into the model because of high correlation ($r = -0.81$, $p < 0.01$) with latitude and the temperature signal is composed from other variables included in the model M2 (i.e., latitude, altitude). We further wished to avoid using climate interpolations, which included error due to oversmoothing, when observations on spatial gradients (i.e., altitude, latitude) with tight climate correlations are available. All variables of the upper hierarchical levels were calculated as the mean of values from the lower hierarchy (for example, stand basal area was calculated as the mean of plot mean basal area within a given stand).

To compare the roles of biophysical site conditions and natural disturbances in driving spatial variation in forest biomass at three hierarchical scales (landscape, stand, and plot; Fig. 1, Table 1), we conducted a series of linear mixed-effect models (LME). To test our first hypothesis regarding the drivers of variation in live-tree biomass at the landscape scale, we conducted linear mixed models (M1). Further, to test our next hypothesis regarding drivers of variation in live-tree biomass at different scales, we conducted a second LME model (M2) by combining the within-stand and between stand models. We used the LME model to fit a combination of predictor variables (plus one interaction of date and severity of disturbances), while additionally considering random spatial effects, which allowed us to account for systematic variability in space (Wood, 2006).

To test our first hypothesis, we used the following set of models (M1):

$$BA\_L(D)_{ijk} = \beta_{0k} + b_{ik} + \varepsilon_{ijk}$$

$BA\_L(D)_{ijk}$ is the basal area of living or dead trees at the j-th plot of the i-th stand (response variable) in the k-th landscape. β_{0k} are (fixed) landscape-specific regression coefficients to be estimated together with landscape-specific variance components (σ^2_{Ck}, σ^2_k) and landscape -specific correlogram's ranges. This is done via (restricted) maximum likelihood function optimization stratified by landscape.

In order to explore the role of variability at coarse and fine scales, we considered not only a coarse/fine scale split of random effects for between and within stand components (as is customary in many studies), but we also split selected fixed effects into coarse- and fine-scale components (for the variables which were found important in the preliminary non-split screening). For an explanatory variable, x, with a fixed effect β, the coarse/fine split means forming two variables, x_C and x_F as stand means and differences between plot and stand means of x, respectively. This leads to the decomposition of the overall β effect into β_C and β_F components. These components can be estimated in the usual way in the LME model and subsequently tested. In addition to the fixed effects, our LME model contains random stand effects (corresponding to random effects, or random intercepts on the coarse scale) and residuals (corresponding to random effects on the fine scale). The residual effect also allows for within-stand autocorrelation (using exponential spatial residual correlation structure). Analyses were performed in the R statistical software (R Development Core Team, 2018) using the nlme package (Pinheiro et al., 2015).

To test our second hypothesis, we used the following Model 2 (M2):

$$\begin{aligned} BA\_L_{ij} = {} & \beta_0 + \beta_1.\, lat_{C,i} + \beta_2.\, lat_{F,ij} + \beta_3.\, lon_{C,i} + \beta_4.\, lon_{C,ij} + \beta_5.\, alt_{C,i} \\ & + \beta_6.\, alt_{F,ij} + \beta_7.\, dist\_date_{C,i} + \beta_8.\, dist\_date_{F,ij} \\ & + \beta_9.\, dist\_date^2_{F,ij} + \beta_{10}.\, dist\_sev_{ij} + \beta_{11}.\, BA\_D_{C,i} + \beta_{12}.\, BA\_D_{F,ij} \\ & + \beta_{13}.\, northeness_{C,i} + \beta_{14}.\, northeness_{F,ij} + \beta_{15}.\, dist\_date_{C,i} \\ & * dist\_sev_{C,i} + \beta_{16}.\, dist\_date_{F,ij} * dist\_sev_{F,ij} + b_i + \varepsilon_{ij} \end{aligned}$$

where

BA_L_{ij} is the basal area of living trees at the j-th plot of the i-th stand (response variable),
lat_{ij} is the latitude (center of gravity was calculated as the mean of all plots positions within a higher unit) of the j-th plot of the i-th stand, $lat_{C,i}$ and $lat_{F,ij}$ are the coarse and fine decomposition terms,
lon_{ij} is the longitude (center of gravity was calculated as the mean of all plots positions within a higher unit) of the j-th plot of the i-th stand, $lon_{C,i}$ and $lon_{F,ij}$ are the coarse and fine decomposition terms,
alt_{ij} is the altitude (center of gravity was calculated as the mean of all plot positions within a higher unit) of the j-th plot of the i-th stand, $alt_{C,i}$ and $alt_{Fij}$is its (orthogonal) decomposition into the coarse and fine components, respectively,
$dist_date_{ij}$is the date (i.e., calendar year) of the largest disturbance detected (, $dist\_date_{C,i}$, $dist\_date_{F,ij}$ are the coarse and fine decomposition terms,
$dist\_date^2_{F,ij}$ is the quadratic term of $dist\_date_{F,ij}$,
$dist\_sev_{ij}$ is the severity of the largest disturbance,
BA_D_{ij} is the basal area of dead trees at the j-th plot of the i-th stand, $BA\_D_{C,i}$ and $BA\_D_{F,ij}$ are the coarse and fine decomposition terms,
$northness_{C,i}$ and $northness_{F,ij}$ are decomposition terms of $northness_{ij}$,
$dist\_date_{C,i} * dist\_sev_{C,i}$ is the interaction of coarse terms for disturbance date and severity,
$dist\_date_{F,ij} * dist\_sev_{F,ij}$ is the interaction of fine terms for disturbance date and severity,
$b_i\ N(0, \sigma^2_C)$ are the stand-level random effects (i.e. the coarse level random effects, or coarse level random intercept), which is assumed to be independent across stands,
$\varepsilon_{ij}\ N(0, \sigma^2)$ is the residual term (fine scale random term) which is independent across stands but spatially autocorrelated within the same stand (with exponential correlogram),
$\beta_0, \beta_1, \cdots, \beta_{16}$ are (fixed) regression coefficients to be estimated together with variance components (σ^2_C, σ^2) and correlograms range. This is done via (restricted) maximum likelihood function optimization.

3. Results

3.1. Landscape-scale

The basal area of *Picea abies* stands in the Carpathian Mountains varied consistently along macroclimatic gradients among the three major landscapes. Among stands, we found a positive relationship between mean annual temperature and basal area of living trees ($p < 0.01$, $r = 0.5$, $r^2 = 0.25$; Sup. Fig. 1) and a similar trend was found in the relationship between latitudinal gradient and basal area of living trees ($p < 0.01$, $r = -0.81$, $r^2 = 0.65$; Sup. Fig. 2). The mean live-tree basal area per stand (56.3 m^2/ha) was highest in the Southern Carpathians (Fig. 2), which is the landscape with the highest mean annual temperature (3.5 °C) and the longest growing seasons. Mean stand-level basal area was lower in the Eastern (45.1 m^2/ha) and Western (44.0 m^2/ha) Carpathians (Fig. 2), where mean annual temperatures are cooler (2.7 °C and 2.2 °C, respectively) and growing seasons shorter, compared to the Southern Carpathians.

Landscapes differed in mean basal area, but the standard deviation among stand-level basal area within landscapes was surprisingly similar. Across the full dataset, the standard deviation (SD) of basal area among plots was 12.48 m^2/ha, and none of the landscapes had a strong departure from this value. The SD of basal area among plots was 11.6 m^2/ha (95% confidence interval range 10.07–13.36), 11.69 m^2/ha (95% confidence interval range 10.20–13.40), and 13.26 (95% confidence interval range 12.07–14.57) in the Southern, Western, and in the Eastern Carpathians respectively. Similarly, in all landscapes the variability in the standard deviations of basal area among the different stands were also low (Table 2).

The three landscapes were remarkably similar in the mean date of the maximal disturbance (1883, 1885, and 1886 in the Eastern, Southern and Western Carpathians, respectively; Fig. 2), suggesting the late 19th century was a period of synchronous, large or severe disturbance throughout the study area. However, there was much higher variability in the disturbance date (i.e., the time available for forest

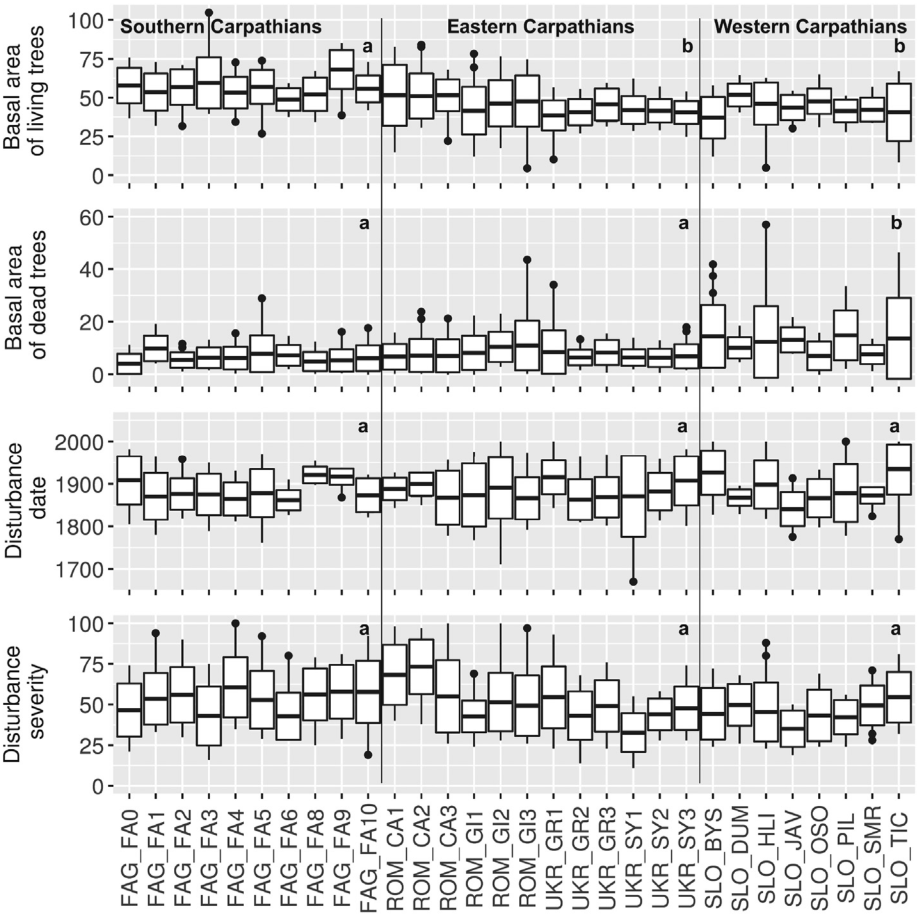

Fig. 2. Stand structural characteristics (Basal area of living and dead trees and Disturbance date and severity) box-plots (solid line indicates mean, box edges indicate standard deviation range, whiskers indicate maximal and minimal values and points indicate outliers) for individual stands. Statistical differences between landscape mean values are indicated by lower case letters and were tested with analysis of variance and post-hoc Tukey HSD test.

development since the last most severe disturbance detected) in the Western Carpathains (SD = 26.4 years) than the Eastern or Southern Carpathians (SD = 0.0 and 1.3 years, respectively). Variability of disturbance severity on the between-stand scale was several times higher in the Eastern Carpathians (mean = 50.9, SD = 9.46) than in the Western (mean = 45.5, SD = 1.29) or Southern Carpathians (mean = 52.7, SD = 0.002). Standard deviation of basal area of dead trees representing recent mortality rates on the within-stand scale was twice as high in the Western Carpathians (mean = 11.7 m^2/ha, SD = 10.08) than in the Eastern (mean = 7.97 m^2/ha, SD = 5.98) or Southern Carpathians (mean = 6.35 m^2/ha, SD = 4.56).

3.2. Coarse-scale (between-stands)

Stand basal area ranged from 37.1 to 68.1 m^2/ha (mean = 47.7 m^2/ha; Table 1). The linear mixed models support our first hypothesis, that variation in basal area among the stands is driven primarily by environmental variables, as indicated by the high importance of environmental variables at the between-stand scale (Table 3). The most important driver of between stand variability of basal area of living trees was latitude ($p < 0.001$, F-value = 87.93). Altitude ($p < 0.05$, F-value = 7.56) and longitude ($p < 0.05$, F-value = 7.13) also played minor roles.

3.3. Fine-scale (within-stand)

Plot basal area ranged from 4.4 to 105 m^2/ha (mean = 48.4 m^2/ha). Unlike the between-stand variability in basal area, which largely followed regional climatic and topographic gradients, the much higher variability in basal area at finer scales within stands was more strongly associated with the timing and severity of recent disturbances (Table 3), in accordance with our second hypothesis that disturbances are the primary drivers of biomass variability at the finest spatial scales. The most important drivers of within stand variability of live tree basal area were time since disturbance ($p < 0.001$, F-value = 57.26) with its polynomial member ($p < 0.001$, F-value = 22.96), and the basal area of dead trees ($p < 0.001$, F-value = 38.73). Northness ($p < 0.001$, F-value = 24.95) and interaction of disturbance parameters ($p < 0.05$, F-value = 5,37) were less important.

4. Discussion

The processes and drivers of spatial variation in forest biomass are well defined theoretically, but are expected to play out over different

Table 2
Standard deviations of Intercepts (between stand scale variability) and Residuals (within stand scale variability) of the LME models.

		Eastern Carpathians	Western Carpathians	Southern Carpathians	Overall pattern
Basal area of living trees	(Intercept)	3.08	3.36	3.33	6.31
	Residual	13.26	11.69	11.6	12.48
Basal area of dead trees	(Intercept)	0.85	0.29	0.74	2.07
	Residual	5.98	10.08	4.56	6.88

Table 3
Results of LME models examining the influence of site conditions and disturbance regime characteristics on basal area of living trees at two spatial scales (BS – between stand scale and WS – within stand scale). The results show: explanatory variables for the model, numDF = degrees of freedom numerator, denDF = degrees of freedom denominator, significance based on F-test, p-value < 0.05 are in bold. Regression coefficients (Reg. coef.) are the fixed effects of the model. Basal area D = Basal area of dead trees.

Explanatory Variable	numDF	denDF	F-value	p-value	Reg. coef.
(Intercept)	1	433	6340.5	< 0.0001	280.26021
Latitude BS	**1**	**22**	**87.928**	**< 0.0001**	**−3.69205**
Latitude WS	1	433	0.451	0.5024	50.75938
Longitude BS	**1**	**22**	**7.129**	**0.014**	**−1.16354**
Longitude WS	1	433	2.556	0.1106	−48.81219
Altitude BS	**1**	**22**	**7.558**	**0.0117**	**0.02569**
Altitude WS	1	433	0.253	0.615	0.0012
Disturbance Date BS	1	22	1.159	0.2933	−0.03368
Disturbance Date WS	**1**	**433**	**57.262**	**< 0.0001**	**−0.07619**
Disturbance Date WS^2	**1**	**433**	**22.956**	**< 0.0001**	**−0.00036**
DisturbanceSeverity	1	433	0.952	0.3298	0.09385
Basal area D BS	1	22	1.657	0.2114	−0.46443
Basal area D WS	**1**	**433**	**38.73**	**< 0.0001**	**−0.49391**
Northeness BS	1	22	1.095	0.3067	−1.90687
Northeness WS	**1**	**433**	**24.953**	**< 0.0001**	**−5.1316**
Interaction between disturbance effects BS	1	22	0.278	0.6033	−0.00002
Interaction between disturbance effects WS	**1**	**433**	**5.373**	**0.0209**	**0.00166**

scales in different geographic contexts, which complicates our general understanding of forest biomass patterns (White and Jentsch 2001). Climate drives structural variation at the largest scales, among biomes for example, but the prominence of variation along climatic gradients within forest regions is typically less clear, largely due to the high degree of variability contributed by disturbances. The primary outcome of disturbances is commonly an increase in spatial heterogeneity, with most disturbances producing a matrix of disturbed and undisturbed areas. On the other hand, simulations of stand dynamics repeatedly emphasize how density dependent processes, especially competition, promote evenness in stand structure; when variation in environmental factors and disturbance history is low, forest biomass is often surprisingly uniform (Kashian et al. 2005). Through extensive sampling along biophysical gradients within a well-defined forest region and a comprehensive reconstruction of disturbance history, we are able to establish clear links between forest biomass across biophysical gradients while simultaneously accounting for local disturbance-induced variability.

4.1. Landscape-scale

Variation in basal area of late-successional primary *Picea abies* forests throughout the Carpathian Mountains has been formed by disturbance regimes and environmental gradients spanning a variety of spatial scales. Our findings confirm the importance of biophysical factors at the coarsest scales. Despite large amounts of disturbance-induced variation in forest structure, we detected a stable gradient in forest biomass across multiple degrees of latitudes. The detected influence of latitude on basal area strongly implies that demographic rates (i.e. growth and mortality) respond to climatic variation. Disturbances contribute variation in forest structure orthogonally to biophysical gradients, which reduces the likelihood of detecting biophysical effects. The added variability will also reduce the size of the detected effect of climatic gradients on basal area. Considering that biophysical gradients and disturbances counteract in this way leads us to believe that climate is an especially strong driver of forest dynamics along the Carpathians. Inspecting the distribution of times since each of our Carpathian study sites encountered disturbance suggests that disturbance rates were somewhat low since earlier in the 20th century (Schurman et al., 2018). These low disturbance rates may be an important factor in allowing us to see such clear environmental effects on old-growth forest dynamics (Luyssaert et al., 2008), but it remain important to understand that disturbance and environmental effects both underlie the observed patterns. Detecting variation in forest structure along broad biophysical gradients despite the large degree of variation contributed by disturbance, reflects the tendency of old-growth forests to exist as a mosaic of age-patches.

The stand-level basal area of living trees (mean = 47.7 m^2/ha; range = 37.1–68.1) closely overlaps with the range of values previously reported from the study landscape (36 – 63 m^2/ha; Holeksa et al., 2007, Korpel 1995, Lamedica et al., 2011), supporting that we accurately account for the full range of stand-level basal area values for primary spruce forests in the Carpathian Mountains observed during last several decades. The disturbance-induced variation in basal area was similar among landscapes (Table 2); the evenness in disturbance patterns importantly contributes to our ability to detect environmental effects on forest structure. These findings further suggest that if disturbance impacts remain low, the latitudinal gradient in forest biomass will likely persist, as low-to-medium severity events continue to cause minor fluctuations in forest structure at a low enough frequency to permit the recovery of basal area (Sup. Fig. 3; see also Turner et al., 1993). The mosaic model of old growth forests suggests that the distribution of age-patches in a landscape should remain stationary through time. However, the fact that the observed forest age structure is somewhat synchronized (Janda et al., 2017) indicates that Carpathian forests do not completely comply with this stationary mosaic model. Old stands throughout the Carpathians exhibit a higher susceptibility to common disturbance agents (Schurman et al., 2018), and implies that the current distribution of age patches is likely to increase if disturbance frequency and severity also increases.

The stability of basal area along biophysical gradients could soon be influenced by increasing mortality, especially in the Western Carpathians, where recent severe disturbances have led to extensive tree mortality (Mezei et al., 2014; Nikolov et al., 2014). The basal area of standing dead trees was highest in the Western Carpathians, and high standard deviation in dead tree basal area among plots indicates that the amount of recent morality is highly variable at fine scales, consistent with local disturbances (Table 2). Recent studies have pointed to high temperature and low precipitation as drivers of disturbances in *Picea abies* forests, particularly where drought-stress predisposes trees to attack by the spruce beetle (Marini et al., 2017, Schurman et al., 2018). Recent forest development in this landscape might be connected with several factors, such as predisposition from past severe disturbances (synchronized development of old stands), coupled with the increasing influence of climate change on forests (Seidl et al., 2017, Senf and Seidl, 2018, Sommerfeld et al., 2018).

4.2. Coarse-scale (between-stands) variability in basal area

The differences in basal area among stands also support our first hypothesis, that variation in forest biomass among landscapes and stands is driven primarily by factors associated with the biophysical environment, as indicated by the high importance of environmental variables at the between-stand scale. The most important driver of between-stand variability in basal area was latitude (Sup. Fig. 2), which is closely related to climate (mean annual temperature decreased with increasing latitude across the sampled stands; $p < 0.01$, $r = -0.81$, $r^2 = 0.65$; Sup. Fig. 4). The growth rates of *Picea abies* trees in these ecosystems is mostly temperature dependent (Primicia et al. 2015), and this tree-level effect may contribute to the observed trend of increasing stand-level basal area as temperatures increase from high to low latitudes (Sup. Fig. 4). Although they had less explanatory power in the model, both altitude and longitude influenced basal area among stands.

The positive correlation between live-tree basal area and altitude may reflect an interaction between environmental gradients and disturbances rather than a direct effect of topography, consistent with our alternative hypothesis, that disturbances and the biophysical environment are interrelated across multiple scales. Natural disturbances tend to occur more frequently and cause larger patches of tree mortality at warmer sites at lower elevations than cooler, high-elevation sites (Korpel, 1995). Further, there can be an additional effect at low elevations, as such sites may represent the boundary of the optimal conditions for *Picea abies* growth, where greater climatic stress at the tree level increases vulnerability to disturbance, particularly by the spruce beetle. This pattern is supported by recent findings regarding the influence of drought on disturbances in *Picea abies* forests (Schurman et al., 2018, Senf and Seidl, 2018). The positive effect of basal area increase in the westward direction could be connected with a general geographical gradient, characterized by a more extreme continental climate (cold and dry) toward the east. In more extreme climates, trees tend to invest more resources to defense and roots than to above ground biomass (Reich et al., 2014).

4.3. Fine-scale (within-stand) variation in basal area

Given that the relatively small size of our sampled stands led to little variation in biophysical environment among the plots within each stand, we infer that the high within-stand variability in basal area was driven mostly by disturbance. This interpretation is consistent with our second hypothesis, and is supported by our findings that both the date of the time since disturbance and the basal area of standing dead trees varied widely among plots within each stand. Time since disturbance was the most important variable in explaining variability in biomass at the within-stand scale, consistent with other studies in the Carpathian Mountains that found strong relationships between biomass and time since disturbance (Trotsiuk et al., 2016, Seedre et al., 2015). The high variability in time since disturbance within stands suggests that individual stands typically represent fine-grained mosaics of smaller patches that have had different time available for forest development since the last severe disturbance. The time since disturbance was not important, however, at the stand scale (between stand scale), suggesting that despite high fine-scale variability in the time since disturbance, this variation tends to average out at the scale of individual stands, possibly in combination with a period of synchronous disturbances in the late 19th century (Schurman et al., 2018).

The second most important variable in distinguishing within-stand variation in the basal area of live trees was the basal area of dead trees. The negative relationship found here is intuitive; with more trees killed by recent disturbances, there was a lower basal area of live trees above 10 cm DBH (the measurement threshold) and there has not been sufficient time since the disturbances for recruitment of new trees. Additionally, the interaction between time since disturbance and severity also influenced the basal area of living trees. We found that the negative correlation between time since disturbance and basal area of living trees was strengthened by disturbance severity (Sup. Fig. 5), indicating that stands recovering from similar disturbance severity follow similar developmental trajectories (Trotsiuk et al., 2016). Our model results showed that northness was moderately important for within-stand scale basal area, but not at the between-stand scale, suggesting that environmental effects can operate at small scales if within-stand variation in environmental characteristics is high. We found a negative relationship between northern aspects and basal area of living trees, further corroborating that the temperature sensitivity of growth in these high elevation forests (Primicia et al., 2015) is behind much of the variation we encounter in basal area.

5. Conclusion

Our study helps to unravel the complexity behind forest biomass by identifying the scale dependence of major drivers. Basal area along the Carpathian arc responds positively to environmental change towards southern latitudes. Disturbance acts orthogonally to this gradient, adding substantial variability and reducing stand-level basal area. It is imperative to recognize that empirical relationships between forest-level attributes and environmental gradients detected over large geographic domains integrate both environmental effects and disturbance-induced variation. The net effect of disturbance is to reduce the apparent effect size of environmental gradients, which has important implications for large-scale representations of vegetative processes. Our findings provide insight into likely future development, and a benchmark for measuring future changes. Both climate changes and shifting disturbance regimes are likely to continue to drive variation in future basal area along the Carpathian arc. Increasing temperatures may permit northern latitudes to increase in basal area, but intensifying disturbances will act to deplete latitudinal gradients, and ultimately reduce basal area.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.12.045.

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6. Discussion

6.1 Contrasting patterns of natural mortality in primary *Picea* forests of the Carpathian Mountains

6.1.1 Mortality and mortality rates

A large dataset of 371 permanent sample plots, spanning over 1000 km geographical gradient, was used to assess the mortality in primary Norway spruce stands in the Carpathians. Mortality rates on large scales were within the range of background mortality reported in studies examining stands in the absence of recent high-severity, large-scale disturbances (Stephenson and van Mantgem 2005, van Mantgem et al. 2009, Das et al. 2016). Small scale, low-severity disturbances should be considered an integral part of background mortality (Turner 1987, Fraver et al. 2009), which to an extent, contradicts the approach applied in many individual-based forest models. Climate can synchronize forest structure over large areas (Schurman et al. 2018) but the finer scale variation has been suggested to be mostly driven by frequent, small- to medium-scale disturbances (Meigs et al. 2017, Janda et al. 2019). Considering that mixed severity regimes (Trotsiuk et al. 2014) with a prevalence of moderate scale and severity disturbances (Čada et al. 2020) have been suggested for montane spruce forests in the Carpathians, the variability in mortality rates fit the expectations.

On 18% of plots the annual mortality rate exceeded the reported 2% upper threshold of background mortality rates (Stephenson and van Mantgem 2005). Such increased mortality can be attributed to relatively dense stands and self-thinning processes (Castagneri et al. 2010, Svoboda et al. 2010) and/or to less frequent, high-severity disturbances (Sproull et al. 2015, 2016, Schurman et al. 2018, Čada et al. 2020), which are the most likely driver behind observed mortalities over 10% per year on several plots. The major cause of such disturbances in mountain spruce stands are windthrows and bark beetle outbreaks, which can be confirmed by field observations in the study stands. It is often complicated to distinguish between mixed-severity regimes (Panayotov et al. 2011) and individual disturbance events that cause intermediate severity damage (Woods 2004) based on structural data. These two concepts are not mutually exclusive as intermediate disturbances can be responsible for a substantial portion of tree mortality within the mixed-severity regime. However, the records of multiple mortality agents in most stands further support the concept of a mixed-severity regime.

Analysis of variance detected a significant difference in the variability of plot-level mortality between stands, localities, and regions. This was clearly driven by recently disturbed plots in the Western Carpathian region, and likely also the generally low mortality in the Ukrainian part of the Eastern Carpathians. The increased variability in the observed mortality rates in the most disturbed Western Carpathian region is in contrast to the generally lower, but evenly distributed mortality in Northern Romania, which resulted in a higher plot-level median in Northern Romania. The large area sampled, size of the dataset, and variability in stand structure at the time of plot establishment allow for an assumption that the observed patterns are representative of a longer timeframe, although, it is necessary to consider the possible influence of stochastic disturbance events (Čada et al. 2020). Structural stand parameters, disturbance history (Schurman et al. 2018) and local topography (Senf and Seidl 2018) are considered key factors driving the observed mortality patterns in primary forest stands. Still higher, yet also highly variable mortality rates were reported by other studies conducted in the spruce stands in the Western Carpathian region (e.g., Sproull et al. 2015, 2016). These studies, however, were focusing on stands during bark beetle outbreaks and reported mortality rates were comparable to the mortality rates observed in those stands in our dataset that were affected by recent high-severity disturbances. Similarly, the mortality rates detected prior to the recent outbreak period (e.g., Sproull et al. 2015) were close to the levels we observed. Our results seem to be representative of the spectrum from low to high mortality periods, thus further highlighting the spatio-temporal heterogeneity in primary stands and its importance for forest development and stability.

6.1.2 Size class distribution of mortality

The observed diameter class distribution of recently dead trees for individual stands indicates substantial variability. The overall distribution shows even numbers of recently dead trees among DBH classes up to 40 cm followed by a continuous decrease towards larger classes, which is influenced by a comparably lower abundance of huge trees. Sampling threshold should be considered as the smallest size classes are expected to have the highest mortality. It is also important to note the shape of the distribution becomes unimodal, centered on 41 – 50 cm DBH class when the trees are weighted by their respective basal area, which can be related to the combined relatively high BA per tree and still relevant densities in this size class. The composition of different mortality agents in each stand may be a key consideration, as certain mortality modes are more frequent in particular size classes, indicating the importance of forest spatial structure (Das et al. 2008). A relatively short timeframe could have influenced the distribution because some disturbance events with severe impact on large trees have substantially longer return intervals (Hurst et al. 2011, Čada et al. 2020), however, the extent and variability within the dataset should mitigate this effect.

6.1.3 Mortality agents

Competition is an important mortality agent in stands that have not been affected by a higher severity disturbance in recent years, especially in the smaller size classes, and its overall contribution is likely to increase when DBH threshold is lowered. However, the proportion of dead trees associated with competition varied substantially across stands. This variability is assumed to be driven by stand density and prevalent stage of development.

The most frequently recorded mortality agent across all stands (75% of all mortality), regardless of the overall mortality rate was bark beetle infestation. Trees, for which bark beetle was recorded as the mortality agent, were often clustered on certain plots, following the expected behavior of this insect (Wermelinger 2004). The distribution of trees most likely killed by bark beetle was unimodal, centered on the 31 – 40 cm DBH class, as observed in other stands impacted by bark beetle. Small trees severely affected by bark beetle infestation, however, were found also in stands with low mortality rates, therefore clearly not experiencing outbreak conditions. Bark beetle is often not the only mortality agent detected on a particular recently dead tree, which supports the role of an infestation either as an inciting factor – making the tree more vulnerable to subsequent agent like fungi; or a contributing factor – often just accelerating the already ongoing decline caused by another mortality agent like competition, drought, or physical damage (sensu Manion 1991). The significant and frequent role of bark beetle infestation is evident, however, in the heterogeneous forests the higher proportion of bark beetle-related mortality does not always have a severe impact on the large scale.

Tree deaths associated with abiotically-caused physical damage (structural failure) were frequent (11% of all mortality cases, ranging from 0 to 41% for individual stands). The contribution of the three modes of physical damage (crown break, stem break, uprooted), however, substantially varied among stands. The distribution of trees with crown or stem breakage was decreasing towards higher DBH classes, likely driven by smaller trees facing higher risk of being severely damaged by another falling tree (Woods 2004, Das et al. 2008, Holzwarth et al. 2013). The stands with higher stand density and/or a lot of advanced regeneration are likely to experience higher mortality rates during periods without severe wind-related disturbances but are likely to recover faster after such event than stands with bigger trees and closed canopy. Stand structure, disturbance legacies (Schurman et al. 2018) and local topography (Senf and Seidl 2018), are therefore a key consideration. Given the contribution of abiotic agents to overall mortality the results do not confirm their suggested overrepresentation at the expense of intrinsic causes in mortality models (Das et al. 2016).

Climatic extremes were reported as major mortality agent in a limited number of cases. It is very complicated to accurately identify impacts of climate in the presence of another mortality agent, which can usually be visually detected. Considering the global climatic trends, the role of climatic extremes might be underestimated in results of this study. Based on other studies from primary Norway spruce stands in the region, the dominant climatic factor is drought (Schurman et al. 2018, Bjorklund et al. 2019, Schurman et al. 2019, Svobodová et al. 2019).

The critical step in improving our understanding of climate change impacts on forests lies in evaluating the role of climate in the context of developmental drivers and various mortality agents. The presence of multiple mortality agents on more than one third of the plots with any mortality detected during the remeasurement period emphasizes the complexity of mortality processes and simultaneous effects of different agents in primary forests.

6.2 Past disturbances influence current *Picea abies* mortality in primary Carpathian forests

6.2.1 Relationship between past canopy area removal and current mortality

The study was conducted in primary Norway spruce forests over a wide geographic gradient, spanning roughly 1000 km, and contains sample plots and stands with very variable trajectories of past canopy area removal (disturbance history). The stands in our dataset are considered mostly driven by mixed-severity disturbance regimes with infrequent high-severity disturbances (e.g., Trotsiuk et al. 2014, Meigs et al. 2017, Čada et al. 2020). Current annual mortality rates based on a five-year re-census period ranged from 0 to 100% across the study plots (Synek et al. 2020, Chapter 5.1). The mortality rates are highly variable both between and within stands. The extremes are attributed to the ongoing bark beetle disturbance in the Western Carpathians. The annual mortality rates are based on relatively short resampling period, however, the variability in stand structure at the time of plot establishment and disturbance histories along with extent of the dataset and the extensive area sampled, allow us to assume the observed patterns in current mortality should be representative of a longer timeframe. The increased mortality rates related to bark beetle event in some stands enable us to consider the full range of variability that can occur in this forest type.

A significant relationship was detected between past canopy area removal (proxy for disturbances) and current mortality rates. The importance of disturbance history for future development has been suggested previously (e.g., Panayotov et al. 2011, Janda et al. 2019). When coupled with studies evaluating the relationship between disturbance history and current stand structure (e.g., Janda et al. 2017) or stand structure and mortality (e.g., Clyatt et al. 2016) our results indicate that all three aspects (disturbances, mortality, stand structure) of the cyclical process should be considered in context of each other. The inverse character of the relationship could be simplified as generally younger stands experiencing lower mortality rates; however, this explanation is not covering the whole situation in uneven-aged stands with the rare occurrence of stand replacing events. It is clear the vulnerability of forest stand to high-severity disturbances increases with time since last disturbance (Pickett and White 1985, Schurman et al. 2018).

However, disturbances can interrupt natural forest developmental cycle (Meyer 1999), allowing younger growth cohorts to regenerate alongside mature ones, thus substantially altering forest structure horizontally and vertically, and improving its heterogeneity (Trotsiuk et al. 2012, Mikoláš et al. 2017). The variable, yet continuous creation of canopy openings seems to be a critical driver of the observed relationship. Stands developing in such a dynamic way are more likely to have high diversity in tree ages, dimensions, and spatial structure, which improve the stands resilience (Aussenac et al. 2017); especially since the drivers of disturbances are affected by ongoing global processes, namely climate change, but the response to these drivers varies at finer scales (Sommerfeld et al. 2018).

The strength of the relationship changes with increasing length of the period of past stand development reaching its peak at 120 and 130 years for stand- and plot-level respectively, which indicates a major influence of infrequent higher-severity disturbances. The period with strongest relationship corresponds with expected return intervals of high-severity disturbances (Čada et al. 2020) and the time estimated for complete decay of large logs (Holeksa et al. 2008). Deadwood represents important disturbance legacy (Hunziker and Brang 2005, Zielonka 2006) in insect- and wind-driven forests (Grodzki et al. 2004, Krumm et al. 2011, Panayotov et al. 2011). Average tree longevity can be another factor influencing the length of the period with strongest relationship (Čada et al. 2020). In such case the length of the period is assumed to be species specific.

The amount of variability explained by single parameter of past canopy area removal is low on the plot-level, however, on the stand-level it is substantial enough to be considered in more complex models. The relevance of the relationship is further supported by increase in explained variability when random effect of stand is added to plot-level analysis. A measure of variability of past disturbances is at least equally important as its mean value. The combination of the two variables should be considered to improve precision of complex stand dynamics models, because tree mortality remains one of the highest uncertainties in large-scale vegetation dynamics models (Bugmann et al. 2019). The relationship is significant and follows a similar pattern when all plots with no current mortality are excluded, which suggests low mortality periods are integral part of the stand development, just like higher severity disturbances.

6.2.2 Patterns on different scales

When the dataset is split to subregions, the pattern observed for the whole gradient was only detected for some of them. The generally observed pattern can be best seen in the Western Carpathians, which experienced the widest spectrum of recent mortality (Synek et al. 2020, Chapter 5.1), therefore we might assume the possibility to detect the pattern in stands that are undergoing low mortality periods, with low variability among plots being limited. Significant relationships were detected for most subregions, but they differ in length of the period with the strongest relationship. Such variability can be linked to differences in local topography (Senf and Seidl 2018). Asynchronous effects of high-severity stochastic events (Čada et al. 2020) are another possible cause of the variation. These infrequent events can disrupt our ability to detect the relationship within the timeframe we are working with due to their specific legacies. However, their impacts are not permanent and are part of the long-term dynamics.

The general pattern does not change with changing size of the individual samples (plot vs. stand), however, bigger samples provide stronger results (more variability is explained by the model). This finding can be explained by the relatively small areas of the plots, which can easily avoid part of the range of the disturbance severities in the area during observation period. Another possible explanation can be seen in the smaller effect of random single tree or small gap events on a broader scale (Janda et al. 2019), resulting in a more pronounced effect of more severe, larger scale events which are likely to have synchronized effects across the stand (Janda et al. 2017). The difference in period lengths with the strongest relationships on both plot- and stand-levels may be explained by the effects of progressively spreading disturbances, such as insect outbreaks. In such cases, some individual plots would be substantially affected earlier than the stand as a whole, consistent with our results – the period on the plot-level is longer, meaning the events started earlier. Based on observations of bark beetle outbreak progress (e.g., Sproull et al. 2015, 2016) and the importance of bark beetle as a mortality agent in Norway spruce stands in the region, regardless of mortality rates (Synek et al. 2020), this explanation seems to be reasonable. Some differences can be attributed to the most frequent mortality agents and are therefore assumed to be species-specific (Holzwarth et al. 2013, Vanoni et al. 2016) and related to stand conditions (Das et al. 2016).

6.2.3 Changes in the relationship patterns through time

To verify that the observed relationship and its pattern with changing length of considered past period are consistent throughout time, we attempted to reconstruct the relationship for several previous decades. Since exact mortality data for previous decades are not available, they have been approximated by canopy area removal in the same way used for disturbance reconstruction. Significant relationships were detected in several cases, however, the period with the strongest relationship was not consistent with the pattern observed for the most recent years. The amount of variability explained was still increasing with the extending length of the observation period several decades past the period length showing the strongest relationship with the most recent mortality. Limited canopy area removal data for some stands prior to 1800, however, make it impossible to follow the relationship further into the past and we are therefore unable to identify the exact period with the strongest relationship. We can therefore argue that the critical disturbance period driving current morality dynamics is decreasing in length. The shift can be attributed to increasing frequency of disturbances under global changes (Seidl et al. 2014, Schurman et al. 2018) and/or increased susceptibility of the stands to such disturbances again because of climatic changes (Čada et al. 2016). Climate-induced changes in environmental drivers and disturbance regimes are reportedly forcing forests toward shorter-statured and younger stands (McDowell et al. 2020), however, within our results it is uncertain if the change is indeed a result of global changes or a consequence of changing stand conditions following development after disturbances.

It is important to consider that canopy area removal based on tree ring data is not an exact measure of tree mortality, although it is a very good proxy for that purpose. Some release events of surrounding trees are not induced by actual tree deaths but by substantial damage to canopy from which the affected trees might recover. However, we argue that the associated potential biasing effect is limited in spruce stands compared to stands comprised of tree species with high resprouting ability (Roženbergar et al. 2020).

6.3 Diverse patterns of mortality in primary beech-dominated mixed forests of the Carpathians

6.3.1 Mortality rates

Using a dataset of 227 permanent sample plots (almost 14,000 trees) the study focused on observing mortality rates and patterns in European beech-dominated primary forests across a wide gradient. The observed overall annual mortality rate was well within the range of background mortality reported in forests unaffected by recent high-severity disturbances (Stephenson and van Mantgem 2005, van Mantgem et al. 2009, Das et al. 2016). However, at finer scales the mortality rates varied, and the variability is even more pronounced when individual species are considered. It is also important to note that besides competition and intrinsic causes, the background mortality is an outcome of lower intensity (in terms of scale and/or severity) disturbances (Turner 1987, Fraver et al. 2009).

Annual mortality rates exceeding 2% were detected on less than 10% of plots and could be, in many cases, attributed to dense stand conditions and self-thinning process (Castagneri et al. 2010, Svoboda et al. 2010) and/or relatively higher mortality of Norway spruce - mostly related to bark beetle infestation. Species-specific mortality of Norway spruce and European silver fir represents the only cases (12) where a plot-level annual mortality was higher than 5%. The mortality rates detected for Norway spruce in mixed stands are, however, still substantially lower than the rates detected in spruce-dominated primary forests in the Carpathian region (Sproull et al. 2015, 2016, Synek et al. 2020) or in even-aged spruce monocultures across Europe. Similar to the results from the higher elevation spruce stands, our findings in beech-dominated mixed forests match the concept of mixed-severity disturbances – with severity substantially variable over larger areas (Panayotov et al. 2011, Trotsiuk et al. 2014, Schurman et al. 2018). The intermediate-severity damage caused by individual events (Woods 2004) is likely an integral part of the disturbance regime, however, the records of multiple mortality agents in most stands suggest multiple mixed-severity disturbances rather than single major event.

Significant difference in the variability of plot-level mortality between the Western Carpathians and other regions was found. The indicated substantial heterogeneity on different scales supports the concept of mixed-severity regime reported from some mixed stands in the region (Frankovič et al. 2021). The variability is likely driven by relatively higher Norway spruce mortality. The role of species-specific mortality rates has been further highlighted by significant difference between mortality rates of fir and spruce as compared to beech. Local disturbances are considered the major driver of structural variability on a fine scale, while climatic factors are likely the most important characteristic on a coarse scale (Janda et al. 2019). The limits of short observation period should be offset by the extensive sampled area, large dataset and substantial variability in stand conditions. However, it is still necessary to consider the possible impact of stochastic disturbance events which can also lead to a shift in species composition and subsequently the relative frequency of mortality agents. Structural stand parameters, disturbance history (Schurman et al. 2018) and local topography (Senf and Seidl 2018) are likely crucial factors underlying the variability in the periods without major disturbance events and substantially influencing the impact of these. Several studies of mortality rates in the Carpathian region lately reported substantially higher mortality rates, but most of these studies were conducted in higher elevation spruce-dominated stands during bark beetle outbreak (e.g., Sproull et al. 2015, 2016). However, spruce-dominated stands are apparently subject to higher mortality rates even in non-outbreak conditions (Sproull et al. 2015, Synek et al. 2020) and our results suggest this statement remains valid even when spruce trees only are considered within mixed stands. The expected role of drought was not confirmed as the region generally least affected by drought conditions, the Southern Carpathians, had the highest mortality rate.

6.3.2 Size class distribution of mortality

The diameter class distribution of recently dead trees follows similar pattern for both regions. Overall distribution shows the highest number of recently dead trees in DBH class 11 to 20 cm followed by continuous decrease towards larger classes. Due to 6 cm DBH threshold, the smallest recorded tree class is narrower than the rest (6 – 10 cm as opposed to 10 cm size classes) in order to keep the other size classes comparable with the results from spruce stands, where the threshold was 10 cm. The shape of the distribution differs from the distribution found in Norway spruce stands in the same region, where the amounts of recently dead trees were balanced up to 50 cm DBH. The difference can be attributed to the more vertically complex structure of mixed stands, resulting in higher competition for light, however, the distribution of Norway spruce mortality found in mixed stands resembles the pattern reported from spruce-dominated stands. Species-specific patterns have been previously reported (e.g., Holzwarth et al. 2013) and further emphasize the role of species-specific composition of mortality agents, as particular mortality agents are more frequent in specific size classes (Holzwarth et al. 2013). Considering the differences across species and regions we hypothesize the species-specific dynamics might be a stronger driver than site conditions, provided the site conditions are appropriate for a given species. In terms of basal area, however, the highest proportions of mortality can be found in size classes between 50 and 90 cm DBH. Thus, size classes relatively abundant within the stands with substantially high basal area per tree. It is necessary to consider relatively short timeframe as certain infrequent disturbance events with expected higher impact on larger size classes might not occur during the given observation period (Hurst et al. 2011). The spatial and structural variability, however, should mitigate the potential bias.

6.3.3 Mortality agents

Climatic extremes recorded as mortality agents were more frequent in mixed stands than in spruce stands in the same region. However, the contribution to overall mortality is still limited and the difficulties in identifying this mortality agent in the field remain. It is usually only possible to detect the role of climatic extremes when there is no subsequent agent present. Climatic data for our study stands indicate drought affected the majority of the stands during the period between censuses, suggesting climatic conditions could have operated as a predisposing factor in many cases of tree mortality and therefore, the role of climatic extremes in our results may be underestimated. In one of the subregions, the Southern Carpathians, the stands with mostly positive water balance over past few years were also the stands with the lowest mortality, although the same does not apply to the other subregions. However, it has been reported that the response to climatic change can be highly altered by changes in the disturbance regime in temperate forests (Seidl et al. 2011, Thom et al. 2017) and the impact of specific climatic drivers can be affected by increasing temperatures (Schurman et al. 2019). Our findings suggest the important role of shifts in temperature and precipitation is indeed strongly influenced by other stand conditions (e.g., topography, stand structure, disturbance history) and only when considered together the real implications can be properly assessed.

Despite the variability among stands, competition was a crucial driver of mortality in primary beech-dominated mixed stands during periods without a high severity, large-scale disturbances. The evident abundance of trees assigned to this mortality mode is further supported by the higher mortality among suppressed or lower layer trees based on the distribution of recently dead trees across the DBH classes. The contribution of competition to total mortality was expected to be highest in the smallest size classes and the results confirm that. Competition as a mortality agent was less frequently recorded for Norway spruce compared to the other species and all data. The impact of competition in this case might be underestimated due to vulnerability of spruce trees to insect infestation when weakened.

The overall role of insects was limited; however, bark beetle infestation was a major mortality agent for Norway spruce. Considering the abundance of this tree species in our study stands and low mortality rates observed, we surely cannot talk about outbreak conditions. The proportion of insect-related mortality in spruce trees in mixed stands complements the report of bark beetle as a dominant mortality agent in spruce stands regardless of overall mortality (Synek et al. 2020). These findings indicate that the presence of bark beetles in a heterogeneous stand does not have to lead to any large-scale effects, quite contrary the insects represent important aspect of primary stand dynamics. Insects as a mortality agent are often not a sole agent leading to death of a given tree and should be therefore considered in the context of stand conditions and other possible mortality agents.

Trees damaged by abiotic factors (crown or stem breakage, or uprooted) represented roughly the same portion of all mortality as competition. Wind damage is considered the main disturbance type in these forests (Splechtna et al. 2005, Nagel and Svoboda 2008). Infrequent ice-storms are another major source of abiotically-caused damage (Nagel et al. 2016). The composition of the three different modes is similar between regions but varies among species, suggesting the susceptibility to above-ground abiotic damage is species-specific, and likely related to the role of fungi. Severe physical damage as a mortality agent was in general less frequent in spruce trees compared to other species. We argue it might be driven either by lower vulnerability of spruce trees to wind damage in relatively denser mixed stands or simply the common combination of less severe physical damage operating as an inciting factor for insect infestation. The number of trees for which broken crown was considered a mortality agent were decreasing towards higher DBH classes, likely driven by smaller trees facing a higher risk of being severely damaged by another falling tree (Woods 2004, Das et al. 2008, Holzwarth et al. 2013). Stem breakages have comparably higher shares in the larger size classes. A possible explanation can be seen in the massive damage to the crown needed to induce the death of a large tree, while stem break, usually causing loss of the whole crown, is lethal in most cases, regardless of tree size. The increased frequency of fungi affecting the stem or root system in larger trees represents another likely cause. Based on the similarity in composition of physical damage modes across subregions, abiotic factors in mixed stands are likely more connected to regional or global conditions and are somewhat random within the region. Stand structure and time since last severe disturbance are factors that influence abiotic-related mortality on finer scales (Čada et al. 2020, Schurman et al. 2018), alike the local topography (Senf and Seidl 2018), which is less evident in mixed stands compared to higher elevation spruce stands.

The uncertainty in the identification of the mortality agents, especially for large dominant trees and in difficult-to-access parts of trees, is likely even more critical in mixed stands than in coniferous forests. Another major consideration is proper evaluation of combinations of mortality agents (Das et al. 2016, Synek et al. 2020). A substantial share of plots with a record of multiple mortality agents during the five-year re-census period further accentuates the complexity of mortality processes and simultaneous effects of different agents in primary forests.

6.4 Drivers of basal area variation across primary late-successional *Picea abies* forests of the Carpathian Mountains

The processes and drivers of spatial variation in forest biomass are theoretically well-defined but are expected to act differently over various scales in different geographic contexts, which complicates the general understanding of forest biomass patterns (White and Jentsch 2001). Climate is the dominant driver of structural variation at the largest scales, however, the prominence of variation along climatic gradients within forest regions is often reduced, largely due to the high degree of variability introduced by disturbances. Disturbances result in increases in spatial heterogeneity, usually creating a matrix of disturbed and undisturbed areas. Simulations of stand dynamics, however, emphasize how density-dependent processes, especially competition, promote evenness in stand structure. If the variation in environmental conditions and disturbance history is low, forest biomass can be surprisingly uniform (Kashian et al. 2005). Through extensive sampling along biophysical gradients within a well-defined forest region and a comprehensive reconstruction of disturbance history, forest biomass can be evaluated across biophysical gradients with respect to the local disturbance-induced variability.

6.4.1 Landscape-scale

Variation in basal area of late-successional primary Norway spruce forests throughout the Carpathians has been formed by disturbance regimes and environmental gradients spanning a variety of spatial scales. The findings of the study confirm the importance of biophysical factors at the largest scales. Stable gradient in forest biomass across multiple degrees of latitudes have been detected. The influence of latitude on basal area implies that demographic rates (i.e., growth and mortality) respond to climatic variation. Disturbance-induced variation in forest structure reduces the likelihood of detecting biophysical effects and decreases the strength of the detected effect of climatic gradients on basal area. Considering the effect was detected despite the counteracting influence of disturbances, we argue that climate is an especially strong driver of forest dynamics along the Carpathians. The relatively low disturbance rates since early 20th century (Schurman et al. 2018) might be an important factor allowing us to see such clear environmental effects on primary forest dynamics (Luyssaert et al. 2008). However, it is necessary to consider both disturbances and environmental effects as crucial drivers of the observed patterns. The stand-level basal area of living trees (mean = 47.7 m^2 /ha; range = 37.1–68.1) matches the range of values previously reported from the study landscape (36 – 63 m^2 /ha; Holeksa et al. 2007, Lamedica et al. 2011), indicating that the full range of stand-level basal area values for primary spruce forests in the Carpathian Mountains was captured. The disturbance-related variation in basal area was similar among landscapes; the evenness in disturbance patterns substantially contributes to the possibility to detect environmental effects on forest structure. These findings suggest that the latitudinal gradient in biomass can persist under the impacts of low- to moderate-severity disturbances, as the minor fluctuations in forest structure permit the recovery of basal area. The distribution of age-patches in a landscape should remain stationary through time according to the mosaic model of old-growth forests. However, the certain extent of synchronization in age structure (Janda et al. 2017) indicates that Carpathian forests do not strictly follow this stationary mosaic model. The stability of basal area along biophysical gradients can be affected by increases in mortality in near future, especially in the Western Carpathians, where recent severe disturbances have led to extensive tree mortality (Mezei et al. 2014, Nikolov et al. 2014, Sproull et al. 2015, 2016, Synek et al. 2020). The high standard deviation in dead tree basal area among plots indicated high variability in recent morality at fine scales, consistent with local disturbances, which has been confirmed by the mortality study based on re-census of the study plots (Synek et al. 2020). Predisposition from the last disturbances and the increasing influence of climate change, namely higher temperatures and low precipitation, are likely the major factors behind recent forest development (Marini et al. 2017, Seidl et al. 2017, Schurman et al. 2018, Sommerfeld et al. 2018, Schurman et al. 2019).

6.4.2 Coarse-scale (between-stands) variability in basal area

The differences in basal area among stands indicate the variation in forest biomass among landscapes and stands is predominantly driven by factors associated with the biophysical environment, as supported by the high effect of environmental variables at the between-stand scale. The main driver of between-stand variability in basal area is latitude, which is closely related to climate (mean annual temperature decreases with increasing latitude across the sampled stands). Temperature-dependent growth rates of Norway spruce (Primicia et al. 2015) are a logical explanation of the observed relationship. Altitude and longitude also affect the basal area, however, the effects in the model were weaker. The positive correlation between live-tree basal area and altitude probably reflects interactions between climatic conditions and disturbances rather than topography itself. For example, low elevations, representing the boundary of the optimal conditions for Norway spruce growth, can be easier affected by climatic stress (Jump et al. 2009, Allen et al. 2010), which increases vulnerability to bark beetle-related disturbances. Recent findings regarding the influence of drought on growth and disturbances in montane Norway spruce forests support this concept (Schurman et al. 2018, Senf and Seidl, 2018, Bjorklund et al. 2019, Schurman et al. 2019, Svobodová et al. 2019). The positive effect of basal area increase in the westward direction can be related to increasingly more extreme continental climate (cold and dry) toward the east. In extreme climate, trees tend to invest more resources to defense and root system than to above ground biomass (Reich et al. 2014).

6.4.3 Fine-scale (within-stand) variation in basal area

The little variation in biophysical environment among the plots within each stand is likely due to the relatively small size of our sampled stands, and we therefore infer that the high within-stand variability in basal area is driven mostly by disturbances. This interpretation is consistent with substantial variability in time since last disturbance and basal area of standing dead trees among plots within individual stands (Chapter 5.4) and is further supported by within-stand variability in observed annual mortality rates and mortality agents (Synek et al. 2020). Our finding that time since disturbance is the most important parameter in explaining within-stand variability in biomass is consistent with other studies conducted in the Carpathians that report strong relationships between biomass and time since disturbance (Seedre et al. 2015, Trotsiuk et al. 2016). The high variability in time since disturbance within stands indicate the individual stands consist of mosaics of patches that are developing without severe disturbance events for periods of different length. The time since disturbance was not important, however, at the between-stand scale, indicating that the fine scale variability averages itself out over larger scales. The basal area of standing dead trees is the second most important variable defining within-stand variation in the basal area of living trees. The relationship detected was negative and the reasoning is intuitive; with more trees killed by recent disturbances, there is a lower basal area of live trees and there was not enough time for newly recruiting trees to reach the measurement threshold of 10cm DBH. Furthermore, the interaction between time since disturbance and severity of the last event strengthened the negative correlation between time since last disturbance and basal area of living trees. Such finding suggests that stands recovering after events of similar severities follow similar developmental trajectories (Trotsiuk et al. 2016).

7. Management implications

Common forest management approaches used in Central and Eastern European forests typically generate a limited range of structural variation compared to that found in natural forests. The homogeneous techniques of current approaches mostly result either in a combination of highly opened and shaded conditions in even-aged systems, or equally shaded conditions over continuous forest cover, produced under selective cutting management. However, such conditions differ from the heterogeneity and complexity of conditions observed in natural forests subject to moderate-severity disturbances (Meigs and Keeton 2018). The findings of this thesis, like other studies (e.g., Čada et al. 2020), suggest that current management treatments are often extremely severe, with considerably smaller areas of effect and shorter return intervals compared to the observed spectrum of natural disturbances. Based on the concept of the "historical range of variability" (Keane et al. 2009) - which presents the idea that specific regimes of past disturbances are the primary driver of forest conditions that native forest species have adapted to over extensive periods of time, and from which they are likely to benefit in the future - we can assume that deviating from the more natural scheme might induce substantial changes to forest development and biodiversity, and ultimately result in vulnerability of such stands to extreme disturbances. Current management practices are often outside the range of variation reported from primary forests (Čada et al. 2020). Shorter rotation periods shift the age distributions towards younger forests, thus magnifying the effects of climate change which is forcing the forests in the same direction (McDowell et al. 2020). Among other impacts, old trees and related late developmental structures are frequently absent in managed forests and the lack of such habitats can substantially affect biodiversity (Asbeck et al. 2021). The biological legacies of natural disturbances and mortality are often not taken into consideration (Meigs and Keeton 2018) and the related structures, such as dying trees or standing and lying deadwood, are therefore missing in managed stands. The results of this thesis should complement previous findings on disturbance regimes and patterns and could provide further information to guide efforts to emulate natural disturbance patterns in logging operations (Keane et al. 2009, Long 2009), and to improve the recommendations for retention forestry concepts (Fedrowitz et al. 2014, Mori and Kitagawa 2014).

An acknowledgement of the wide spectrum of natural disturbance effects, mortality and composition of mortality agents, and their subsequent biological legacies by forest management might greatly improve ecological benefits. Heterogeneous treatments should be preferred to mimic the observed spectrum of mortality rates and relative prevalence of mortality agents. The crucial role of low-to-moderate-severity and small-to-moderate-size disturbances should be reflected by spatially and temporally diverse distribution of forestry operations following the natural patterns in order to increase landscape connectivity and forest resilience. Even though high-severity disturbances are apparently part of the natural disturbance regimes (Čada et al. 2020, Synek et al. 2020) the recommended severity of management treatments should be significantly lower than 100 %. Certain shares of trees, optimaly large living and dead trees of multiple species (where applicable) and other structural attributes (e.g. deadwood) should be retained in a stand perpetually to facilitate stand resilience and continuity. The level of retention should be set accordingly to the structural legacy amounts needed, the cumulative effects of natural and human disturbances, landscape structure, and reconstructed disturbance or mortality rates. A combination of appropriate retention levels with spatially- and temporally-variable treatment shapes and severities has the potential to enable the application of management treatments to moderate-scale areas, corresponding to the scale generally considered under current approaches (Meigs and Keeton 2018). Patches without any logging operations should be included and some degree of natural disturbances and mortality within managed areas should also be allowed to maintain the associated legacies.

The observed patterns of mortality also have implications for forest conservation areas that are critical for maintaining diversity. The strict conservation of primary forest remnants and natural forest restoration should be a major interest of nature conservation managers (Sabatini et al. 2020). These areas should be large enough and sufficiently connected to ensure forest resilience to severe events. Based on the variability in mortality rates up to a regional level and composition of mortality agents dependent on stand structure, which highlights heterogeneity, the proposed minimum reserve area in the order of hundreds of hectares (e.g., Čada et al. 2020) and even two orders higher in specific scenarios (geographical isolation, homogeneous age structure) (Lehnert et al. 2013, Mikoláš et al. 2017) seems to be reasonable.

8. Conclusions

The findings of the presented dissertation thesis contribute to the scientific knowledge on the mortality rates and composition of mortality agents in primary forests in the context of structural characteristics and disturbance regimes. The thesis focuses on 1) mortality rates and mortality agents in the context of stand structure in primary Norway spruce stands, 2) the relationship between disturbance history approximated by canopy area removal and current mortality rates, 3) overall and species-specific mortality and composition of mortality agents in primary European beech-dominated mixed forests, and 4) the most important drivers of basal area variability in primary forests.

Our findings suggest that the mortality rates in primary mountain Norway spruce forests are comparable to the published range of background mortality. However, the observed variability across the Carpathian region is substantial, with extremes in current plot-level mortality in the Western Carpathians. Mortality rates detected in beech-dominated mixed forests in the same region are also within the range, yet comparably lower, with less pronounced extremes, although the variability in plot-level mortality is still evident. The results also indicate bark beetle infestation is the most frequent mortality agent even in low mortality periods in high elevation Norway spruce stands and the most prevalent mortality agent in Norway spruce within mixed stands regardless of composition and overall mortality rate. Higher proportions of bark beetle-related mortality, however, did not always have a severe impact at larger scales, although short-term inventory data might not provide sufficient information to precisely define the mortality processes at different scales; coupling these findings with dendrochronological data could provide better insight. Permanent study plots used in the study will also provide a baseline to evaluate any future bark beetle outbreaks and the role of increased insect-related mortality in the

inherent dynamic in these forest ecosystems. The obtained results imply that bark beetles, even during low overall mortality phases, strongly influence mountain primary Norway spruce forests and, to an extent, also primary beech-dominated mixed stands. A significant difference in mortality rates for individual species was detected, and these differences are likely driven by species-specific composition of mortality agents. While the mortality of Norway spruce is mostly driven by insects in both evaluated forest types, the most frequent mortality agents for European beech are competition and abiotically-caused damage. The species-specific composition of mortality agents is reflected in distribution of mortality along the DBH gradient as particular mortality agents are more frequent in specific size classes. The results suggest that high mortality rates reported in the Carpathian region relate to specific forest type with its characteristic conditions, structure and species composition which emphasizes the need for structural and compositional heterogeneity, not only in primary forests but also in managed ones.
Quantification of mortality is an aspect of the disturbance and stand structure relationship which should not be neglected. Primary Norway spruce stands with higher average canopy area removed per decade in the last 120 years are currently experiencing lower annual mortality rates. A measure of variability in canopy area removed per decade during the observed period seems to be equally important as the average canopy area removal. The detected relationship is stronger on stand-level than plot-level. However, the pattern was not detected for all subregions, and appears to be changing over time as the same pattern was not confirmed for periods further in the past. It remains uncertain, whether the change is related to global change and is working towards shortening the period with the strongest effect on observed mortality, indicating accelerated stand dynamics, or it is a consequence of developmental changes in forest stands after disturbances. Nonetheless, the influence of past stand development on current mortality supports

the concept of emulating natural disturbances in managed stands. Using the historical range of variability in canopy area removal or disturbances in general to guide forest management can help sustain forest ecosystem structures, composition, and functions (Seymour et al. 2002, Long 2009, Kulakowski et al. 2017). Natural disturbance characteristics can provide guidelines to important management decisions, such as extent and intensity of operations, and rotation periods, that can be linked to natural disturbance patch size, severity, and frequency, respectively (Seymour et al. 2002, Keane et al. 2009). Such consideration might in turn lead to improved stability of target stands.

Identifying the scale dependence of major drivers brings a key insight to the complexity behind forest biomass variation. Basal area along the Carpathians reacts positively to environmental change towards southern latitudes. Disturbances affect the stands in a way highly independent on this gradient, generating substantial variability, reducing stand-level basal area, and hindering the apparent effect size of environmental gradients. It is imperative to realize that the observed relationships between forest-level attributes and environmental gradients over large geographic areas integrate both environmental effects and disturbance-induced variation. Increasing temperatures might allow forests in northern latitudes to increase in basal area, but intensifying disturbances are expected to deplete latitudinal gradients, and ultimately reduce basal area. Shifting disturbance regimes and climate change are likely both going to continue to drive variation in future stand structure and mortality along the Carpathians. Disturbances, mortality and stand structure should be considered different aspects of the same cyclical process, highly variable through space and time. It becomes crucial to review these aspects in context of each other to properly evaluate the forest dynamics under the ongoing climate change.

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