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**Disturbance dynamics, stand structure and growth pattern of the primary
forest in Europe**

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I hereby confirm that this Ph.D. thesis “Disturbance dynamics, stand structure and growth pattern of the primary forest in Europe” was elaborated independently with the usage of quoted literature and based on consultations and recommendations of my supervisor.

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Abstract

Disturbances influence forest structure, dynamics, ecosystem function and services. There is widespread concern that climate change is leading to shifts in natural disturbance regimes, and subsequent changes to the structure, composition, and function of forest ecosystems. How past disturbances have shaped forests at the scale of decades or centuries is crucial to understanding long-term forest development and biomass accumulation. This understanding will increase the capacity to manage forests more resilient to climate change.

The main objective of the thesis is to reconstruct and characterize historical disturbance regime in the mountain Norway spruce forest and to describe the impact of disturbance legacies on ecosystem services. Analysis of tree-ring widths has been shown to be the only approach to reconstruct forest history with annual resolution over centuries. Thus I first aimed to i) test the efficacy of tree-ring methods for detecting past disturbance events (section 5.1); then ii) assess spatiotemporal characteristics of disturbance regime on the plot, stand, landscape, and region level (section 5.2); and finally iii) evaluate the influence of natural disturbances on the magnitude and dynamics of biomass accumulation and maintaining lichen survival and diversity (section 5.3). To achieve first aim I compare each method against a dataset of tree growth with likelihood of a growth release calculated based on competition change from an experimental canopy disturbance mimicking a hurricane in a northern hardwood forest Massachusetts, USA. For the following aims, I compile a globally unique dendroecological dataset, which includes 12000 cored trees sampled over 560 plots located across the Czech Republic, Slovakia, Ukraine, and Romania, to examine regional scale patterns of past disturbance in primary Norway spruce forests, and impact of its legacies on ecosystem services.

The main findings of the thesis are:

i) Each tree-ring method demonstrated efficacy in the detection of canopy disturbance across experimental and observational data. Recognizing the conditions under which each disturbance detection method performs best will help avoid possible pitfalls related to reconstructing past disturbance histories and facilitate comparisons of forest histories using different methods (section 5.1.1).

ii) Evidence of a combination of variable severity disturbances that fails to fit the classical scheme of gap or patch dynamics with sharply defined sizes and borders, but is more consistent with a mixed severity disturbance regime across the landscape (sections 5.2.1 & 5.2.2). Central and Eastern Europe mountain spruce forest has been affected by series of mixed severity disturbances; these events were clustered in a period from 1800 to 1900, resulting in a broad scale peak and associated non-equilibrium of age and biomass across the regional scale under high probability to be disturbed in the near future (section **Error! Reference source not found.**).

iii) The period of time that a tree is in the canopy, and not tree age, modulates the trajectory of tree level AGBI. Time since disturbance and disturbance severity are important co-predictors for stand-level AGBI and AGB (section 5.3.1). Tree age was the strongest variable influencing lichen diversity and composition. Recent (<80 years ago) severely disturbed plots were colonized only by the most common species, however, old trees (>200 years old) that survived the disturbances served as microrefuges for the habitat specialized and/or dispersal limited species (section 5.3.2).

To conclude, recognizing the conditions under which each disturbance detection method performs best will help avoid possible pitfalls related to reconstructing past disturbance histories and facilitate comparisons of forest histories using different methods. It is critical to better understand past disturbance legacies over the larger region to assess the potential of future outbreaks and to guide decisions on post disturbance management in these key conservation areas. Management should recognize disturbances as a natural part of ecosystem dynamics in the mountain forests of Central Europe, account for their stochastic occurrence in management planning, and mimic their patterns to foster biodiversity in forest landscapes. Even late-seral forests can rapidly regain biomass lost to low intensity disturbance, and additionally survival of old trees after disturbances could maintain and/or recover large portions of epiphytic lichen biodiversity even in altered microclimates.

Key words:

Biodiversity, carbon sequestration, dendroecology, disturbance ecology, Norway spruce, forest dynamics, old-growth forest, tree-rings.

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1. Introduction

Climate change is expected to alter disturbance regimes around the globe (Seidl et al., 2014b). Interactions between disturbance regimes (Frelich, 2002; Pickett and White, 1985; Turner, 2010) influence ecosystem development at different spatial and temporal scales. Moreover, uncertainties exist on how timing and frequency of disturbances vary through time and space (Pederson et al., 2014). Understanding how past disturbances have shaped natural forests at the scale of decades or centuries is crucial to informing forest management towards increasing ecosystem resilience in the context of climate change.

Quantifying past forest disturbance events provides perspective on current forest composition, structure, and function. Tree-ring reconstructions of past disturbances cover the time not only of consecutive censuses in contemporary forest inventory plots, but also of periods before written records of forest disturbance, potentially back several centuries in time. When precisely-dated, tree rings are assigned a specific calendar year (Douglass, 1920). Increased confidence in the timing of disturbance occurrence allows ecologists a greater chance of attributing disturbances to potential driving agents or teleconnection patterns (Black et al., 2016). Relative to the lifespan of a tree, disturbance events are typically fast processes occurring over hours (e.g., windstorm) to months or years (e.g., drought) (Pickett and White, 1985). The ability to document disturbance events on an annual basis across a landscape and over centuries is a powerful method of quantifying past forest disturbance dynamics and revealing mechanisms of long-term forest development.

Our understanding of natural dynamics has largely been based on studies that characterized disturbance regimes through two opposing perspectives: either small-scale patch dynamics, traditionally seen in old-growth temperate forests (Korpel, 1995; Seymour et al., 2002), or large infrequent disturbances, often described for boreal forests (Kuuluvainen and Aakala, 2011). However, there is a continuum of natural disturbances in forests ranging from single canopy tree death to widespread low mortality all the way to severe stand-replacing events. Recent studies have demonstrated that disturbances may commonly be complex and variable, such that the dichotomous characterization of disturbance regimes as

following large infrequent disturbances or patch dynamics is too simplistic (Angelstam and Kuuluvainen, 2004).

Likewise, understanding how forest structure and composition respond to variation in past disturbances may provide insight into future resilience to climate-driven alterations of disturbance regimes (Tepley and Veblen, 2015). The complex, stochastic nature of natural disturbances, and the extent and magnitude of new disturbances are influenced by a combination of physiography, previous disturbance history, and severity of new disturbance (Bouchard et al., 2006; Splechtna et al., 2005; Wallenius et al., 2004), thus, defining clear disturbance regimes in the landscape is problematic.

A major obstacle to integrating natural disturbance patterns into stand and landscape forest management planning is the lack of landscape scale reference conditions where disturbance processes and forest dynamics can be studied. Recent research shows that spatial and temporal variability in disturbance processes is greater than that suggested by traditional models. This would imply that landscape scale management should not only mimic late successional forest structure and composition, but successional stages and structural complexity that arise from moderate to high severity disturbances as well. Understanding the common pathways to stand and landscape structures and their historical range of variability to inform forest management often requires retrospective studies in primary forests that have been relatively uninfluenced by human activities.

2. Literature review

2.1. Dendroecological methods for reconstruction disturbance dynamic

A number of tree-ring-based release-detection methods have been developed to differentiate disturbance-induced changes in growth from those caused by interannual climate variability, tree biometry, or tree life history traits (Black and Abrams, 2004; Druckenbrod et al., 2013; Fraver and White, 2005; Lorimer and Frelich, 1989; Nowacki and Abrams, 1997). This advance creates the opportunity to easily use each of these methods, including parameter adjustments within each method. Yet, faced with the diversity of approaches and parameter values, researchers likely ponder: *“How should one choose which method or parameter level to use given particular research goals and specific forest conditions?”*

The growth response of trees to disturbance has been used to quantify disturbance regimes across a variety of landscapes and biomes (Frelich, 2002; Fritts and Swetnam, 1989; Lorimer, 1980). Tree-ring reconstructions of historical disturbance are an important bridge between longer records with low temporal resolution and highly-resolved records that cover short time spans. Since the formalization of tree-ring methods of disturbance detection (Lorimer and Frelich, 1989), there has been an explosion of methods (Black and Abrams, 2004; Druckenbrod et al., 2013; Fraver and White, 2005) that introduce alternative approaches. Only Rubino and McCarthy (2004) examined differing methods. Altman et al. (2014) created a new program that contains a majority of these methods, but neither they nor Rubino and McCarthy (2004) have made a direct comparison of the newer methods. Some old and newer methods could result in inaccurate reconstructions of disturbance and forest development (Altman et al., 2014; Copenheaver et al., 2009; McEwan et al., 2014; Pederson et al., 2014). Therefore, a rigorous examination of these methods is vital as we enter a period of unprecedented ecological change.

Developers of the various release-detection methods have independently discussed the strengths and weaknesses of their specific approach (Black and Abrams, 2004, 2003; Druckenbrod et al., 2013; Fraver and White, 2005; Lorimer and Frelich, 1989), and several authors have examined the sensitivity to varying

parameters and thresholds of the growth-averaging method (Bouriaud and Popa, 2007; Rubino and McCarthy, 2004; Stan and Daniels, 2010). To date, no work has provided a detailed comparison of the different methods available on datasets with highly-resolved records of disturbance. Such datasets allow the opportunity for researchers to assess the ability of each method to detect disturbance in terms of timing and magnitude. A rigorous examination of these methods is critical because some methods could create uncertainties in the timing of disturbance reconstruction and forest development (Altman et al., 2014; Bouriaud and Popa, 2007; Copenheaver et al., 2009; McEwan et al., 2014; Pederson et al., 2014; Rubino and McCarthy, 2004; Šamonil et al., 2015).

2.2. Disturbance dynamic in the natural forest landscapes

There is widespread concern that climate change will alter natural disturbance regimes and thereby impact forest ecosystems (Dale et al., 2001; Turner, 2010). Recent changes in disturbance regimes in some regions, such as increased wildfire activity and large-scale insect outbreaks in North America, have already been attributed to climate change (Weed et al., 2013). However, in order to gauge ongoing and future changes to disturbance regimes, it is necessary to establish a solid baseline against which to evaluate these changes. This is particularly important given that disturbances are discontinuous processes that usually occur as infrequent events or episodes. Quantifying the natural range of disturbance variation over time periods of several centuries is thus important for understanding potential changes in severe large-scale events with long return intervals (Jarvis and Kulakowski, 2015).

Natural disturbance regimes, and variation in disturbance size, frequency, and severity, play key roles in shaping forest structure and development at stand and landscape levels (Abrams and Orwig, 1996; Frelich, 2002; Pickett and White, 1985). Understanding the influence and importance of natural disturbances is needed for designing forest management that maintain forest functioning and biodiversity (Angelstam, 1998; Lindenmayer et al., 2006). Recognizing the influence of disturbance on fluctuations in tree biomass and carbon balance has global implications (Hicke et al., 2012). Given increasing

extremes in disturbances under future climate variation (Schelhaas et al., 2003), the last opportunity to explore and understand the influence of disturbances under current and historic natural conditions may be to characterize the disturbance histories of the few remaining primeval forest remnants.

Variability in disturbances over the landscape has been shown with respect to the extent, magnitude, and impact on forest ecosystems, depending on geographical characteristics, previous disturbance history, and the severity of new disturbances (Bouchard et al., 2006; Stueve et al., 2011; Wallenius et al., 2004; White and Jentsch, 2001). Ecologists have come to recognize that disturbance intensity/severity without accompanying information on the spatial and temporal pattern is a limited criterion for evaluating disturbance history. However, precisely this combination of factors makes it difficult to define a clear disturbance regime for landscapes subject to such disturbances, particularly when the resulting damage is more severe than the baseline of a single tree patch dynamic, but not severe enough to represent large infrequent disturbance (Stueve et al., 2011).

The lack of large-scale reference conditions where disturbance processes can be studied is a major obstacle to evaluating natural disturbance patterns at the stand and landscape levels. Although some very extensive primeval forest remnants still remain in North America (Frelich, 2002; Turner et al., 1998), they are quite scarce in Europe (Hamor et al., 2008; Veen et al., 2010). In addition, forest disturbances are often unpredictable and rare events (Pickett and White, 1985), which makes it difficult to capture them by traditional long-term monitoring or, more recently, even with a remote sensing approach.

The interpretations of disturbance history reconstructions are necessarily dependent on the scale of study, yet the extrapolation of results to coarser spatial scales is problematic because different factors operate on different scales (Everham and Brokaw, 1996; White, 1979). For instance, White and Jentsch (2001) mention that the smaller the study plot is relative to disturbance patches, the more likely it will be entirely disturbed by a single event and that the post-disturbance forest will be relatively homogeneous. Because spatially extensive intensive sampling is very time consuming and

costly, dendroecologists are often forced to restrict sampling to a single large plot (in stands driven by patch dynamics) or to regularly distributed dominant trees (in stands driven by large infrequent disturbances). However, studies that have applied more intensive sampling over larger areas have obtained more accurate and complete pictures of disturbance history, which have revealed high disturbance complexity and heterogeneity (D'Amato and Orwig, 2008; Panayotov et al., 2011; Svoboda et al., 2014). This suggests that the overall heterogeneity of a disturbance history is poorly captured when relying on either of these restricted approaches.

Few empirical studies, however, have addressed century long dynamics of bark beetles and forests over sufficiently large regions to quantify the scale and synchrony of past events. Recent work in western N. America, based on dendroecological reconstruction of past mountain pine beetle outbreaks, found that some historical outbreaks were synchronized across the region, suggesting that the subcontinental synchrony of the ongoing outbreak may not be entirely unprecedented (Jarvis and Kulakowski, 2015). Reconstructing historical natural disturbances at a subcontinental scale is particularly challenging in Europe, where a long history of intensive land use has largely replaced natural disturbances throughout most of the region.

Most of these studies have been carried out within single stands or forest landscapes. The few that have addressed past disturbance patterns across larger regions (i.e. over two forest landscapes) document a complex mixed severity regime across space and time, with a predominance of intermediate severity events (Svoboda et al., 2014; Trotsiuk et al., 2014). Moreover, to date no analyses exist that link past disturbance regimes with current patterns of forest structure and composition for these forest types (D'Amato et al., 2008; but see Zenner, 2005). Such analyses would not only provide an important baseline for understanding how future changes in disturbance regimes might influence forests, but would also be valuable for informing post-disturbance management and quantifying forest resilience (Seidl et al., 2014a). In Slovakia, for example, following the recent disturbances, there was much debate among forest managers regarding the future forest development and integrity of these recently disturbed

mountain forest ecosystems. The outcomes of this discussion, e.g. with regard to the question of salvage logging and re-planting, have important implications for biodiversity and provisioning of ecosystem services (Thom and Seidl, 2015).

Disturbance change is particularly relevant for the mountain forest ecosystems of Central Europe, which are dominated by Norway spruce (*Picea abies* (L.) Karst.). Over the past decades, large areas of these forests have been severely damaged by windstorms (Schelhaas et al., 2003). Wind disturbances are commonly followed by bark beetle outbreaks, and together these two agents have resulted in widespread mortality of spruce forests throughout the region. For example, in the Tatra National Park in Slovakia, wind damaged 12,000 ha of forest in a single event in 2004 (Mezei et al., 2014). Subsequently, with the abundance of wind-felled trees serving as low-defense hosts for bark beetles, a large-scale bark beetle outbreak was triggered in the surrounding unmanaged forest reserves (Nikolov et al., 2014). Similarly, a combination of windstorms and bark beetle outbreaks resulted in widespread spruce mortality in the Bavarian Forest and Šumava National. Determining whether these recent disturbance events are still within the natural range of variability of the system, or whether they exceed this range as a result of drivers such as climate change or past land use, is critical for making informed decisions regarding the management of these forests.

Much recent effort has therefore been made to determine to what degree severe large-scale disturbances such as those observed recently are part of the natural disturbance regime of Norway spruce forests in Central European mountain ranges. This body of work has mainly relied on dendroecological methods to reconstruct the history of disturbance in remnant primary forest ecosystems in the region. However, the findings of these studies remain inconclusive, with some indicating a regime dominated by small-scale, low severity disturbances (Szewczyk et al., 2011) and others finding evidence of larger-scale high severity events having also occurred in the past (Čada et al., 2013; Svoboda et al., 2014, 2012; Zielonka et al., 2010). Most of these studies have been carried out within single stands or forest landscapes. The few that have addressed past disturbance patterns across larger regions (i.e. over two forest landscapes) document a complex mixed severity regime across space and time,

with a predominance of intermediate severity events (Svoboda et al., 2014; Trotsiuk et al., 2014).

Extensive bark beetle outbreaks are thought to require a particular set of conditions, including both favorable temperatures and susceptible host forests, characterized by well-connected stands of large trees (Hart et al., 2014; Jenkins et al., 2004; Kulakowski et al., 2011; Seidl et al., 2014a; Temperli et al., 2015). Consequently, the timing and size of any given outbreak is partly dependent on the legacy left by past disturbance events. For example, large regions of mature conifer forests that originated following a widespread and severe disturbance over a century past may now be vulnerable to a large outbreak, especially under climatic conditions that may be more favorable than in the past. Such links between historic disturbance and subsequent bark beetle outbreaks have been documented both empirically (Kulakowski et al., 2012) and with simulations (Temperli et al., 2015, 2013). These studies indicate that the long-term historic legacies of past disturbances (i.e. severity, timing, and synchrony) are likely to have an important influence on ongoing and future outbreaks under climate change.

2.3. Impact of the disturbance legacies on ecosystem services

To date no analyses exist that link past disturbance regimes with current patterns of forest structure and composition for these forest types (D'Amato et al., 2008; but see Zenner et al., 2015 for analyses in other ecosystems). Such analyses would not only provide an important baseline for understanding how future changes in disturbance regimes might influence forests, but would also be valuable for informing post-disturbance management and quantifying forest resilience (Seidl et al., 2014a).

Recent efforts to quantify dynamics and drivers of productivity in forested ecosystems have included comprehensive overviews of the global biomass variability among different biomes and climatic regions (Burrascano et al., 2013; Keith et al., 2009; Luyssaert et al., 2008), as well as the establishment of comprehensive growth models for managed forests (e.g., Weiskittel et al., 2011). Yet, much work is still needed to understand and quantify biomass dynamics and

the influence of disturbances in the more remote and less well investigated primary forests (Keeton et al., 2011; Taylor et al., 2014). Most research on the impacts of disturbance on the carbon balance in primary forests has focused on stand replacing disturbances (Magnani et al., 2007; Pregitzer and Euskirchen, 2004) where forest responses have been shown to be highly analogous to those in the better investigated managed forest ecosystems (Bradford et al., 2008; Chen and Luo, 2015). This leaves many unanswered questions about the long-term biomass dynamics in primary forests characterized by complex developmental pathways and/or mixed-severity disturbance regimes (Stueve et al., 2011; Woods, 2004).

The dynamics of aboveground biomass (AGB) accumulation in forests are an aggregate of the AGB of individual trees, including the effect of competition and resource availability, and mortality (Berger et al., 2004; Coomes et al., 2014; Jucker et al., 2014). Thus, it is critical to understand the accumulation rate and carbon storage potential of trees considering their age, diameter, and competition status within a stand. In particular, interactions among tree size, tree age, tree life history, and tree lifespan require better quantification for diverse species while considering different disturbance histories (Bigler and Veblen, 2009; Johnson and Abrams, 2009). While the growth of trees as they age has classically been thought to follow an asymptotic sigmoidal curve (e.g., Weiner and Thomas, 2001), recent studies suggest that large trees continually increase their rate of carbon accumulation with increasing size (Stephenson et al., 2014). Investigations of large and/or old trees thus require particularly careful examination, firstly, owing to this interesting recent departure from conventional wisdom, and secondly, because of the disproportionately strong impact large trees have on the carbon dynamics of whole stands (Fauset et al., 2015; Slik et al., 2013).

The broad range of disturbance severities, spatial extent, timing, and return intervals makes it difficult to study and generalize disturbance impacts on forest ecosystems. Moreover, due to the stochastic nature and infrequent occurrences of natural disturbances, many traditional methods (e.g., small permanent plots, short-term remote sensing records) have limited potential to investigate long-time scale processes related to disturbance dynamics. Dendroecological methods have

proven to be a useful tool in the long-term and retrospective investigations including both disturbance dynamics (Frelich, 2002; Pederson et al., 2014) and forest biomass dynamics (Babst et al., 2014a; Foster et al., 2014; Halpin and Lorimer, 2016).

Old-growth forest often provide services, habitat, and biodiversity uncommon in many landscapes, but they too are subject to disturbances of varying severity; thus, uncertainties abound regarding the long-term persistence of many species after disturbances (Johansson, 2008), particularly large-scale windthrow events and bark-beetle outbreaks. If habitat heterogeneity is increased by natural disturbances, the effect on species diversity would be positive (Beudert et al., 2015), but it may also result in the loss of habitat and consequent fragmentation for certain species (Johansson et al., 2006). A network of habitat fragments must satisfy certain necessary conditions in terms of number, size, and spatial configuration of fragments to allow for long-term persistence of the focal species (Hanski and Ovaskainen, 2003). The capacity of individual species to persist and recolonize adjacent areas after disturbances can help us to understand the processes and value of old-growth forests to preserve rare species in altered landscapes.

Epiphytes are long-lived sessile organisms that persist on trees until tree fall; other threats to local extinction are relatively minor, and it is unlikely to go extinct locally until the tree dies (Johansson et al., 2012). Species with a narrow ecological niche and large dispersal propagules have lower colonization rates than species with a wide niche and small, easily dispersed propagules. Colonization rates are substantially higher when habitat connectivity is high (Fedrowitz et al., 2012), in accordance with the metapopulation theory (Hanski, 1999). Isolation of subpopulations in fragmented landscapes greatly increases the risk of future extinction at a landscape scale despite survival of subpopulations, described by Tilman et al. (1994) as extinction debt. Lichens with limited dispersal ability may be restricted to survive in metapopulations in dispersed remnant old-growth forest fragments. Hypothetically, long-lived epiphytic lichens could survive on trees for several hundred years, thereby reducing the risk of extinction with longer time

frames to allow for the creation of suitable conditions for colonization in the surrounding landscape.

In disturbed landscapes, residual individual or small groups of older trees that survive severe disturbance events could serve as micro-refuges until surrounding trees become suitable for colonization (e.g., develop suitable bark structure for the capture of vegetative propagules, presence of compatible photobiont for fungus spores). However, lichen species must be able to survive on micro-refuges in altered microclimatic conditions related to the surrounding canopy dieback (Gauslaa et al., 2007; Johansson et al., 2006); and, despite the possible existence of micro refuges after disturbance, subpopulations of some species could disappear immediately after the disturbance.

3. Aims of the thesis

Thesis aims to reconstruct and quantify historical range of disturbances and their legacy on ecosystem services (carbon dynamics and biodiversity). How past disturbances have shaped forests at the scale of decades or centuries is crucial to understanding long-term forest development and biomass accumulation. This understanding will increase the capacity to manage forests more resilient to climate change. Based on up to 500 permanent plots across several primary *P. abies* forest landscapes we conduct comprehensive analysis to enlarge our understanding of past disturbance history, biomass accumulation dynamics and biodiversity in primary forest ecosystems.

Particular aims of the thesis are:

1. Investigate the efficacy of four of the commonly used tree-ring methods (radial-growth averaging, boundary line, absolute increase, and time series) in the detection of past disturbance events (section 5.1.1).
2. Reconstruct the spatiotemporal pattern of past disturbances at different scales (plot, stand, and landscape) for Central (Slovakia) and Eastern (Ukraine) Europe (section 5.2.1. and 5.2.2).
3. Assess the level of synchronization and variability in disturbance history across the entire Carpathian region (section **Error! Reference source not found.**).
4. Evaluate the influence of natural disturbances on the magnitude and dynamics of biomass accumulation at decadal to centennial time-scale (section 5.3.1).
5. Evaluate the importance of old trees as micro-refuges and microclimate stability in maintaining biodiversity (section 5.3.2).

4. Methods

4.1. Study area and data collection

Study was conducted in two distinct regions: New England, USA (section 5.1) and Carpathian mountain range (all other results).

4.1.1. New England, USA

To test the efficacy of tree-ring methods in the detection of past disturbance events we used: i) the hurricane manipulation experiment located at the Harvard Forest, Petersham, Massachusetts; and ii) long-term monitoring plots located across New England (Harvard Forest, Pisgah State Park, and North Round Pond forests).

The hurricane manipulation experiment (“hurricane pulldown”) was located at the Harvard Forest, Petersham, Massachusetts, USA (72.20 °N, 42.49 °W, 300-315 m a.s.l.) in a ca. 101-year old *Quercus rubra*-*Acer rubrum* forest developed following a clearcut in 1915 (Harvard Forest Archives, *unpub. data*). A 0.8 ha experimental site and 0.6 ha control site were separated by a 30 m forest buffer. Prior work (Rowlands 1941, Foster 1988) that examined the relationship between damage and forest composition and age in the 1938 hurricane provided a benchmark of roughly 80% canopy loss for the treatment effect in this experiment. Prior to the hurricane experiment, all trees ≥ 5 cm DBH were tagged and spatially mapped. In early October 1990, during the peak of the hurricane season, 276 trees were toppled in a northwesterly direction with a winch to effectively simulate the 1938 hurricane disturbance. Immediately following the toppling of trees, all trees were classified as bent, leaning, snapped, or uprooted. Surveys indicated that 80% of the canopy trees and two-thirds of all trees ≥ 5 cm DBH were damaged. Tree survival, recovery, and DBH were measured in 1990, 1996, 2000, 2005 and 2010 (Foster et al., 1997). In 2009, 57 *Acer rubrum* trees from within the hurricane experiment and the adjacent control forest were cored to determine how damage and release affected tree growth. Live *A. rubrum* stems were selected to represent varying damage: bent (n=15), uprooted (n=6), snapped (n=6), and standing or undamaged (n=15) from the pulldown plot, and 15 undamaged trees from the control plot. One core per tree was collected at

approximately breast height (1.3 m). Re-analysis of these samples in 2015 focused on crossdated cores, resulting in 15 trees from the control plot and 32 from the hurricane experiment plot.

Additionally, vegetation and tree-ring sampling were conducted in long-term monitoring plots at the Harvard Forest (Lyford Grid and around the environmental measuring site (EMS) eddy flux tower), and in Pisgah State Park, New Hampshire (Pisgah Tract and North Round Pond forests). Trees were sampled in 2-3 plots per site in a nested design; all trees >10 cm DBH censused, mapped (distance and azimuth from plot center), and cored from 0-13 m from plot center, trees >20 cm DBH censused, mapped, and cored from 13-20 m from plot center, and trees >30 cm DBH censused, mapped, and cored from 20-30 m from plot center. The 20-30 m nest was only employed in forests that were potentially old growth. Three plots with a similar nested design from the old-growth forests in the Palmaghatt Ravine at Minnewaska State Forest (New York) were used here as a control because little damage is expected in this sheltered ravine that is roughly 125 km west of the path of the 1938 hurricane. The gradient of hurricane disturbance ranges from severe in the old-growth forests of Pisgah State Park, moderate at the Harvard Forest, and little to no disturbance in the Palmaghatt Ravine. In all sites within the gradient, two to three cores were removed per tree. For more information on study area, see section 5.1.

4.1.2. Carpathian range, Central and Eastern Europe.

To access and quantify past disturbance history and its impact on ecosystem services study areas were selected in the most preserved forests remnants along the Carpathian primary mountain belt spanning the gradient from North-West (Slovakia) to South-East (Romania). Using remote sensing data, a review of scientific and popular literature, and visual inspections, in each location the most preserve stand were selected ranged from ~ 15-50 ha (Fig. 4.1). Often poor access on the steep and stony slopes protects those stands from selective logging or grazing. Study stands cover the altitudinal range from 1200 (Ukraine) to 1700 m (Romania). Predominant bedrock is: Romania – volcanic and

crystalline (Svoboda et al., 2014); Ukraine – sandstone (Valtera et al., 2013); Slovakia – Granitoids and Limestones (Janda et al., n.d.).

In each stand, we placed 15-25, 1000 m² (500 m² in rare cases) circular plots using a stratified random design (Svoboda et al., 2014) for a total of 560 plots. In each plot, the positions, diameters, social status (Lorimer and Frelich, 1989), and species of all living trees with a DBH >10 cm were recorded for a total of ca. 33000 trees. Using a random generator, we selected up to 25 non-suppressed trees per plot for the dendrochronological analysis and age estimation. For more details please see sections 5.2 and 5.3.

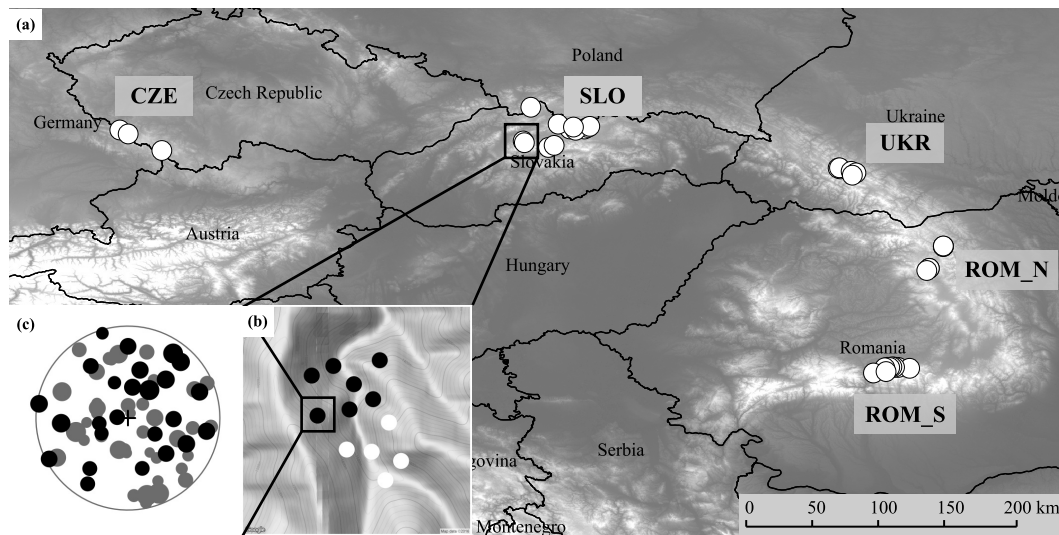


Fig. 4.1 Geographical location of the 37 study stand with 560 plots (0.1 ha each). B: example of the plot distribution within a stand. Black dots represent plots that experienced a disturbance event in the period 1900-1910. C: All trees within the plot were mapped (grey dots) and 25 randomly selected were cored (black dots). Source of digital elevation model: <http://www.reverb.echo.nasa.gov> and Google; country boundaries: <http://www.diva-gis.org>.

4.2. Data analysis

4.2.1. Dendroecological methods for reconstruction disturbance dynamic

We used four widely applied release detection methods. Growth release methods used here can be divided into two broad groups: radial-increment averaging (radial growth-average GA, boundary line method BL, absolute increase method AI) and time-series analysis (TS). All methods were originally

designed and developed for different forest types or species in eastern North America: Radial-growth averaging for trees in the deep shade of northern hardwood forests (Lorimer 1985; Lorimer and Frelich 1989), which was later adapted for overstory oak (Nowacki and Abrams, 1997); Boundary Line for eastern hemlock, pine, and oak (Black and Abrams, 2004, 2003); Absolute Increment for red spruce, balsam fir, American beech (Fraver and White, 2005); and Time Series for eastern hemlock, white pine, and American beech (Druckenbrod, 2005).

Before testing the four growth-release methods, we developed an independent method to determine the likelihood of a growth release in each individual tree via the change in its competitive status before and after the pull-down event as determined from the tree census data. We estimated the competition status of each tree using a distance-weighted size competition index (Tomé and Burkhart, 1989) $CI = \sum \frac{(d_j - d_i)}{(dist_{ij} \times rad)}$ where d_i , the DBH of focal tree, d_j is the DBH of neighbouring tree, $dist_{ij}$, the distance between the neighbouring tree and focal trees, and rad , the radius beyond which competition between trees is considered negligible (10 m in this study). Change in competition (CC) was estimated as the difference of CI for the year immediately before the induced disturbance and 5 years after in both the control and experimental plots in the hurricane-simulation experiment. We applied linear discriminant function analysis (DFA) with jackknifed prediction to changes in competition at the individual tree level to empirically determine whether surviving trees had responded to the reduction in competition after the experimental hurricane disturbance.

We also conducted a sensitivity analysis to identify and quantify how different window length and thresholds influence the stand level reconstruction of disturbance history for the hurricane pull-down experiment at the Harvard Forest and the impact of the 1938 Hurricane at the severely disturbed Pisgah Tract. The precision and intensity of detected disturbance events for each combination of window length and threshold was quantified.

4.2.2. Disturbance dynamic in the natural forest landscapes

The disturbance history was evaluated based on two main types of tree response to decrease in competition (Fig. 4.2): i) rapid early growth rate (open canopy recruitment and ii) abrupt, sustained increases in tree growth. We applied the absolute increase (AI) method (Fraver and White, 2005) to reconstruct the disturbance history based on the tree-ring series (results from section 5.1).

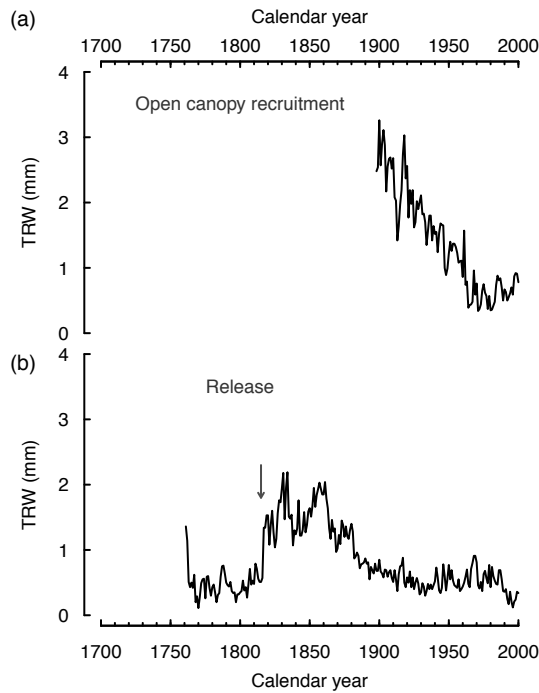


Fig. 4.2 Examples of trees categorized as recruited in the gap (a) and having a release after suppression (b). Release after suppression was identified using absolute increase method.

Tree level canopy accession events were recalculated to the proportion of the canopy area on the plot level that is currently covered by the subject tree (Frelich, 2002; Svoboda et al., 2014). The current tree crown areas were modeled based on tree DBH ($R^2=0.61$, $p<0.001$). Tree level events were summed annually and expressed as the proportion of the available canopy area to represent the plot level disturbance chronology. We fit a kernel density function over the reconstructed disturbance history, weighted by the canopy area (Trotsiuk et al., 2014). Plot level densities of disturbance history were combined to represent the stand level disturbance histories. For each stand we identified the year when maximum proportion of the canopy area was disturbed (Fig. 4.3), and indicate it

as time since last main disturbance event (TSD). Proportion of the canopy area disturbed during that event was used as a maximum disturbance severity (MDS).

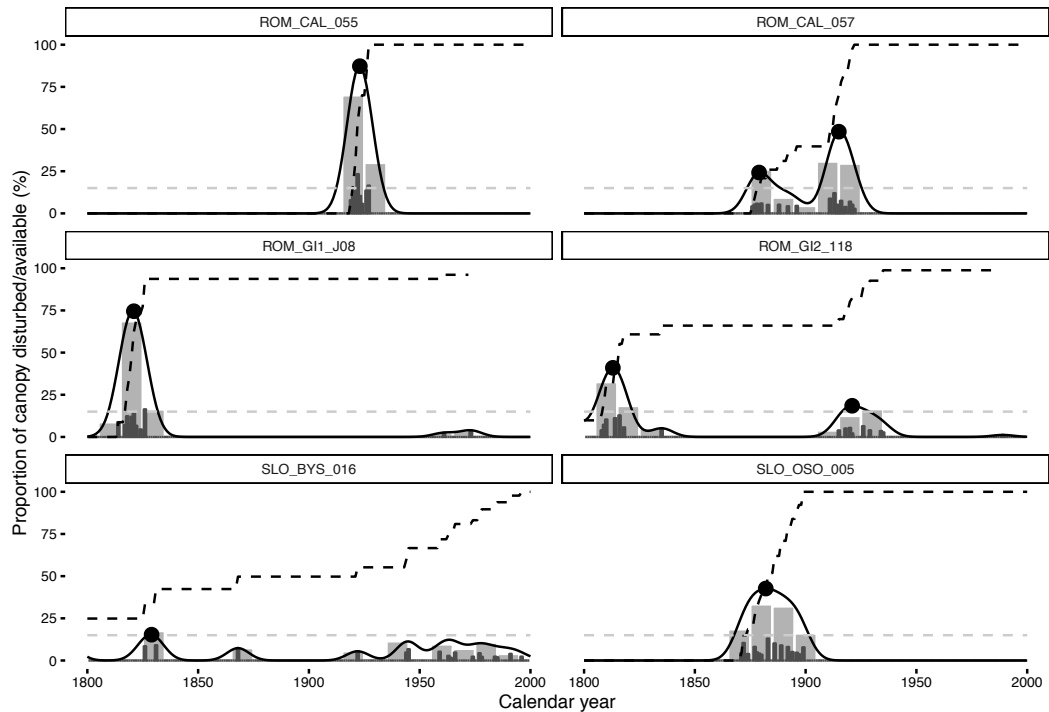


Fig. 4.3 Plot level disturbance history represented as proportion of the trees canopy area responded to disturbances binned by year (black bars) or decade (grey bars). Peaks of disturbances (solid circles) were identified based on the standardized density function (black line) for events with more than 15% of intensity. The dashed grey line shows available tree canopy area.

4.2.3. Impact of the disturbance legacies on ecosystem services

We used aboveground biomass accumulation as one of the important ecosystem service. To estimate biomass based on a trees' DBH, we considered allometric equations for spruce based upon output parameters (AGB in kg), the species and diameter range used to develop the equation, as well as the geographical location of the allometric study site. The equation developed for the Czech Republic spruce forest (Zianis et al., 2005) was found to be the closest match to our study region. Individual tree diameters were reconstructed back in time based upon the method of Bakker (2005). Using these reconstructed diameters, we then computed the historical AGB and AGBI for each tree and year

(Babst et al., 2014b). Stand-level AGB and AGBI were calculated as a sum of AGB and AGBI of all living trees on each plot.

To access individual tree aboveground biomass accumulation we fitted a generalized additive mixed model (GAMM) with a linear combination of smooth functions of DBH and tree age and their interaction as explanatory variables on AGBI, considering random effects (Tree). The pertinence of the random effect and interaction effect was determined by comparing the different models using the Akaike Information Criterion (AIC) value (Burnham and Anderson, 2002). We calculated significance of the explanatory variables and the overall variance explained by the model.

To explain patterns and variability of lichens (as a proxy of biodiversity) based on stand age and disturbance history we used linear mixed effects model and general additive models. We analysed individual species relationships to tree age and presence of old trees at the plot level in comparison to microclimate change. We used general additive models (GAM) from the with binomial distribution and with Plot as a random effect to test the influence of age variables (age and maximum age) and microclimatic change, simplified to two categories, high (extreme and heavy disturbance) and low severity (light and moderate); for high severity events, we assumed substantial microclimatic changes existed in historical development of the canopy.

5. Results

The dissertation thesis consists of 4 published manuscripts one submitted and one to be submitted manuscript. The first part focuses on the comparing four dendroecological methods for detecting past disturbance events (section 5.1). The second part aims at analysis the spatiotemporal dynamic of disturbances on the plot, stand, landscape and region levels (section 5.2). The third part presents an assessment of the impact of disturbance legacies on ecosystem services (section 5.3).

5.1. Dendroecological methods for reconstruction disturbance dynamic

5.1.1. Testing the efficacy of tree-ring methods for detecting past disturbance events using experimental data and known events

In review as:

Trotsiuk, V., Druckenbrod D. L., Pederson N., Orwig D. A., Bishop D. A., Barker-Plotkin A., Fraver S., Martin-Benito D. 2017. Testing the efficacy of tree-ring methods for detecting past disturbance events using experimental data and known events. *Methods in Ecology and Evolution*.

Author contributions:

V.T., D.D., D.M-B. and N.P. conceived ideas and designed the study;

D.O., D.B., A.B-P. and N.P. performed the sampling;

V.T., D.D., D.M-B., D.B. and N.P. performed the dendrochronological analyses;

V.T., D.D. and D.M-B. performed data and statistical analysis;

V.T. and N.P. wrote the manuscript and all authors commented on it.

Testing the efficacy of tree-ring methods for detecting past disturbance events using experimental data and known events

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Running-title: Comparison of growth release detection methods

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Summary

1. Disturbances influence long-term forest structure and function. Accurately quantifying the precise timing and intensity of past events provides insight into the legacy of disturbance and will increase capacity to manage forests that are more resilient to climate change. Tree-ring analysis of abrupt and sustained growth increases in surviving trees (i.e., ‘releases’) is the only approach capable of reconstructing past forest disturbances with annual resolution at centennial scales.

2. Here, we: i) investigate the efficacy of four commonly used tree-ring methods to detect past disturbance events and ii) assess the sensitivity of each method’s detection parameters and thresholds. We first compare each method using a dataset of measured diameter expansion (census) for two decades following an experiment mimicking a hurricane. We then evaluate each method across an observed gradient of hurricane impact. Finally, we compare each method against census data in a forest without any significant disturbance observed during a 45-year period.

3. We used discriminant function analysis (DFA) to identify the likelihood that surviving *Acer rubrum* trees experienced a significant reduction in competition as a result of the hurricane experiment. Disturbance detection methods agreed with 62-84% of the growth releases categorized by DFA. The absolute-increase and original radial-growth averaging method had the highest temporal precision for dating growth releases and produced the lowest rate of false negatives. The modified radial-growth averaging method produced the highest rate of false positives. Sensitivity analysis indicated a significant negative

relationship between detected stand-level intensity of disturbance severity and detection window length and threshold across all methods ($p < 0.001$).

4. We find that each method was effective in detecting canopy disturbance, but the original radial-growth averaging method and absolute increase method had lower levels of overall error in detecting disturbance events. Parameter settings play a key role in the accuracy of reconstructing disturbance history regardless of which method is employed. Time-series and radial-growth averaging methods require the least amount of *a priori* information, but only time-series analysis quantifies the subsequent growth increment. Finally, we recommend yearly binning of disturbances, can likely improve reconstructions of forest history and thus further our understanding of past forest dynamics.

Keywords: Absolute increase, Boundary line, Competition; Forest development; Forest dynamics; Growth releases, Time-series analysis, Release

Terminology:

Tree level

Window length parameter – number of consecutive years used to calculate average growth for radial-growth averaging disturbance detection methods prior to and following a potential disturbance event. For the time-series approach, window length is the number of years used to calculate residuals.

Threshold parameter – criteria to determine if the disturbance event exceeds minima to be defined as a growth release (i.e., an abrupt increase in ring widths). Expressed in % with respect to previous growth.

False positive event – an event is detected, but not by discriminant analysis function based on changes of the competition index before and after the release.

False negative event – an event is detected by discriminant analysis function based on change in competition index, but not by method.

Stand level

Disturbance Intensity – the proportion of trees responding to disturbance standardised by moving kernel density estimation function. Intensity is related to

the number of trees with a detected event and their temporal synchrony during the same event.

Peak disturbance year – year with the greatest estimated disturbance intensity.

Accuracy – intensity agreement between actual disturbance and peak disturbance year estimated from tree rings.

Precision – temporal agreement between actual disturbance and peak disturbance year.

Introduction

Quantification of past forest disturbances reveals the dynamics that led to current forest composition, structure, and function. Tree-ring reconstructions of past disturbances surpass both the length of time in contemporary forest inventories and, quite often, periods prior to written records. Importantly, precisely dating tree rings to assign them a specific calendar year offer the possibility to reconstruct centuries of forest dynamics with annual resolution (Douglass 1920). Increased confidence in the timing of disturbance allows ecologists a greater chance of correctly attributing disturbances to potential agents of disturbance or teleconnection patterns (Black et al. 2016). Relative to the lifespan of a tree, disturbance events are typically fast processes occurring over hours (e.g., windstorm) to slower processes that occur from months or seasons to years (e.g., drought) (Pickett and White 1985). Documenting disturbance at annual resolution, over centuries, and from the tree to continental scales is a powerful way to better understanding forest dynamics. Such studies have the potential to shed much light on the mechanisms driving long-term forest development.

Almost a century after the publication of a pioneering paper on the potential identification of past forest disturbance from tree rings (Marshall 1927), a number of tree-ring-based disturbance-detection methods have been developed to differentiate disturbance-induced changes in tree growth from those caused by life-history traits, biometry, stresses, or climate variability. Briefly, an abrupt, large, and sustained increase in tree ring width (radial growth) is inferred to be a release from tree-to-tree competition and evidence of past canopy disturbance.

Synthesizing these growth releases into a time series reveals centuries of canopy disturbance (Lorimer 1980). Disturbance detection methods were formalized in the mid- to late-1980s so the frequency and intensity of disturbance could be quantified through time (Lorimer 1985, Lorimer and Frelich 1989). Soon afterward, a series of methods and approaches were developed that either built directly upon these original methods (Nowacki and Abrams 1997, Fraver and White 2005) or used new approaches (Black and Abrams 2003, Druckenbrod 2005, Druckenbrod et al. 2013). The growing interest in studying old-growth forests, ecological restoration, and forest conservation biology increased the use of these methods.

Recent software development has placed the primary methods of disturbance detection into the R package TRADER (Altman et al. 2014) which creates the opportunity to simultaneously compare several methods and adjust the parameters and thresholds for each method. Yet, faced with the diversity of approaches and parameters, researchers likely ponder, *“How should one choose which method, parameters, and thresholds to use given particular research goals and specific forest conditions?”*

Developers of the various release-detection methods have independently discussed the strengths and weaknesses of their specific approach (Lorimer and Frelich 1989, Black and Abrams 2003, Black and Abrams 2004, Fraver and White 2005, Druckenbrod et al. 2013). A few studies have examined the sensitivity to varying parameters and thresholds of the growth-averaging method (Rubino and McCarthy 2004, Bouriaud and Popa 2007, Stan and Daniels 2010). To date, however, no work has provided a detailed comparison on the performance of the main detection methods with datasets of controlled or observed records of disturbance. This kind of data would allow assessing the ability of each method to detect the timing of a disturbance and estimate its magnitude. A rigorous examination of these methods is critical regarding their ability to correctly identify past disturbances (both false positives and false negatives) and the timing of disturbances (Rubino and McCarthy 2004, Bouriaud and Popa 2007, Copenheaver et al. 2009, Altman et al. 2014, McEwan et al. 2014, Pederson et al. 2014, Šamonil et al. 2015).

Our primary objective was to analyze the performance of four widely used disturbance-detection methods in a forest subjected to an experimentally-induced disturbance. The four methods examined here are: radial-growth averaging (Lorimer and Frelich 1989, Nowacki and Abrams 1997), boundary line (Black and Abrams 2003, 2004), absolute increase (Fraver and White 2005), and time series (Druckenbrod 2005, Druckenbrod et al. 2013). We also examined the performance of both the original (Lorimer and Frelich 1989) and modified (Nowacki and Abrams 1997) radial-growth averaging method. Performance was assessed by a method's ability to detect a disturbance of known timing and magnitude. Our secondary objectives were to: **i)** investigate the efficacy of these methods in forests containing a range of conditions and disturbance histories and **ii)** gain insight into the sensitivity of each method to adjustments in their temporal parameters and growth thresholds. Our study will provide guidance for future tree-ring studies with respect to method selection and interpretation of results.

Materials and methods

To first test the sensitivity of these methods, we used repeated forest census data from an experiment designed to mimic the damage in upland forests caused by the 1938 hurricane in New England (Cooper-Ellis et al. 1999). We also compared each method in forests along a gradient of disturbance severity caused by the 1938 hurricane ranging from old-growth forests directly in the path of the hurricane to a mature forest outside the cone of damaging wind (Boose et al. 2001) (Fig. 1). Finally, we used data from a long-term 3-ha study plot, where no significant canopy disturbance occurred since 1969 (Eisen and Barker Plotkin 2015), to examine how each method performs in forests with no severe canopy disturbance.

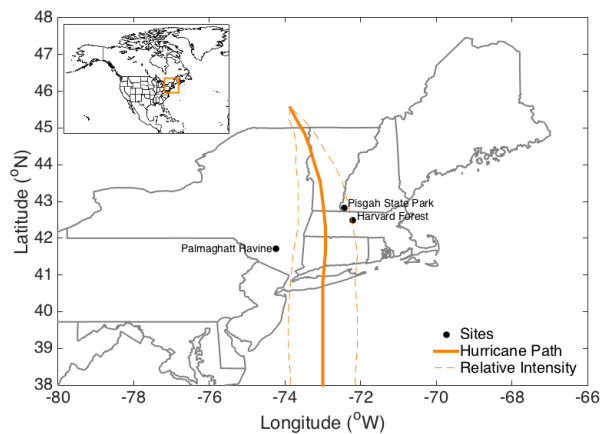


Fig. 1. Map of the study site location (black dots), Hurricane path (solid orange line), and relative maximum sustained wind speed intensity (width between dashed orange lines) (Boose and Foster, 1999).

Study sites and data sets

Hurricane Pulldown Experiment

The hurricane manipulation experiment (“hurricane pulldown”) was located at the Harvard Forest, Petersham, Massachusetts, USA (72.20 °N, 42.49 °W, 300-315 m a.s.l.) in a ca. 101-year- old forest dominated by *Quercus rubra* and *Acer rubrum*. The forest originated following a clearcut in 1915 (Harvard Forest Archives, *unpub. data*). A 0.8 ha experimental site and 0.6 ha control site were separated by a 30 m forest buffer. Prior to the hurricane pulldown experiment, all trees ≥ 5 cm diameter at breast height (DBH) were tagged and spatially mapped. In early October 1990, 276 trees were toppled in a northwesterly direction to effectively simulate the 1938 hurricane disturbance. The impact of the 1938 hurricane provided the benchmark of roughly 80% canopy loss for the hurricane pulldown experiment (Rowlands 1941, Foster 1988). Similarly, surveys immediately following the toppling of trees indicated that 80% of the canopy trees and two-thirds of all trees > 5 cm DBH were damaged (damage was classified as bent, leaning, snapped, or uprooted). For more details on this experiment, see (Cooper-Ellis et al. 1999, Plotkin et al. 2013).

In 2009, a total of 57 *Acer rubrum* trees from within the hurricane experiment and the adjacent control forest were cored once at approximately breast height (1.3 m) to determine how implementation of the hurricane pulldown

experiment affected the growth of surviving trees. *Acer rubrum* is the most numerous species, has a large potential for competitive release, and experienced a wide variety of damage intensity during the experiment. Live stems selected for coring represented varying damage: bent (n=15), uprooted (n=6), snapped (n=6), and standing or undamaged (n=15) from the pulldown plot, and 15 undamaged trees from the control plot.

1938 Hurricane Gradient Sites

Vegetation and tree-ring sampling were conducted in long-term monitoring plots at the Harvard Forest (Lyford plot), and in Pisgah State Park, southwest New Hampshire (Harvard Pisgah Tract and North Round Pond forests). Trees were sampled in 2-3 plots per site using a nested design: 1) all trees 0-13 m from plot center and >10 cm DBH were censused, mapped (distance and azimuth from plot center), and cored, 2) trees 13-20 m from plot center and >20 cm DBH were censused, mapped, and cored, and 3) trees 20-30 m from plot center and >30 cm DBH were censused, mapped, and cored. The 20-30 m nest was only employed in forests that were potentially old growth. Three plots were sampled with a similar nested design in an old forest of the Palmaghatt Ravine at Minnewaska State Forest (New York State). The gradient of hurricane disturbance ranges from severe in the old-growth forests of Pisgah State Park, moderate at North Round Pond and at the Harvard Forest Lyford plot, and little to no disturbance in the Palmaghatt Ravine. In all sites, 2-3 cores were extracted per tree. The number of trees cored per forest are 144 in the Lyford plot, 224 in the Pisgah Tract, 155 at North Round Pond (91 trees in the two broadleaf-dominated plots and 64 in the conifer-dominated plot), and 157 trees at the Palmaghatt Ravine.

Tree core preparation

All cores were dried, sanded, and visually cross-dated following standard dendrochronological methods (Stokes and Smiley 1968). They were later measured to the nearest 0.001 mm and dating was verified with the program COFECHA (Holmes 1983, Grissino-Mayer 2001). Although increased core

replication helps to recover a greater amount of disturbance history (Copenheaver et al. 2009), only the oldest core per tree was used in the hurricane gradient samples so that a parallel comparison could be made to the samples collected in the hurricane pulldown experiment. In the hurricane pulldown experiment, dating control of all cores resulted in 15 crossdated trees from the control plot and 32 crossdated trees from the hurricane pulldown plot. Outside of the hurricane experiment, crossdated time series of radial increments from 699 trees were used for our study.

Disturbance detection methods

Growth release methods used here can be divided into two broad groups: radial-increment averaging (radial growth averaging, boundary line, absolute increase) and time-series analysis (time-series approach) (Fig. 2). Radial-increment averaging methods involve comparing mean growth rates prior to and after year any year t within an *a priori* number of years, hereafter ‘window length’, to determine if a significant increase in growth occurred on year t ; with further constraints involved in boundary line and absolute increase methods. The time-series approach identifies sequences of statistically extreme residual ring widths after accounting for the effects of any biological age trend and autocorrelation (Druckenbrod 2005). All methods were originally designed and developed for different forest types or species in eastern North America: radial growth averaging for trees in the deep shade of northern hardwood forests (*Acer*, *Betula*, *Fagus grandifolia*, *Tsuga canadensis*, etc.) (Lorimer 1985, Lorimer and Frelich 1989), which was later modified for overstory *Quercus* spp. (Nowacki and Abrams 1997) and applied to wide range of forests, including low-density *Pinus palustris* forests (Pederson et al. 2008); boundary line for *Tsuga canadensis*, *Pinus* spp., and *Quercus* spp. (Black and Abrams 2003, Black and Abrams 2004); absolute increase for *Picea rubens*, *Abies balsamea*, and *Fagus grandifolia* (Fraver and White 2005); and time series for *Tsuga canadensis*, *Pinus strobus*, and *Fagus grandifolia* (Druckenbrod 2005).

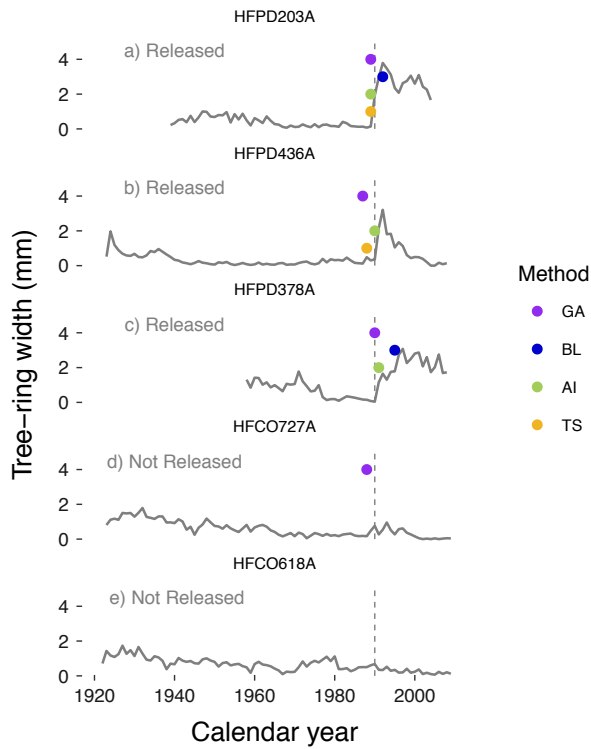


Fig. 2. Examples of trees categorized as having been released (a-c) or not (d-e) based on the DFA of their competition changes following the 1990 hurricane pull-down experiment (dashed vertical line). Colored dots signify identified releases according to method; their locations along the x axis signifies the year that method identified the release. Methods: GA = growth averaging, BL = boundary line, AI = absolute increase, TS = time series. TRW = tree-ring width.

i) Radial-growth averaging methods

One of the earliest developed and still commonly used methods is based on ring width running means with a 15-year window length (Lorimer 1980, 1985, Lorimer and Frelich 1989). The original method averaged radial growth over the preceding 15-year period M_1 (including the target year t), and the average radial growth over the subsequent 15-year period, M_2 (excluding the target year t) to calculate the percentage growth change (PGC) for each annual ring as:

$$PGC = \frac{M_2 - M_1}{M_1} * 100. \quad (\text{Eq. 1})$$

The original thresholds to detect growth releases were $\geq 100\%$ growth increase for a “major, sustained” release and 50-99% for a moderate release (Lorimer 1985, Lorimer and Frelich 1989). These proposed window lengths and thresholds would

minimize potential false positives that could be caused from changes in climate such as a return to normal or wet conditions after a severe drought. The original window lengths were shortened to 10 years to capture more disturbances, especially those from old-aged canopy oak trees (Nowacki and Abrams 1997). Based on thinning studies, Nowacki and Abrams (1997) also determined a 25% increase in growth to be the better growth-release threshold for mature overstory trees, which respond more conservatively to canopy perturbations. Hereafter, the latter method will be called the modified radial growth averaging method. Following up on the original Lorimer and Frelich (1989) window lengths and growth-release thresholds, Pederson et al. (2014) found that indeed, shorter window lengths and lower thresholds could result in an increase of false positives if the climate moved from severe drought to an extreme pluvial. Differing M_1 and M_2 window lengths, as well as thresholds, have been applied to meet species-specific or site-specific criteria (Rubino and McCarthy 2004, Fraver and White 2005).

ii) Boundary-line method

In the boundary-line method, the percentage growth change of each ring width for each tree is scaled by its maximum potential observed growth, as defined by prior growth rates for that species growing at one or several locations (Black and Abrams 2003). Growth pulses exceeding 20% of the prior growth boundary line were classified as a release. The rationale of this method is that standardizing growth should account for the influence of site condition, species, size and tree age on the radial growth rates (Black and Abrams 2003, Black and Abrams 2004, Ziaco et al. 2012). Dividing prior growth into 0.5 mm segments and averaging percentage growth change values of the top 10 values within each segment constructs the boundary line. Defining the boundary line requires a large amount of data from a single species with similar site conditions, in some cases up to 50,000 radial increments, which may make the boundary line difficult to fit for certain stands and species (Appendix S1).

iii) Absolute-increase method

While the two previous methods are based on the relative changes of ring-width averages, the absolute-increase method (Fraver and White 2005) relies on the subtraction of the pre-event mean growth rate (M_1) from the mean post-event rate (M_2), using 10-year window lengths.

$$AI = M_2 - M_1. \quad (\text{Eq. 2})$$

Similar to the boundary-line method, if the difference exceeds a predetermined threshold for a given species, the growth increase is deemed a valid release. This method has the advantage, shared with the boundary-line method, of scaling the release criteria according to prior growth rates, making the threshold more stringent at low rates of prior growth and more lenient at higher rates. The method is meant to detect overhead canopy disturbances, making it similar to the ‘major’ releases referred to in previous methods.

Fraver and White (2005) point out that setting the appropriate species-specific release threshold can be done through an iterative process that requires expert knowledge of the growth potential for the species of interest. They demonstrated the utility of the threshold-selection process by testing it against empirical absolute increases found in different trees responding to dated canopy gaps. In cases where knowledge of species’ growth potential is not available, they suggest selecting a threshold value equal to 1.25 times the standard deviation, or somewhat less than the 90th percentile, of all absolute increases. In the current study, we used the latter procedure (1.25 SD) to determine species-specific thresholds for the absolute increase method.

iv) Time-series analysis method

Time-series analysis is central to the reconstruction of past climate using tree rings (Cook and Kairiukstis 1990) and has only recently been used for reconstructing past ecological changes (Druckenbrod 2005). This method uses intervention detection, accounts for the autocorrelation present in width measurements of sequential tree-rings and removes the long-term growth trend from a series, enabling its release criteria to scale with a tree’s growth rate similar to the boundary-line and absolute increase methods. Unlike previous methods, however, intervention detection disentangles and isolates the subsequent growth

response to a disturbance event in the units of tree-ring widths. This disturbance signal is expressed as a “*disturbance-growth index*” that detects not only the year of release but also the magnitude and duration of a release event. Disturbance growth indices can also be averaged across trees to reconstruct the resulting growth response of a forest or, alternatively can be used to remove the imbedded disturbance signal from tree-ring width measurements in order to reconstruct past climate from tree rings (Rydval et al. 2015).

We used the most recent version of the time-series methods, Curve Intervention Detection (CID) (Rydval et al. 2015). This method captures the growth increase after a canopy release event regardless if the release is either sustained or only temporary. Similar to methods used to reconstruct climate, a time-series of ring widths from each tree is power transformed and detrended to remove each tree’s long-term growth trend. Release events are identified as sequences of unusually large, positive departures from autoregressive residuals over intervals of 9 to 30 years. Using Tukey’s biweight mean as a robust estimate of location and scale, the detection criteria identifies any sequence with a scale greater than 3.29 (or 99.95% of the observations for a one-tailed analysis) as an outlier (Druckenbrod et al. 2013). A Hugershoff curve (Warren 1980, Cook and Kairiukstis 1990) is then fit to the series to quantify the magnitude of growth release. The series is then detrended using this curve to produce a disturbance-standardized series. The method iterates through the entire tree-ring series again to detect any additional release. Then, the series is re-expressed in original ring-width units (mm). Disturbance-growth indices are then calculated as the difference between the initial ring-width measurements and the disturbance-standardized series.

Analysis of disturbance methods

Determining the likelihood of growth release

Before testing each method, we developed an approach to independently determine the likelihood of a growth release in each individual tree based on tree-census data from the hurricane pulldown experiment and Lyford plot. In addition to the tree-core data, these sites have repeated censuses of mapped trees. In the

hurricane experiment, tree survival, recovery, and DBH were measured in 1990, 1996, 2000, 2005 and 2010 (Foster D, Barker Plotkin A. 1999. Vegetation Response in Simulated Hurricane Experiment at Harvard Forest since 1990. Harvard Forest Data Archive: HF002). In the Lyford plot, tree survival and DBH were measured in 1969, 1975, 1991, 2001 and 2011 (Foster D, Barker Plotkin A, Lyford W. 1999. Lyford Mapped Tree Plot at Harvard Forest since 1969. Harvard Forest Data Archive: HF032). During the census period of 1969-2011, this site experienced no major disturbances (Eisen and Barker Plotkin 2015). We estimated the competition status of each tree using a distance-weighted size competition index (CI) (Tomé and Burkhart 1989),

$$CI = \sum \frac{(d_j - d_i)}{(dist_{ij})} \quad (\text{Eq. 3})$$

where d_i is the DBH of the focal tree, d_j is the DBH of the neighbouring tree, $dist_{ij}$ is the distance between the neighbouring tree and focal trees. Change in competition was estimated from inventory data as the difference of CI for the year immediately before the induced disturbance and 5 years after in both the control and experimental plots in the hurricane-simulation experiment. We applied linear discriminant function analysis (DFA) with jackknifed prediction to changes in competition at the individual tree level to empirically determine the likelihood of the trees to respond to the reduction in competition after the experimental hurricane disturbance. DFA was calculated with R library ‘MASS’ (Venables and Ripley 2013).

Sensitivity Analysis of Disturbance Detection Methods

Trees identified as released or not released through DFA were used as the standard for comparing the efficacy of the four disturbance detection methods. Efficacy at the tree level was evaluated by the (1) correct classification of trees identified as having been released through DFA and (2) timing of the detected event compared to the year of the known event (Fig. 3). We considered two types of false detections: 1) a false negative: where DFA classified a tree as released, but a disturbance was not detected in the tree-ring data by the detection method considered, and 2) a false positive: where DFA did not show the tree having a

significant change in competition, but a disturbance detection method identified a release from the tree-ring series in that tree.

We also conducted a sensitivity analysis to identify and quantify how different window lengths and thresholds for each method influenced the stand-level reconstruction of disturbance history for the hurricane pulldown experiment and the impact of the 1938 Hurricane on trees in the Harvard Pisgah Tract (Table 1). Thresholds varied depending on the method used. For the radial-growth averaging methods, moving averages were calculated for window lengths between 5 and 15 years with a 1-year time step. For the time-series method, window lengths from 1 to 22 years were used to calculate residuals (Table 1).

Table 1 Ranges of window lengths and thresholds used for the sensitivity analysis of disturbance detection methods.

Method	Window length ($M_1 = M_2$, in years)	Threshold
Modified radial-growth averaging		From 25% to 175% by 25% increments
Boundary line	From 5 to 15 by 1 step	From 20% to 80% by 10% increments
Absolute increase		From 70% to 130% of default absolute increase threshold
Time series	Time step of 1,2,3,4,5,7,12,17,22	From 70% to 130% of default time series threshold

We used the R package TRADER (Altman et al. 2014) for all methods based on the modified radial-growth averaging approaches, and an executable program for the time-series approach (Druckenbrod et al. 2013) in Matlab (Mathworks 2014). All subsequent analyses were done using R statistical software ver. 3.0.1 (R Core Team 2013). We fitted a species-specific boundary line for our analysis (Appendix S1) using the “boundaryFit” function in the R package TRADER (Altman et al. 2014). We also evaluated how different prior growth lengths influence the curvature of the boundary line (Appendix S1).

Stand level data interpretation of release events

Summing or binning annual disturbances into decadal classes, as has commonly been done in many studies, causes large uncertainties in determining the precise timing of past disturbance (obscuring the cross-dated signal) and the severity of each event. For example, decadal binning of the 1990 hurricane experiment here split detected disturbance into the 1981-1990 and 1991-2000 bins (see Results). In an attempt to solve this issue, we fit a kernel density estimation (KDE) function to reconstructed disturbance histories to better characterize the timing and severity of disturbance events at the stand level. The KDE function is a non-parametric method to estimate the probability density function of random variables (Duong 2007). The moving KDE function was fit to 15-year windows, and the value for a particular year was extracted from the distribution at the midpoint. All values were standardized by the maximum value calculated by fitting the KDE to the normal distribution with 1 standard error and a 15-year window. After 1,000 replications, the maximum value here was determined to be 0.28184 (Appendix S2). Peaks in disturbances (e.g., years when more than 20% of sample trees responded) were identified using a peak detection function applied to the KDE data.

Using outcomes from the KDE analysis, we derived an intensity of disturbance, which incorporates both the proportion of trees showing response and synchrony in the timing of response to a release from competition. That is, we reasoned that a disturbance of greater intensity would result in more trees registering a growth response and greater synchrony in their responses. Peaks in disturbances detected represent the standardized proportion of trees responding to a disturbance. Our approach allows one to account for temporal alignment of the detected release events without losing the temporal resolution and precision due to binning the data in 10-year bins. Ultimately, our approach creates a clear and statistically-correct break between neighbouring disturbance events. These calculations were performed using the R statistical software (R Core Team 2012) with the ‘density’ function and the ‘pracma’ package (Borchers 2015) and ‘findpeaks’ function in the ‘quantmod’ package (Ryan 2008).

Results

Determining the likelihood of trees released in the hurricane pulldown

Based upon changes in estimated tree competition and growth after canopy disturbance in the hurricane pulldown experiment, discriminant function analysis classified 85% of surviving *Acer rubrum* trees as having been released from competition. A decrease of 0.10 of the competition index, translating to a 30% loss of basal area around tree within 5 years, was determined to result in a significant chance ($p < 0.001$) of a growth release for trees in the pulldown plot versus those in the control plot (Fig. 3a). This CI value is only 0.06 lower than two standard deviations of the calculated change in competition on the control plot between 1990 and 1995. Compared to trees that were less likely to have been released, trees classified as released by DFA experienced a significantly higher relative increase in diameter growth (an increase of $4.9\% \pm 5.0\%$ per year, versus a $0.9\% \pm 1.0\%$ per year for unreleased trees, t -test $p < 0.001$).

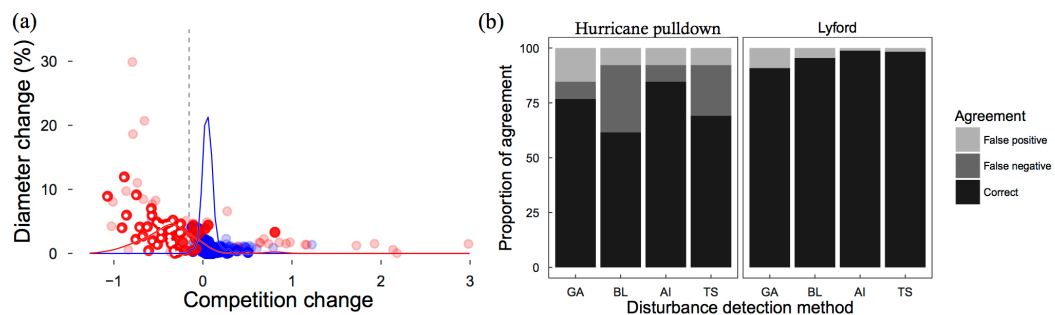


Fig. 3. (a) - Relative diameter increase (between 1990 and 1995) expressed by change in the competition index for all species on the control (blue) and experimental plots (red). *Acer rubrum* trees are bold in color; other species are designated with lighter, transparent coloring. *Acer rubrum* trees identified as released according to discriminant function analysis are represented by red hollow dots. The dashed vertical line represents competition index threshold for tree to be considered as likely to have release. **(b)** - Agreement between the classification of tree growth from the (i) hurricane pulldown experiment (left panel) and the (ii) Lyford plot (minor 1938 hurricane damage, right panel) using discriminant function analysis (DFA) and the four commonly-used disturbance detection methods tested for this study.

Evaluation of disturbance event detection

The four disturbance detection methods correctly identified 62-85% of the growth releases determined by discriminant function analysis in the hurricane experiment plots (Table 2). The absolute-increase method achieved the highest agreement (85%), while the boundary-line method achieved the lowest agreement (62%). The proportion of false positives incurred using the modified radial-growth method was 15%, while the proportion incurred by using the other three methods was only 8% (Fig. 3b). False negatives were more common than false positives, with the modified radial-growth averaging and absolute-increase methods having the least number of false negatives (8%) and boundary line having the most (31%).

Better agreement between methods in detecting growth releases identified by DFA occurred in the Lyford Plot, the forest with the lowest disturbance rates. The rates of correctly identified releases ranged from 91% to 99% (Table 2). The modified radial-growth averaging method identified the highest proportion of false positives (9%), while the other three methods identified between 1% and 5%. No false negative events were identified in the Lyford plots.

Table 2 Comparison of the efficacy of each method to different parameters of disturbance detection. The calculated sensitivity of disturbance is tested using default settings on the Harvard Forest hurricane pulldown experiment. Sensitivity is a measure of parameter robustness; if changing detection parameters greatly changes the reconstructed disturbance history, the sensitivity is considered to be high, which we view as detrimental.

Parameters	Modified Radial-growth Ave. (10/10/25%)	Boundary Line	Absolute Increase	Time Series
Correct				
Hurricane pulldown	77%	62%	85%	69%
Lyford	91%	95%	99%	98%
False Positive				
Hurricane pulldown	15%	7%	7%	8%
Lyford	9%	5%	1%	2%
False Negative				
Hurricane pulldown	8%	31%	8%	23%
Lyford	0%	0%	0%	0%

Temporal Precision of Disturbance (range, in years)	-1 – 1	-1 – 5	0 – 1	-1 – 2
Calculated Intensity of Disturbance	52%	25%	54%	18%
Sensitivity to Parameter Thresholds	high	high	n.s	high
Large Amount of Data Required	no	yes	yes	no
<i>A priori</i> Information Required	no	yes	yes	no
Additional Information Returned	no	no	no	yes

Event Detection Comparison at the Stand-level

The performance of each method on the timing and intensity of detected disturbance events at the stand level was evaluated using data from the hurricane pulldown experiment (Fig. 4). While all methods identified peaks in disturbances within a year of the hurricane experiment, the temporal offset of all series analyzed ranged from -6 years (six years prior to the experiment) to +7 years (7 years after the experiment). The absolute-increase method appears to have the best temporal accuracy overall. It had the smallest standard deviation ($sd=1.88$), but highest kurtosis ($k = 7.12$), and positive skewness ($sk=2.00$) in identifying the correct year of disturbance, suggesting correct identification of most releases but a tendency to detect releases several years after the disturbance event. Here, a lower standard deviation equals greater temporal precision. A high kurtosis indicates a narrower spread around the mean date identifying the year of disturbance while a positive skewness indicates more detections in the years following the pulldown experiment. In comparison, time-series and boundary-line methods had the largest standard deviations (2.71 and 2.50 respectively), the lowest kurtosis (1.91 and 2.03 respectively), and skewness (-0.32 and 0.46 respectively), reflecting a wider temporal spread of detected releases and in the case of the time-series method releases detected several years before the actual disturbance.

The absolute-increase and the modified radial-growth averaging methods identified the highest percentage of trees responding to disturbance (i.e., peaks of the kernel density function, 54% and 52%, respectively). In contrast, the

calculated intensity of disturbance for the time-series and boundary-line methods showed roughly half those values (18% and 25% respectively).

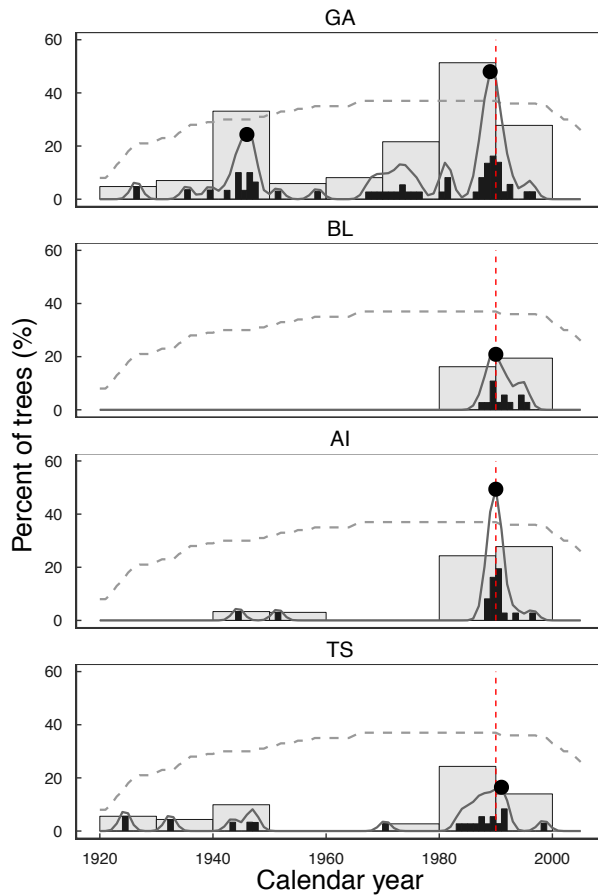


Fig. 4. Plot-level disturbance history in response to a simulated hurricane in 1990 (represented by the red line) at the hurricane pulldown experiment. The proportion of trees responding to disturbances is binned by year (black bars) and decade (grey bars). Peaks of disturbances (solid circles) were identified based on the standardized running kernel density estimation function (solid black line). The dashed grey line shows number of trees. See Figure 2 for method codes.

Stand-level Sensitivity Analysis of Disturbance Detection Methods

When conducting the sensitivity analysis of all methods at the stand level by modifying window length parameters and threshold levels within pre-established ranges, the modified radial-growth averaging and the absolute-increase methods had the narrowest range of temporal detection with the data from the hurricane pulldown experiment (0-1 years post experiment), while the boundary-line method was the least precise with values from one year prior to up

to five years following the experiment (Fig. 5). All methods but the absolute-increase method showed strong negative correlations ($p < 0.001$) between estimated disturbance intensity and the increase in window width and thresholds (r^2 : GA = 0.82, BL = 0.81, AI = 0.27 (n.s), TS = 0.87) (Appendix S3). Both the window length and threshold level significantly impact this relationship for modified radial-growth averaging, absolute increase, and time series methods. Only adjusting threshold levels for the boundary-line method significantly impacts the intensity of reconstructed disturbance. The absolute-increase method is less sensitive to the temporal parameter than the radial-growth averaging method.

With all methods, temporal detection of the 1938 hurricane event in the Harvard Pisgah Tract was more precise than at the hurricane pulldown experiment. Intensity of disturbances, however, were more sensitive to the choice of method, window length, and threshold at the Harvard Pisgah Tract than at the hurricane pulldown experiment showing stronger correlations between threshold and disturbance intensity ($r^2 = 0.75-0.93$, $p < 0.001$) (Fig. 5, Appendix S3). The boundary-line method still had a longer period of temporal offset in detecting the 1938 Hurricane than other methods. In this forest, however, it only ranged from -1 to +3 years.

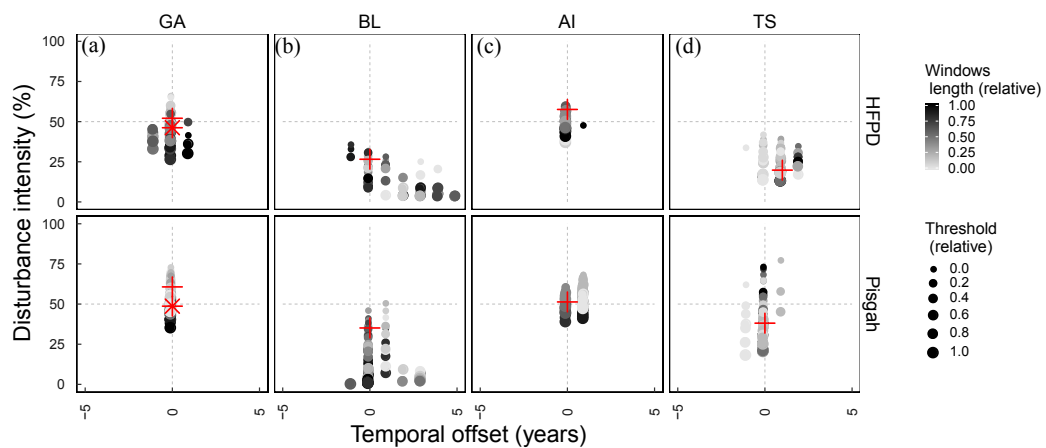


Fig. 5. Analysis of sensitivity of the four method to changes in their parameters of window length and threshold for release detection. Accuracy, precision, and intensity of release events are identified here based on default settings (red cross) and those with different windows length (grey color) or thresholds (symbol size) for the hurricane pulldown experiment (upper panel) and the 1938 hurricane at the Harvard Tract in

Pisgah State Park (lower panel). Windows length and criteria threshold represent the range tested from Table 1, ranging from 0 to 1. See Methods for more details on parameters.

Comparison of reconstructed disturbance histories along a 1938 hurricane gradient

Detecting the impact of the 1938 hurricane differed among methods and forest sites (Fig. 6). In the Harvard Pisgah Tract, all four methods identified a peak in disturbance the year after the hurricane, with the modified radial-growth averaging and absolute-increase methods having the narrowest periods of temporal detection. Disturbance intensity ranged from 35%-38% (boundary line and time series) to 51%-60% (absolute increase and modified radial-growth averaging). In the forest used as control for the 1938 Hurricane, the Palmaghatt Ravine, all four methods detected some disturbance around 1938 with most returning low levels of intensity (5-10%). The exception to this pattern is modified radial-growth averaging, which estimates a level of intensity that is more than twice than that of the absolute increase and time series methods (Fig 6). For the time-series method, the disturbance growth indices show that the magnitude and duration of forest response to hurricane disturbance is greatest for the most severe site (Harvard Pisgah) and decays subsequently through time.

We explored how these methods performed in different forest types by comparing data from plots of broadleaf forest at North Round Pond (NRP) in Pisgah State Forest to conifer-dominated plots located 500m away. In the NRP broadleaf forest, temporal detection was centered around 1938 for the modified radial-growth averaging and boundary-line methods and 1939 for absolute-increase and time-series methods. All methods detected a disturbance intensity >20% in North Round Pond broadleaf forest (modified radial-growth averaging = 50%, boundary line = 22%, absolute increase = 25%, and time series = 20%). In the NRP conifer forest, the range in temporal detection was slightly lower than that of the broadleaf forest. Only three methods in this forest (modified radial-growth averaging, boundary line, absolute increase) identified disturbance intensity above 20% (39%, 21%, and 25%, respectively).

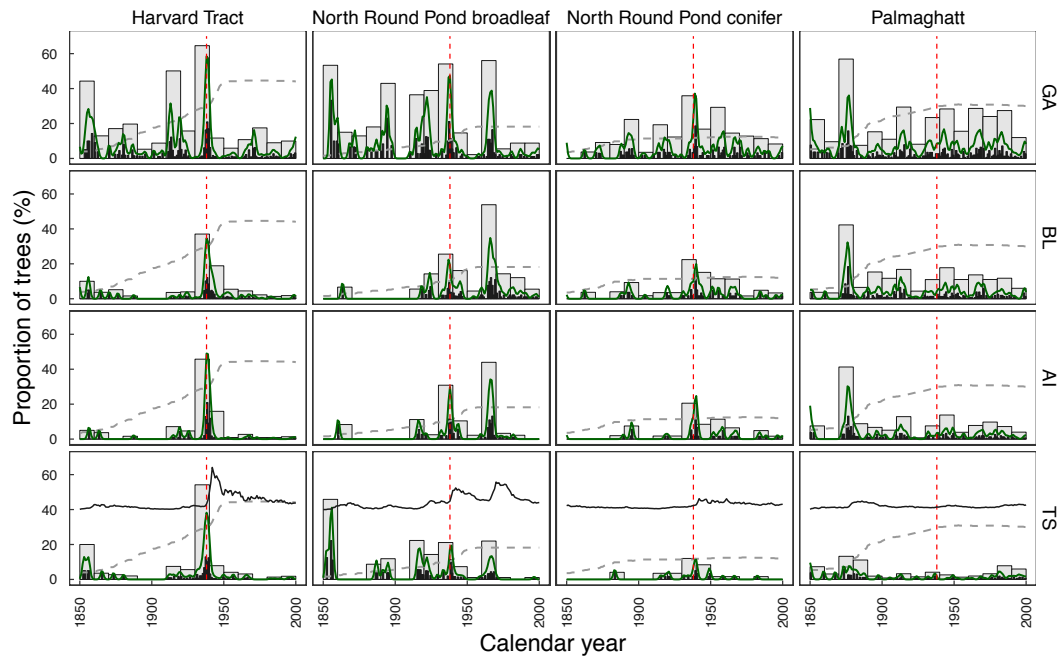


Fig. 6. Comparison of time-series disturbance history for the 1938 hurricane gradient (from high to low damage, left to right) reconstructed using default settings, 1 years (black bars) or binned by 10 (grey bars). The solid green line represents intensity of the events derived from the moving kernel density function and the dashed grey line represents sample depth (divided by 5). The solid black line represents the disturbance-growth index (mm) for the time-series method.

Discussion

We found a range of efficacy among the four methods in reconstructing canopy disturbance events in New England forests. All methods correctly identified the proportion of expected growth releases in the hurricane pulldown experiment. Performances improved (i.e. greater detection rates) and differences among methods were minor during a period with a relatively low rate of canopy disturbance (Table 2). Uncertainties in the temporal precision of the disturbance detection varied depending on the method used, as previously reported (Fraver and White 2005, Copenheaver et al. 2014). Our results showed that these uncertainties were greatest with the boundary-line and time-series methods. Temporal precision in reconstructing disturbance histories is crucial for a better understanding of forest ecological dynamics as it reveals disturbance rates, the severity and frequencies of disturbance, and impacts of disturbances on forests

ecosystems. Importantly, temporal precision will likely greatly enhance our ability to attribute the drivers of disturbance.

Altering the window lengths and thresholds influenced the rates of false positive and false negative events. Some methods (modified radial-growth averaging) show higher sensitivity, which results in the detection of more false-positive events, or the events that did not occur. In contrast, some window lengths and thresholds may be too rigid, resulting in actual events being undetected (boundary line, time series), the false-positive results. These findings indicate a trade-off between the identification of false-positive and false-negative events. Methods with higher constraints, such as a requirement of *a priori* data (boundary line or absolute increase), or more complex calculations (time series) had fewer false positives (Fig. 3b). Previous studies comparing release detection methods found a similar result in the production of false positive and negative events (e.g. Rubino and McCarthy 2004, Black et al. 2009, Copenheaver et al. 2014). While conducting the sensitivity analysis, we noticed that the original formulation of the radial-growth averaging method (Lorimer, 1985; Lorimer and Frelich, 1989) produced fewer false positives compared to the modification of Nowacki and Abrams (1997) (Fig. 5), suggesting a detectable difference in results from common methods. The modified radial-growth averaging method, for example, returned an intensity of disturbance that is twice that found with other methods in the 1938 hurricane control forest (Fig 6). While differences in the production of false negative and false positives are small, they have the potential to have a substantial influence in interpreting forest development.

All methods showed a substantial limitation in reconstructing the estimated intensity of canopy disturbance. The modified radial-growth averaging and absolute-increase methods estimated the disturbance intensity of 60-65% at the hurricane pulldown experiment, while the boundary-line and time-series methods estimated ca. 20-25%. While each method may detect the same number of trees showing a release around the time of a known disturbance event, performance in temporal precision influences the estimation of disturbance intensity by nearly 30%. It is clear that temporal precision of the various methods needs to be considered carefully when estimating disturbance intensity.

Forest structure and composition had an impact on the performance of the different methods. The modified radial-growth averaging and absolute-increase methods performed better in younger forests with, presumably, smaller trees than the boundary-line and time-series methods. All methods performed better in older forests or forests with little to no levels of substantial canopy disturbance. We surmise that tree age has less of impact on performance in young versus old forests. Hypothetically, older forests are composed of a greater proportion of large trees that create larger gaps with canopy disturbance. Interestingly, the range in temporal precision was smaller in the conifer-dominated forest in Pisgah State Park compared to the broadleaf-dominated forest in the same landscape. Estimation of disturbance intensity using the other methods was not affected by forest type, but understanding the impact of forest structure and type on performance needs further investigation before understanding interactions between disturbance detection performance and forest structure and composition.

Uncertainties, Parameter Sensitivity, and an Advance

Our comparison of four commonly used methods of disturbance detection from forests with well-documented past disturbance events leads to three considerations. First, we find that the tree-level temporal uncertainties in determining release dates create large uncertainties in reconstructing disturbance history at the stand level. Temporal precision was greater with absolute increase and radial-growth averaging and weaker with boundary-line and time-series methods. We found that these uncertainties were consequential when estimating disturbance intensity. Although the modified radial-growth averaging and absolute-increase methods estimated just over one half of the expected disturbance intensity, they estimated more than twice the amount of the boundary-line and time-series methods. We do note that the time-series method does capture additional information about the magnitude and duration of release events. For example, mean disturbance growth indices at Pisgah increased by > 1.5 mm/yr and gradually decreased over the next half century, showing the greatest magnitude and duration to this disturbance event. Given the variability in temporal precision among different methods, users should be aware of their

limitations and recognize the uncertainties in reconstructed disturbance produced by these methods. Overall, the absolute-increase and radial-growth averaging methods had the highest temporal precision for dating growth releases following disturbance.

Second, parameter settings are among the most critical and still largely unsettled issues in disturbance detection analysis. Parameter settings can lead to over- or under-estimation of the timing and intensity of disturbance events (Rubino and McCarthy 2004, Bouriaud and Popa 2007, Copenheaver et al. 2014; Pederson et al., 2014). Here, our parameter sensitivity test showed that the absolute-increase and modified radial-growth averaging methods were least influenced by parameter selection. We recommend additional tests utilizing a greater number of tree species, in species-rich forests with varied structure, and forests experiencing a greater range of disturbances than the forests in which the four methods were developed. Results from these types of studies may challenge traditional assumptions used for the construction and development of these disturbance detection methods. In general, we found that the modified radial-growth averaging method and absolute-increase methods had lower levels of overall error in detecting canopy disturbance events with the original formulation of the radial-growth averaging method producing fewer false positives than the modified radial-growth averaging method.

Third, a significant constraint in some of these methods is the quantity of data and/or expert knowledge required prior to disturbance analysis. The boundary-line and absolute-increase methods require a significant amount of *a priori* information while radial-growth averaging and time-series methods require the least amount. Considering these constraints, the application of these two methods should be primarily limited to large datasets representative of a single species or locations where growth information of many species is already available (Black and Abrams 2003, Fraver and White 2005, Ziaco et al. 2012). We view the *a priori* need for large data sets regarding expected species growth patterns or expert knowledge to be a limitation for studies in forests with high tree-species diversity or projects that have short timeframes for completion.

Further research is needed for improving data-dependent constraints in disturbance detection methods.

Finally, our results indicate that annual binning of canopy disturbance, combined with kernel density estimation, would improve reconstructions of forest disturbance history and understanding of long-term forest dynamics. Most important, annual binning requires cross-dated tree-ring series. We find that binning disturbances into decades indicates nearly continuous canopy disturbance. In contrast, annual binning revealed improved agreement with the documented events at our study forests and suggested disturbance was more episodic (Figs. 4 & 6). Annual binning has revealed an episodic disturbance regime with a range of disturbance frequencies and intensities of forest dynamics (Pederson et al. 2014). In that investigation, that might not be obvious with decadal binning. In that investigation there were periods with no disturbance, periods dominated by background disturbance or gap dynamics (frequent, low intensity disturbance), and the occurrence of synchronous, intense, and large-scale canopy disturbance (Pederson et al. 2014). We propose that binning disturbance annually will improve our understanding of disturbance dynamics.

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5.2. Disturbance dynamic in the natural forest landscapes

5.2.1. A mixed severity disturbance regime in the primary *Picea abies* (L.) Karst. forests of the Ukrainian Carpathians

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V.T., M.S., and P.J. conceived ideas and designed the study;

All co-authors performed the sampling;

V.T., P.J., M.M., H.R., and M.S. performed the dendrochronological analyses;

V.T. performed data and statistical analysis;

V.T. and M.S. wrote the manuscript and all authors commented on it.



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A mixed severity disturbance regime in the primary *Picea abies* (L.) Karst. forests of the Ukrainian Carpathians



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ABSTRACT

Natural disturbance regimes play key roles in shaping forest structure and development at stand and landscape levels. Disturbances are commonly complex and variable, such that classical dichotomous characterization of disturbance regimes as following large infrequent disturbances or patch dynamics is too simplistic, especially when the resulting damage is more severe than the baseline of a single tree patch dynamic, but not severe enough to represent large infrequent disturbance. Ongoing climate change affects mountain *Picea abies* forests in Central, East and Southeastern Europe by an increasing frequency of storms and bark beetle outbreaks. We present a unique study based on extensive dataset aimed to reveal the spatiotemporal pattern of the disturbance history and role of the mixed severity disturbances in primary spruce mountain forest landscapes in the Ukrainian Carpathians.

We reconstructed canopy disturbance history and maximum disturbance severity using ca. 2396 tree cores in 96 sample plots. Neither large-scale stand-replacement nor fine scale dynamics was the prevailing disturbance over the last four centuries. Rather, we observed a complex spatiotemporal pattern of mixed severity disturbances. Canopy turnover time ranged between 50 and 300 years and depended on the maximum severity of the disturbance event. Spatial analyses revealed no similarity in spatiotemporal pattern across disturbance histories or maximum disturbance severities. We observed evidence of a combination of variable severity disturbances that fails to fit the classical scheme of gap or patch dynamics with sharply defined sizes and borders, but is more consistent with a mixed severity disturbance regime across the landscape. Windstorms were likely the most important past disturbance agent. The probability of an epidemic bark beetle attack was low, although the possibility of small local outbreaks cannot be excluded. An additional, potentially overlooked, agent of disturbance could be historic periods of extreme cold.

This reconstructed disturbance regime may challenge existing silvicultural systems in the Carpathians, calling for a more complex spatiotemporal forest management approach. However, mimicking a mixed severity disturbance regime can be done at the forest management level by applying a range of disturbance severities at the stand level.

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1. Introduction

Natural disturbance regimes, and variation in disturbance size, frequency, and severity, play key roles in shaping forest structure and development at stand and landscape levels (Abrams and Orwig, 1996; Frelich, 2002; Pickett, 1985). Understanding the influence and importance of natural disturbances is needed for designing forest management that maintain forest functioning and biodiversity (Angelstam, 1998; Lindenmayer et al., 2006). Recognizing the influence of disturbance on fluctuations in tree

biomass and carbon balance has global implications (Hicke et al., 2012). Given increasing extremes in disturbances under future climate variation (Schelhaas et al., 2003), the last opportunity to explore and understand the influence of disturbances under current and historic natural conditions may be to characterize the disturbance histories of the few remaining primeval forest remnants.

Our understanding of natural dynamics has largely been based on studies that characterized disturbance regimes through two opposing perspectives: either small-scale patch dynamics, traditionally seen in old-growth temperate forests (Korpel, 1995; Seymour et al., 2002), or large infrequent disturbances, often described for boreal forests (Kuuluvainen and Aakala, 2011). However, there is a continuum of natural disturbances in forests ranging from single canopy tree death to widespread low mortality all the way to severe stand-replacing events. Recent studies have demonstrated that disturbances may commonly be complex and variable, such that the dichotomous characterization of disturbance regimes as following large infrequent disturbances or patch dynamics is too simplistic (Angelstam and Kuuluvainen, 2004). Variability in disturbances over the landscape has been shown with respect to the extent, magnitude, and impact on forest ecosystems, depending on geographical characteristics, previous disturbance history, and the severity of new disturbances (Bouchard et al., 2006; Stueve et al., 2011; Wallenius et al., 2004; White and Jentsch, 2001). Ecologists have come to recognize that disturbance intensity/severity without accompanying information on the spatial and temporal pattern is a limited criterion for evaluating disturbance history. However, precisely this combination of factors makes it difficult to define a clear disturbance regime for landscapes subject to such disturbances, particularly when the resulting damage is more severe than the baseline of a single tree patch dynamic, but not severe enough to represent large infrequent disturbance (Stueve et al., 2011).

The lack of large-scale reference conditions where disturbance processes can be studied is a major obstacle to evaluating natural disturbance patterns at the stand and landscape levels. Although some very extensive primeval forest remnants still remain in North America (Frellich, 2002; Turner et al., 1998), they are quite scarce in Europe (Hamor et al., 2008; Veen et al., 2010). In addition, forest disturbances are often unpredictable and rare events (Pickett, 1985), which makes it difficult to capture them by traditional long-term monitoring or, more recently, even with a remote sensing approach. Therefore, much of our understanding of disturbance histories stems from dendroecological studies, which can provide precise spatiotemporal reconstruction over a large-scale.

The interpretations of disturbance history reconstructions are necessarily dependent on the scale of study, yet the extrapolation of results to coarser spatial scales is problematic because different factors operate on different scales (Everham and Brokaw, 1996; White, 1979). For instance, White and Jentsch (2001) mention that the smaller the study plot is relative to disturbance patches, the more likely it will be entirely disturbed by a single event and that the post-disturbance forest will be relatively homogeneous. Because spatially extensive intensive sampling is very time consuming and costly, dendroecologists are often forced to restrict sampling to a single large plot (in stands driven by patch dynamics) or to regularly distributed dominant trees (in stands driven by large infrequent disturbances). However, studies that have applied more intensive sampling over larger areas have obtained more accurate and complete pictures of disturbance history, which have revealed high disturbance complexity and heterogeneity (D'Amato and Orwig, 2008; Panayotov et al., 2011; Svoboda et al., 2014). This suggests that the overall heterogeneity of a disturbance history is poorly captured when relying on either of these restricted approaches.

Understanding the dynamics and landscape pattern of natural disturbances thus requires intensive sampling over large-scales in remnant primary forests. Our approach has been to employ a precise design of intensive sampling and new methodological techniques to reconstruct the past disturbance history and landscape dynamics of an extensive untouched remnant of primary forest in Europe. The specific aims of our study were to: (i) reconstruct the spatiotemporal pattern of past disturbances and integrate the results across plot, stand and landscape scales; (ii) determine disturbance rates in different forest stands; and (iii) describe the features of the identified disturbance regime. We also discuss the possible causal agents of such a disturbance regime.

2. Material and methods

2.1. Study area

The study was conducted in a primary montane spruce forest in the Ukrainian Carpathians (Appendix A). The Gorgany Mountain range (part of the Carpathians) spreads approximately 75 km from Northwest to Southeast and represents one of the largest remnants of primary montane spruce forests (*Picea abies* (L.) Karst, Hamor et al., 2008). The mean monthly temperature of the warmest month (July) is +16.4 °C, and of the coldest (January) is –7.6 °C. Precipitation in the region varies from 853 to 1007 mm/year, peaking in June and July. Snow cover remains for 79 days. Leptosols and albic podzols predominate on sandstone bedrock (Chernyavskyy and Shpylchak, 2011; Valtera et al., 2013). Ridge tops are usually shielded by revealed stones or covered by *Pinus mugo* Turra. Due to poor access on the steep and stony slopes, the area has not been subject to forestry or grazing (which is otherwise the typical historical land use on Central European mountain ridges in the recent centuries); bottoms of the valley were selectively or clear cut to approximately 1200 m a.s.l.; primeval *Picea abies* forests have been preserved at higher altitudes up to the mountain ridges covered by *Pinus mugo* or bare stone screes.

Based on the literature and remote sensing and field surveys, two protected areas were chosen for inclusion: the Gropha landscape reserve and the nearby Syvulya mountain range. In each area, 3 spruce dominated stands were chosen for sampling as the best preserved stands representative of the overall forest condition, i.e., omitting tree line and extreme sites, without footprints of any human activities, primary forest features according to field observation (Wirth et al., 2009). We designed the sampling strategy to have four levels of spatial extent: landscape (whole study region), localities (Gropha and Syvulya), stands (three within each locality) and plots (ninety-six in total).

2.2. Data collection

Within each stand, 15–20 1000 m² (horizontal radius 17.84 m) plots (Table 1) were placed according to a regular randomized design (Svoboda et al., 2014). For this purpose, each stand was overlain with a 141.4 × 141.4-m grid (2-ha). Sampling plot centers were randomly allocated within each grid cell in the inner 0.5 ha core, such that the distance between the nearest two plots could vary from 106.7 to 176.1 m. When the tree density was over ~80 trees per 1000 m² (visual assessment), the plot size was reduced to 500 m² (N = 8). Most plots were on western and northern aspects (36% and 33%, respectively), with some on eastern and southern aspects (20% and 11%, respectively). Elevation averaged 1370 m a.s.l., ranging from 1240 to 1515 m a.s.l. In all plots, *Picea abies* was the dominant tree species and accounted for 94% of the basal area. Accessory tree species were *Pinus cembra* and *Sorbus aucuparia*.

Table 1

Main stand structural characteristics of the study stands. Values were averaged across 1000 m² plots. All trees with DBH ≥ 10 cm were identified and 25 randomly selected non-suppressed trees were cored.

Study stands	GR1	GR2	GR3	SY1	SY2	SY3	Average
Geographic position (E°, N° in WGS84)	23.93026; 48.59596	23.89917; 48.60814	23.91924; 48.61309	24.09306; 48.56017	24.16411; 48.53734	24.11095; 48.50298	
N of plots	16	15	15	20	15	15	96 (sum)
Elevation (m a.s.l.)	1400 ± 28	1372 ± 43	1359 ± 61	1452 ± 47	1389 ± 51	1318 ± 40	1385 ± 62
Slope (%)	26 ± 7	32 ± 4	32 ± 5	28 ± 9	27 ± 5	30 ± 9	29 ± 7
DBH (mm)	321 ± 56	322 ± 51	285 ± 68	267 ± 51	303 ± 59	272 ± 64	294 ± 60
Tree density (stems ha ⁻¹)	444 ± 136	425 ± 101	631 ± 207	662 ± 227	490 ± 178	635 ± 334	553 ± 228
Basal area (m ² ha ⁻¹)	39.8 ± 7.5	40.7 ± 8.7	44.2 ± 11.8	42.3 ± 8.8	41.2 ± 8.7	40.6 ± 7.7	41.5 ± 8.8
Non-suppressed trees (% BA)	91 ± 4.7	93 ± 3.6	88 ± 5.9	88 ± 5.0	91 ± 4.9	91 ± 6.3	90 ± 5.3

All live trees ≥ 10 cm diameter at breast height (DBH) were identified, labeled and mapped in each study plot. We recorded diameter at 1.3 m height, social status (suppressed or non-suppressed (Lorimer and Frelich, 1989), and species of all tree individuals. Tree height and crown projection were measured for five randomly selected trees in each plot. Using a random generator, we selected 25 non-suppressed trees per plot for the dendrochronological analysis; we took one core per tree at 1 m height. Rotten trees were replaced by additional trees of similar DBH. For open canopy growth rate determination we sampled 3–4 trees (DBH ≤ 8 cm) growing under the closed canopy and in the patches of different sizes.

2.3. Dendrochronological analysis and disturbance chronology

Cores were dried, cut by a core microtome (Gärtner and Nievergelt, 2010), measured on a LINTAB 3 digital positioning table (Rinntech, Heidelberg, Germany), and cross-dated using TSAP-Win™ software (Rinntech, Heidelberg, Germany) followed standard dendrochronological methods (Stokes, 1996). All tree-ring series were first visually cross-dated (Yamaguchi, 1991) and verified with COFECHA software (series intercorrelation 0.48) (Holmes, 1983). In total, 2394 tree cores (361,176 radial increments) were used for the analysis of disturbance history. The pith was reached in 49% of trees, and an additional 41% were within 0.5 cm of the pith. When the pith was missing, age was estimated based on Duncan's method (Duncan, 1989).

The disturbance history was evaluated based on two main types of canopy accession: (1) rapid early growth rate (open canopy recruitment) and (2) abrupt, sustained increases in tree growth (Frelich and Lorimer, 1991; Svoboda et al., 2014). For identifying open canopy recruited trees, we determined the growth rate threshold that separates trees that recruited under an open canopy from those that originated under a closed canopy (Frelich and Lorimer, 1991; Svoboda et al., 2014). We compared the juvenile growth of saplings (DBH ≤ 8 cm) growing in patches over 500 m² (N = 54) with those under a closed canopy (N = 119). Logistic regression was used to determine the optimal threshold between these two groups by the intersection of specificity (an expression of the likelihood of false negatives) and sensitivity (likelihood of false positives) (Hosmer Jr. and Lemeshow, 2004). Trees were considered as open canopy recruited if the average growth rate over the first 15 years was ≥ 1.3 mm·year⁻¹ (likelihood ratio $\chi^2 = 129.4$, $P < 0.001$).

To detect release events, the boundary line approach was used (Black and Abrams, 2004, 2003), which has proven to be one of the most efficient in detecting release events. To account for the bioclimatic influence on tree growth (Ziaco et al., 2012), we fit a specific boundary line curve for study sites based on 361,176 radial increments (Appendix C). Release was defined as any growth change in excess of 20% of the boundary line (Black and Abrams, 2003) that was sustained for at least 7 years (Fraver et al., 2009).

The disturbance chronology reconstruction was done by using canopy accession events of the trees, following the approach of Lorimer and Frelich (1989). Open canopy recruitment was most common among all study stands: the percent of open canopy recruited trees range from 53% (GR2) to 70% (SY1). To avoid a sampling-depth bias toward recent events, all detected events were converted to the percent of the canopy area disturbed in each plot to scale the evidence of disturbance according to each tree's current crown area (Lorimer and Frelich, 1989; Svoboda et al., 2014). Current crown areas were predicted from DBH based on a linear regression of DBH on crown area from the stratified sample ($R^2 = 0.61$, $P < 0.001$, crown area = $0.4631 \cdot \text{DBH} + 0.8948$). To calculate the disturbance chronology, we summed the percent of the canopy disturbed area by decade.

Canopy turnover time was calculated as the minimum sum of subsequent years to remove a certain percent of the canopy. For each study plot we calculate the minimum time needed to remove 5%, 10%... up to 90% of the canopy. For severe disturbances, the minimum time needed to remove a certain percent of the canopy was much shorter and did not exceed 30 years (Svoboda et al., 2014). Moreover, since the recruitment of regeneration after disturbances might span a few decades (Holeksa et al., 2007; Svoboda et al., 2014; Svoboda et al., 2012; Szewczyk et al., 2011), we calculated the maximum possible percent of the canopy removed within the subsequent 10, 20 or 30 years.

2.4. Maximum severity and spatiotemporal pattern of disturbances

Because every new disturbance tends to override the evidence of the previous one, we used the maximum disturbance severity (MDS) of the event to interpret the severity on disturbances in the single study plot. MDS represents the severity of the strongest disturbance event that can be detected in a sampling year. To estimate MDS at the plot-level, we fit a kernel density estimation function (KDE) to the temporal distribution of the percent canopy removed in each study plot (Appendix D). KDE is a non-parametric method to estimate the probability density function of random variables. Kernel density estimation is a fundamental data smoothing problem, where inferences about the population are made based on a finite data sample (Duong, 2007). To fit the density function, we used the distribution of years in which canopy accession events occurred multiplied by the percent of the canopy area disturbed in a given year. For each plot, the maximum value of the density was estimated and represents the MDS. The maximum value of the KDE (0.08) was achieved when 100% of the canopy was removed within one year (Appendix D). The calculation was done using the R statistical software (R Development Core Team, 2012) under library 'stats', using the 'density' function.

Four severity classes were defined based on the amount of canopy removed: light 0–20%, moderate 20.1–40%, heavy 40.1–60% and extreme > 60% (adopted from Frelich and Lorimer, 1991). The year in which the MDS occurred is referred to as the year of the

main disturbance event. This does not refer to the exact date of the disturbance, but generally to the middle of the time period within which trees expressed their reaction to a disturbance event.

Non-metric multidimensional scaling (NMDS) was used to reveal the two-dimensional relation between disturbance chronologies and topographic characteristics and climate using the library 'vegan' (Oksanen et al., 2013) and 'mgcv' (Wood, 2011), based on the function 'metaMDS' using the Bray-Curtis similarity metric. As input variables we used a plot-by-decade matrix (96 plots, 35 decades), with the proportion of canopy area disturbed in each cell. Physiographical attributes (elevation, slope, aspect, landform and hillform) were then passively projected onto the ordination space (using the 'envi' function) to examine their relationship with disturbance pattern. Aspect values were transformed using the formula proposed by D'Amato and Orwig (2008). The MDS were included in the ordination using a function ("ordisurf") that creates

a smooth surface and plots the result (as contour lines) on the ordination diagram.

For the spatial analysis of the disturbance patterns, two common approaches in spatial ecology were used: Mantel's tests and Moran's *I* tests. While Mantel's test evaluated the overall correlation between disturbance histories and plots location, Moran's *I* estimated spatial similarity between plot location and plot feature on a different distance scale. The Mantel's test evaluates the correlation between two plot by plot matrixes, in this case one containing the geographical distance between all pairs of plots and the other containing a measure of similarity between plots based on decadal disturbance metrics. Moran's *I* is calculated from both feature location and future values simultaneously and varies between 1 and -1 (Borcard et al., 2011). A positive *I* indicates spatial clustering, while a negative *I* reveals that data are spatially dispersed. Moran's *I* was calculated for each stand separately at distances of

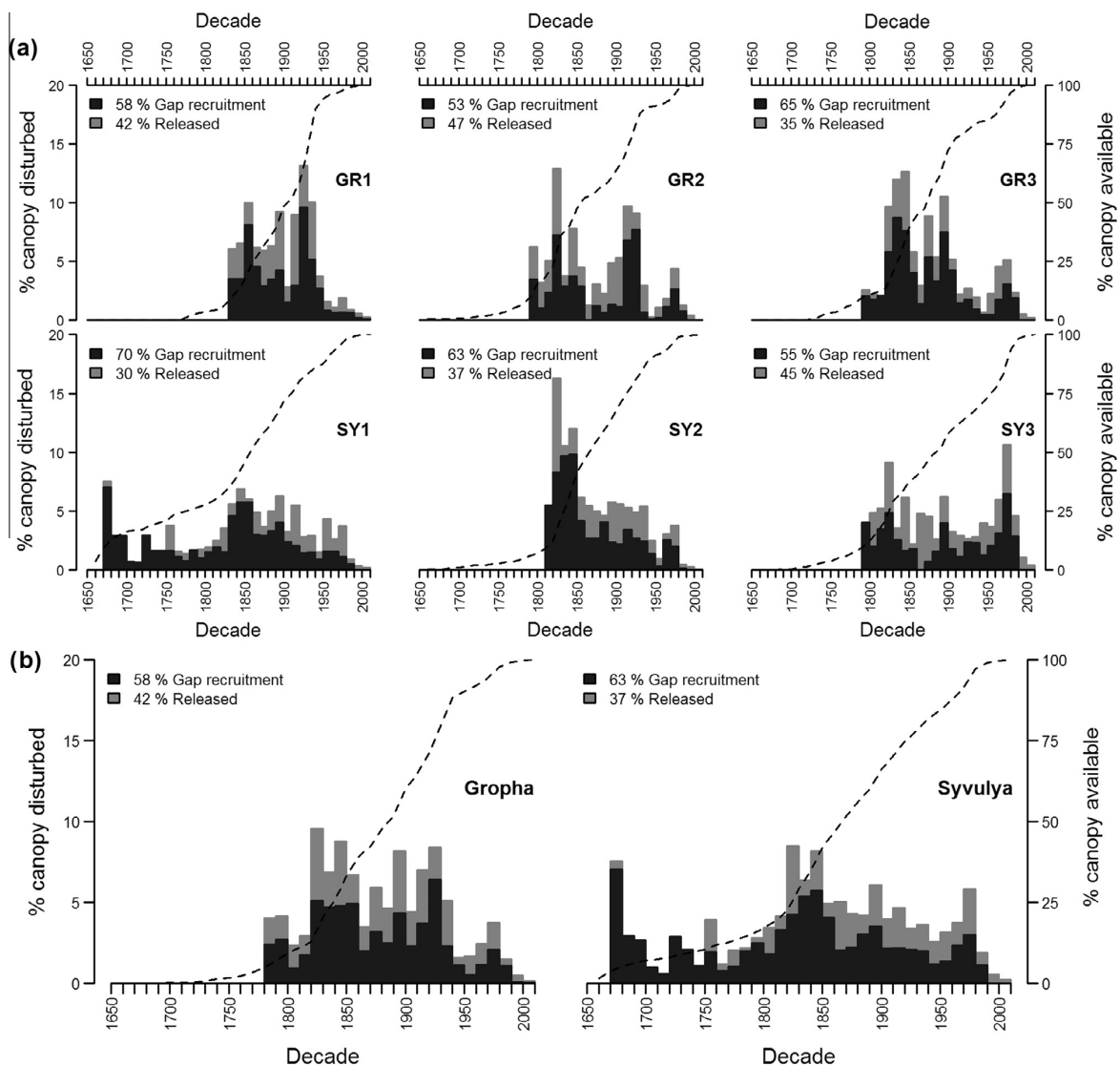


Fig. 1. Mean canopy area disturbed by decade for each of the six study stands (a) and averaged for two landscapes (b). Canopy area disturbed was calculated from two types of canopy accession events: open canopy recruitment (black bars) and release after suppression (grey bars). Twenty-five non-suppressed trees from each plot were used for the analysis and the % canopy available (dashed line, right axis) represents the percent of the total canopy available for the analysis. Chronologies were truncated when the percent of the tree canopy available for the analysis dropped below 10% (5%) of the total stand (landscape) canopy.

50–400 m in 50 m steps in relation to the MDS. The Mantel's and Moran's *I* tests were performed in the *R* statistical software under libraries "vegan" (Oksanen et al., 2013), "plyr" (Wickham, 2011), "ape" (Paradis et al., 2004). All the above mentioned analysis were done using *R* statistical software ver. 3.0.1 (R Development Core Team, 2012).

3. Results

The reconstructed disturbance chronology covered a time span of more than 350 years (starting ca. 1650) and indicated variability in disturbance histories across the study stands (Fig. 1). There was no evidence of a single stand-replacing event that would have covered a stand or landscape scale or heavily removed the canopy on a majority of study plots. Conversely, on the majority of the plots (56%, *N* = 54) a moderate MDS, representing 20.1–40.0% canopy removed, was observed. Light MDS was observed on 28% (*N* = 27) of plots, while heavy and extreme MDS was only seen on 11% and 4%, respectively (Fig. 2). Although similarity of the MDS

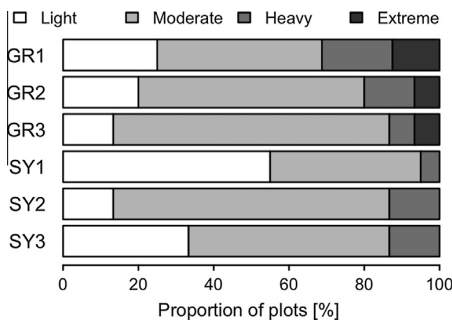


Fig. 2. Proportion of the plots in the stand sharing a similar maximum disturbance severity. Each horizontal box represents a study stand, with colors indicating maximum disturbance severity. The moderate category of maximum disturbance severity was the most frequent, while the categories of heavy and extreme were not so common.

distribution was observed across stands, none of the plots experienced extreme MDS in Syvulya while in Gropha ca. 10% showed heavy and extreme MDS in the past.

The minimum time needed to remove a given percentage of the canopy varied considerably among plots and increased with increasing percent canopy removed. In one 10 year period a maximum of 75% (median 28%) of the canopy area was removed at the plot-level (Fig. 3), while within 30 years up to 95% of canopy (median 45%) was removed. On average, it took 24 subsequent years (range from 3 to 112 years) to remove 40% of the canopy. For 60% of the canopy to be removed, the medium minimum time was 54 subsequent years (from 7 to 250 years). The minimum time needed to replace a given percentage of the canopy varied highly between plots with different MDS: plots with light MDS needed five to ten times longer compared to plots with extreme MDS.

The plot-level disturbance chronology allowed us to fully explore temporal variability in past disturbances on a small-scale (Fig. 4). The oldest recorded event occurred in SY1 between 1650 and 1680 and affected the majority of the plots available for analysis (*N* = 9 plots, 90% from available). The largest disturbance event, which affected around 60% of the study plots over the entire landscape, happened between 1820 and 1840 and showed variability in percent canopy removed across decades (Fig. 4). A high proportion of the affected plots (38%) experienced their MDS during this period, indicating a greater disturbed canopy. However, a majority of the plots (85%) experienced only a moderate MDS event. The disturbed plots were distributed throughout the study area, with somewhat more in the GR2 stand (Fig. 4). A few other events affecting a large number of plots (40–50%) occurred in 1840–1860, 1890–1900 and 1910–1930. Fewer plots (18–24%) exhibited MDS in that period, but those that did mainly experienced heavy and extreme MDS (36–57%). The most recent event in 1970–1980 affected 26 plots (27%), 8 (31%) of which had their MDS at that time.

The ordination analysis (Fig. 5) revealed only partial synchronicity in disturbance history among plots. There was no clear tendency that disturbance history regime was more synchronized

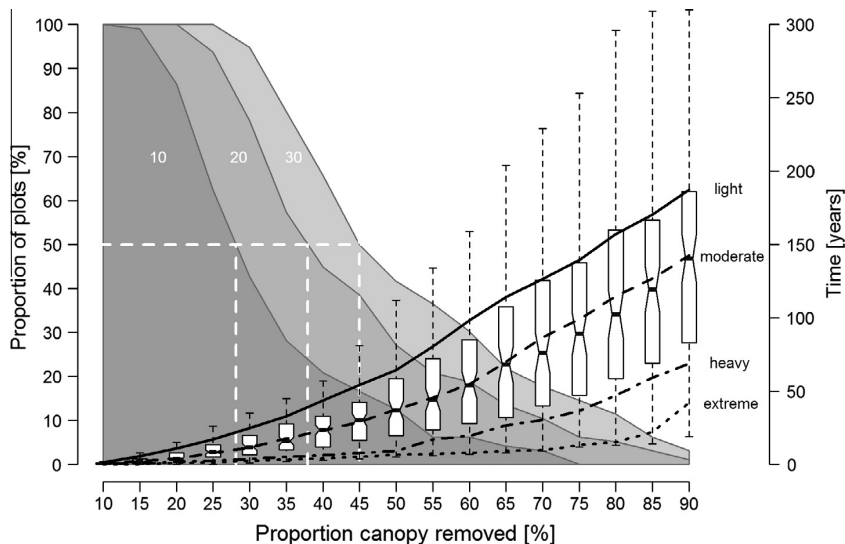


Fig. 3. Minimum time needed to remove *n* percent of the canopy on the plot-level. The median (the horizontal bold line in the box), first and third quartile (the box), and minimum and maximum (the vertical dashed line) minimum time are shown for each 5% step of canopy area. Plots with heavy and extreme maximum disturbance severity (two lower lines) needed much less time to disturb *n* percent of the canopy than plots with light and moderate (two upper lines) disturbance severities. The shaded area indicates the proportion of plots with *n* percent of the canopy removed within 10, 20, 30 subsequent years. Within 30 subsequent years, 50% of the plots had at least 45% of the canopy removed.

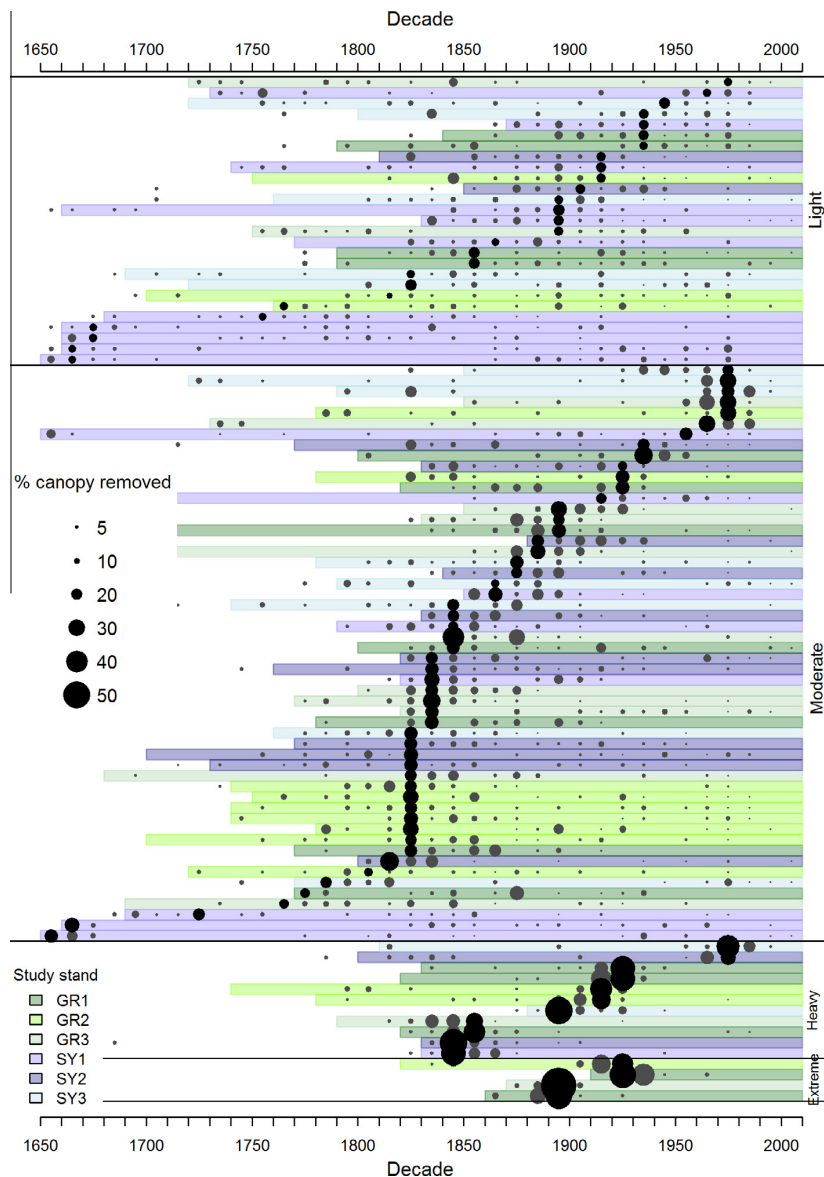


Fig. 4. Plot-level disturbance chronology. Each horizontal bar corresponds to one study plot, with the color of the studied stand. Size of the point represents the proportion (%) of the canopy area removed per decade. Black point show the midpoint of the decade in which each MDS event occurred. Plots are ordered by the time of the main disturbance event and horizontal bars were truncated when the percent of available canopy dropped below 10%. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

among the plots within a given stand, with the exception that plots within the GR2 stand created a distinct cluster in the ordination space in the 1820–1840 period. None of the physiographic features were significantly correlated with the ordination axes. Further, distinct groups of plots with similar dates of MDS can be seen in the ordination space. Plots that experienced their MDS in the 1650–1680 and 1820–1840 periods had lower disturbance severities compared to other periods. However, variability, rather than uniformity, of disturbance severities appeared to be the prevailing.

Stands did not show evidence that geographically proximal plots had similar decadal disturbance histories, with the exception of stand GR2 (Mantel test $r = 0.31$, $P < 0.01$). This stand was influenced by two main disturbance periods (1820–1840 and 1910–1930), which affected 60% and 35% of plots, respectively (Fig. 6).

During the first event, the majority of plots experienced moderate MDS, while in the second heavy and extreme MDS prevailed. These findings were supported by the Moran's I test, which only revealed significant similarity in MDS among the plots situated 100–150 m apart ($r = 0.51$, $P < 0.05$) in one stand (GR2). For three other stands, a significant negative correlation was observed at the distances of 150–200 m (GR3) and 300–350 (SY1, SY2).

4. Discussion

Our results indicate that the overall pattern of the disturbance history on the whole study landscape was diverse in temporal and spatial scales. We revealed that the forests did not originate

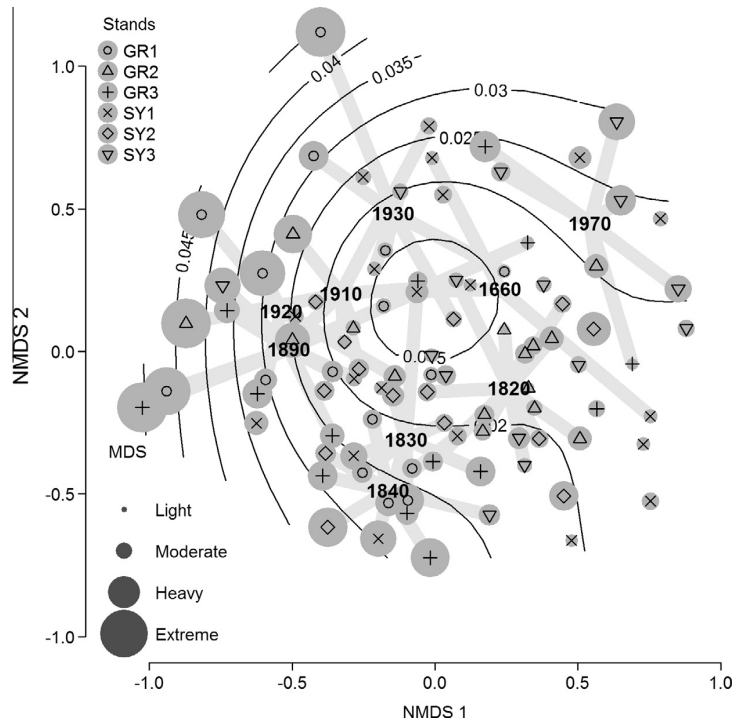


Fig. 5. Non-metric multidimensional scaling (NMDS) ordination of the disturbance histories from the six study stands, based on the decadal disturbance rates. Black isolines show the gradient of maximum disturbance severity (MDS), with the lowest severity in the center and increasing in all directions. Years indicate the period when the maximum disturbance severity occurred for the plots sharing similar disturbance histories, which are connected by grey lines.

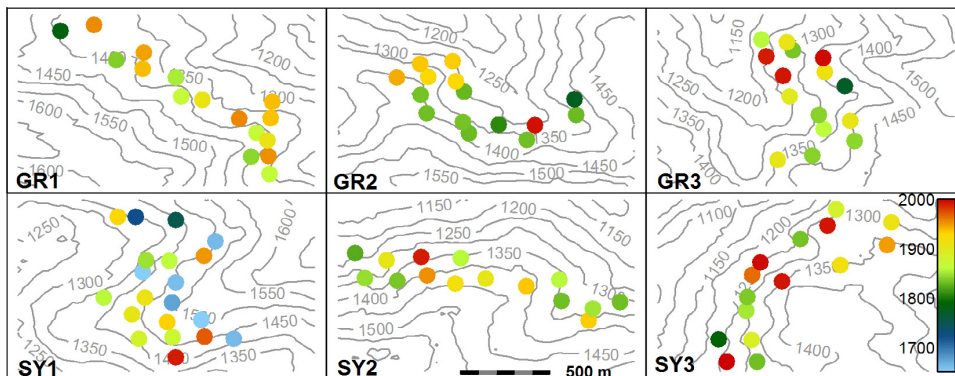


Fig. 6. Map showing spatial and temporal variability in the time when the maximum disturbance severity event occurred in the study plots. Each point represents one study plot, with the color corresponding to the time when the maximum disturbance severity event occurred. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

after one stand-replacing disturbance event, nor were shaped by single tree patch dynamics, but rather were affected by numerous events of different severities, extents and timing, which resulted in a complex pattern of disturbance history. The observed spatiotemporal pattern, combined with different maximum severities of disturbances, created high heterogeneity and complexity, which indicates that a mixed severity disturbance regime prevailed in this forest over the last few centuries.

4.1. Disturbance history

Primary montane spruce forests in the Ukrainian Carpathians were shaped by disturbances of different severities, the majority

of which were attributed to the moderate disturbance severity class (Fig. 2). Such a range of disturbance severities affected canopy turnover time, with a lower mortality rate (3–5% of the canopy removed per decade) in plots with light MDS. The spatial heterogeneity of the distribution of affected patches was also high and there was no evidence of synchronicity of disturbance events or disturbance history in adjacent plots, with the single exception of one stand (GR2) that was characterized by two main disturbance events. The observed patterns of spatiotemporal variability and severity of past disturbances (Figs. 4–6) were highly heterogeneous.

Such mixed patterns of disturbance, which fit neither the small-scale patch dynamics nor the large-scale catastrophic disturbance

models, have recently been described as mixed severity (a.k.a. moderate, intermediate) disturbances (Hanson and Lorimer, 2007; Stueve et al., 2011; Woods, 2004). Such disturbances may create patchy but severe or widely dispersed yet moderate canopy damage (Panayotov et al., 2011; Stueve et al., 2011; Woods, 2004). While mixed severity disturbances of forest ecosystems were mostly discussed in fire communities (Perry et al., 2011) they are more rare in the scientific literature on forests driven by other disturbance agents (Stueve et al., 2011; Woods, 2004) and there is still no clear definition of what constitutes a mixed severity disturbances regime, common characteristics include variability in patch size and number and broad ranges in the amount of canopy removed (Greenberg and McNab, 1998; Hanson and Lorimer, 2007; Nagel et al., 2006; Stueve et al., 2011; Woods, 2004). This may arise from a single disturbance hitting a large area with variable intensity and extent within the landscape, or from a combination of numerous disturbance events occurring in different parts of the landscape that may be driven by different disturbance agents. Importantly, the consequences of both are read in the spatiotemporal heterogeneity and complexity of forest structure. Nevertheless, mixed severity disturbances are often an important link that is missing in the discussion between fine scale patch dynamics and large infrequent disturbances.

The mixed severity disturbance regime observed in this study is in keeping with that previously reported for European spruce forests (Janda et al., 2014; Panayotov et al., 2011; Svoboda et al., 2014). The variability in disturbance severity and spatial distribution of patches creates a mosaic on the forest landscape. However, despite, some previous studies that have shown a relationship between disturbance history and geographical characteristics, in our study no clear evidence between disturbance history and geographical characteristic was observed. This may be a result of the sampling design (low gradient along the physiographical range), but also can indicate that the influence of disturbance agents is simply too variable over the landscape to be easily modeled or predicted.

4.2. Disturbance regime evaluation

Primary forest is not a simple functioning ecosystem, but rather has a complex hierarchical structure (Mori, 2011). Interpreting landscape dynamics based on single plot-level data is thus inappropriate (White and Jentsch, 2001), making it impossible to evaluate disturbance history at local, stand and landscape scales based on small sampling datasets or preferential selection. While interpreting the disturbance regime, the area of observations must therefore be taken into account. The results from this study showed high variability of disturbance severities on the plot-level, but greater balance at the stand level (Figs. 1 and 3). If only a subset of the plots had been used for the analysis, the overall picture of the disturbance histories would have been incomplete and may have given inappropriate results. For example, if the sample had only observed plots with high and extreme MDS, we would have concluded that high severity disturbances were prevailing in this forest. Or conversely, if the sample had only observed plots with light disturbances, the conclusion would have been that a patch disturbance regime prevailed. Therefore, our data support the conclusion that an extensive and balanced sampling design can better uncover the true complexity of the disturbance history of a forest.

Criteria for identifying a mixed severity disturbance regime are not yet well defined. But the important element appears to be disturbance events that are markedly less severe, and more frequent, than the rare benchmark of large infrequent disturbances, and yet strong enough to inflict patchy catastrophic damage not considered patch disturbance (Stueve et al., 2011). Our results indicate, and support, the previous observation that mixed severity

disturbance regimes are characterized by the periodic, unpredictable occurrence of disturbance events that create patches of different size and disturbance severity within the affected area (Hanson and Lorimer, 2007; Woods, 2004). Although our data do not allow precise evaluations of the size of the disturbed area, the results suggest that almost 10 ha can be affected during a single such disturbance event. Patches with higher severity of disturbances were typically spatially isolated and infrequent, yet contributed importantly to the overall heterogeneity of the disturbance history.

Every new disturbance event overrides the evidence of the previous one, and therefore it is difficult to conduct retrospective studies of disturbance. The individual plots may have experienced a different severity in previous disturbance events, but we can only interpret the last most important event, which likely overrode the evidence of previous ones (by killing trees), especially for recent heavy disturbances. These limitations should be taken into greater consideration during retrospective analysis of disturbance histories. However, it is difficult to interpret the main disturbance event of plots that only experienced light disturbances. Due to frequent single tree mortality, a single main event cannot be identified (Fig. 4 upper panel). Moreover, the area affected by past events is even more difficult to estimate (Shimatani and Kubota, 2011). For example, the event of 1820 could have had an even larger extent in the GR2 stand; however, the next event at the beginning of the 20th century has obscured the traces. The area of past disturbance histories might be much larger; however we are not able to fully reconstruct it.

4.3. Disturbance agents

Disturbance agents play a leading role in creating heterogeneity in the forest and defining the development and extent of disturbance regimes, and yet retrospective studies are limited in their ability to determine the agents responsible for historic disturbances. Separating the biotic and abiotic factors, their roles, and their interaction is difficult (Everham and Brokaw, 1996; Fischer et al., 2013). Wind and insect outbreaks are typically the main disturbance agents shaping the development of the conifer dominated forests in temperate Europe and America (Raffa et al., 2008; Schelhaas et al., 2003; Temperli et al., 2013; Zielonka et al., 2010).

Storms are responsible for 50% of the damage by volume in Europe (Gardiner, 2010), and cause large-scale blowdowns in Central and Western Europe (Brüna et al., 2013; Čada et al., 2013; Zielonka et al., 2010). However, the majority of strong winds come from the west (Donat et al., 2010; Gardiner, 2010; Lavnyy and Lässig, 2003), and the easterly geographical situation of our study sites in Ukraine may buffer it from such storms. By the time such winds reach the study sites, wind speed and intensity have declined and storms are less severe compared to those in Central and Western Europe (Donat et al., 2010). At the same time, damage caused by storms can vary considerably across landscape, due to variability in the storms themselves, the interaction with forest and land features, and the remnant structures of previous disturbances (Everham and Brokaw, 1996; Foster and Boose, 1992; Panayotov et al., 2011; Stueve et al., 2011), creating mosaics across the study landscape and affecting forests strongly only in a few, limited localities. Because this effect may be especially complex in mountainous regions, we consider windstorms to be a likely and an important past disturbance agent for our study area, although perhaps to a lesser extent than in Northeast Europe (Donat et al., 2010; Lavnyy and Lässig, 2003).

In contrast, the spatial and temporal variability of the observed disturbance histories is not typical for epidemic bark beetle outbreaks, which usually create more severe disturbances and cover much larger areas in a synchronized time period (Temperli et al., 2013). Recent studies have shown that warm temperatures and

low precipitation, resulting in drought, are favorable for epidemic bark beetle populations by weakening trees and improving conditions for successful breeding (Aakala et al., 2011; Chapman et al., 2012; Hart et al., 2014; Raffa et al., 2008; Temperli et al., 2013). However, in our study area a climate growth response analyses revealed a positive response of the trees to the higher summer temperature and low precipitation (Appendix E), suggesting that the trees are not suffering from drought, as it might be observed in other places. The low summer temperatures and short warm period of this mountainous region may also not allow for multiple bark beetle generations in a given year. Thus, although we do not exclude small, local bark beetle attack as an agent of disturbance in our study area because populations of beetles are always present in the forest (Raffa et al., 2008), we surmise that the probability of an epidemic attack in the past was quite small.

An additional, potentially overlooked agent of disturbance may be the influence of cold periods on forest development (Kullman and Öberg, 2009; Kullman, 1989). Abnormal temperature fluctuations and cold periods might cause high needle loss in spruce stands, which could create a partial canopy opening that corresponds to a moderate disturbance regime Kullman (1996). This could explain why the disturbance events (1650, 1820) that occurred during the coldest periods in the last few centuries (Buntgen et al., 2013) were those that affected the largest proportion of plots in the study region.

4.4. Management implications

There are many forest management systems that account for natural patterns of disturbance. Understanding the disturbance regime of a forest, in particular the severity, frequency and spatial pattern of individual disturbances, can provide a framework for forest management plans. Mimicking small-scale patch dynamics by human intervention often leads to the promotion of late successional species, while large clear-cuts are favorable for early-successional stages. But a combination of disturbances (on different spatiotemporal scales) may contribute to the environmental heterogeneity and thereby increases species diversity (Connell, 1978). Mimicking a mixed severity disturbance regime might be a valuable tool in forest management, where the unplanned development of forests is not the target (Hanson and Lorimer, 2007; Mori, 2011; Nagel et al., 2014).

We observed remarkable spatiotemporal complexity in natural disturbances, which is likely impossible to precisely mimic through anthropogenic perturbations (Kuuluvainen, 2009; Nagel et al., 2014). Nonetheless, mimicking natural disturbances through management can be used successfully in forests where species diversity and structural heterogeneity are the primary objectives. Heterogeneity on the plot-level is created through single disturbances while heterogeneity at the stand level is a result of a combination of different plot-level disturbances. Forest management can thus model disturbances at the forest compartment level. Forest management compartments, which are commonly used by forestry enterprises, can represent the units affected by a single disturbance within the range of natural disturbance severities (Hanson and Lorimer, 2007; Seymour et al., 2002). In those units, management could be oriented to have a range of disturbance severities, targeting moderate canopy disturbances (Nagel et al., 2014; Woods, 2004). If those compartments were spatially and temporally distributed, disturbance conditions approximating a mixed severity disturbance regime could be achieved. Although our results indicate the importance of the mixed severity disturbances regime, it alone is not a panacea of forest management. The key will lie in finding the right mixture of management disturbance severities to create an appropriate level of heterogeneity.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.09.005>.

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J.P. and V.T. performed data and statistical analysis;

P.J., V.T., T.N., R.S., and M.S. wrote the manuscript and all authors commented on it.



The historical disturbance regime of mountain Norway spruce forests in the Western Carpathians and its influence on current forest structure and composition [☆]



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ABSTRACT

In order to gauge ongoing and future changes to disturbance regimes, it is necessary to establish a solid baseline of historic disturbance patterns against which to evaluate these changes. Further, understanding how forest structure and composition respond to variation in past disturbances may provide insight into future resilience to climate-driven alterations of disturbance regimes.

We established 184 plots (mostly 1000 m²) in 14 primary mountain Norway spruce forests in the Western Carpathians. On each plot we surveyed live and dead trees and regeneration, and cored around 25 canopy trees. Disturbance history was reconstructed by examining individual tree growth trends. The study plots were further aggregated into five groups based on disturbance history (severity and timing) to evaluate and explain its influence on forest structure.

These ecosystems are characterized by a mixed severity disturbance regime with high spatiotemporal variability in severity and frequency. However, periods of synchrony in disturbance activity were also found. Specifically, a peak of canopy disturbance was found for the mid-19th century across the region (about 60% of trees established), with the most important periods of disturbance in the 1820s and from the 1840s to the 1870s. Current stand size and age structure were strongly influenced by past disturbance activity. In contrast, past disturbances did not have a significant effect on current tree density, the amount of coarse woody debris, and regeneration. High mean densities of regeneration with height >50 cm (about 1400 individuals per ha) were observed.

Extensive high severity disturbances have recently affected Central European forests, spurring a discussion about the causes and consequences. We found some evidence that forests in the Western Carpathians were predisposed to recent severe disturbance events as a result of synchronized past disturbance activity, which partly homogenized size and age structure and made recent stands more vulnerable to bark beetle outbreak. Our data suggest that these events are still part of the range of natural variability. The finding that regeneration density and volume of coarse woody debris were not influenced by past disturbance illustrates that vastly different past disturbance histories are not likely to change the future trajectories of these forests. These ecosystems currently have high ecological resilience to disturbance. In conclusion, we suggest that management should recognize disturbances as a natural part of ecosystem dynamics in the mountain forests of Central Europe, account for their stochastic occurrence in management planning, and mimic their patterns to foster biodiversity in forest landscapes.

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1. Introduction

There is widespread concern that climate change will alter natural disturbance regimes and thereby negatively impact forest ecosystems (Dale et al., 2001; Turner, 2010; Easterling et al., 2000). Recent changes in disturbance regimes in some regions, such as increased wildfire activity and large-scale insect outbreaks in North America, have already been attributed to climate change (Westerling et al., 2006; Bentz et al., 2010; Weed et al., 2013). However, in order to gauge ongoing and future changes to disturbance regimes, it is necessary to establish a solid baseline against which to evaluate these changes. This is particularly important given that disturbances are discontinuous processes that usually occur as infrequent events or episodes. Quantifying the natural range of disturbance variation over time periods of several centuries is thus important for understanding potential changes in severe large-scale events with long return intervals (Jarvis and Kulakowski, 2015).

Likewise, understanding how forest structure and composition respond to variation in past disturbances may provide insight into future resilience to climate-driven alterations of disturbance regimes (Tepley and Veblen, 2015; Kneeshaw et al., 2011; Kulakowski et al., 2017). Disturbances are by definition short events relative to the extended time frames of forest dynamics, yet they can have long-lasting effects on forest structure and composition. Disturbances can for instance, alter the age structure of forest landscapes, favor early-seral species, and change the developmental trajectories of forest ecosystems, effects that can persist for centuries after a disturbance event (Frellich, 2002; Johnstone et al., 2010; Nagel et al., 2014). Given such long-lasting impacts of disturbances on forest structure and composition, past disturbances can also strongly influence the current and future provisioning of ecosystem services to human society (Thom and Seidl, 2016). Yet, since the long-term effects of disturbances are poorly understood, the disturbance history of landscapes is currently rarely considered in forest management despite its importance for many ecosystem processes and its bearing on what constitutes “close-to-nature” management.

Disturbance change is particularly relevant for the mountain forest ecosystems of Central Europe, which are dominated by Norway spruce (*Picea abies* (L.) Karst.). Over the past decades, large areas of these forests have been severely damaged by windstorms (Fink et al., 2009; Holeksa et al., 2017; Schelhaas et al., 2003). Wind disturbances are commonly followed by bark beetle outbreaks (Schroeder and Lindelöw, 2002; Schelhaas et al., 2003; Wermelinger, 2004; Mezei et al., 2014), and together these two agents have resulted in widespread mortality of spruce forests throughout the region. For example, in the Tatra National Park in Slovakia, wind damaged 12,000 ha of forest in a single event in 2004 (Mezei et al., 2014). Subsequently, with the abundance of wind-felled trees serving as low-defense hosts for bark beetles, a large-scale bark beetle outbreak was triggered in the surrounding unmanaged forest reserves (Nikolov et al., 2014). Similarly, a combination of windstorms and bark beetle outbreaks resulted in widespread spruce mortality in the Bavarian Forest and Šumava National Parks (Lausch et al., 2011; Seidl et al., 2016a). Determining whether these recent disturbance events are still within the natural range of variability of the system, or whether they exceed this range as a result of drivers such as climate change or past land use, is critical for making informed decisions regarding the management of these forests.

Much recent effort has therefore been made to determine to what degree severe large-scale disturbances such as those observed recently are part of the natural disturbance regime of Norway spruce forests in Central European mountain ranges. This

body of work has mainly relied on dendroecological methods to reconstruct the history of disturbance in remnant primary forest ecosystems in the region. However, the findings of these studies remain inconclusive, with some indicating a regime dominated by small-scale, low severity disturbances (Sproull et al., 2016; Szweczyk et al., 2011) and others finding evidence of larger-scale high severity events having also occurred in the past (Svoboda et al., 2012, 2014; Zielonka et al., 2010; Panayotov et al., 2015; Čada et al., 2016; Holeksa et al., 2016).

Most of these studies have been carried out within single stands or forest landscapes. The few that have addressed past disturbance patterns across larger regions (i.e. over two forest landscapes) document a complex mixed severity regime across space and time, with a predominance of intermediate severity events (Svoboda et al., 2014; Trotsiuk et al., 2014). Moreover, to date no analyses exist that link past disturbance regimes with current patterns of forest structure and composition for these forest types (but see D'Amato et al., 2008; Lecomte et al., 2006; Zenner, 2005 for analyses in other ecosystems). Such analyses would not only provide an important baseline for understanding how future changes in disturbance regimes might influence forests, but would also be valuable for informing post-disturbance management and quantifying forest resilience (Seidl et al., 2016b). In Slovakia, for example, following the recent disturbances, there was much debate among forest managers regarding the future forest development and integrity of these recently disturbed mountain forest ecosystems (Nikolov et al., 2014). The outcomes of this discussion, e.g. with regard to the question of salvage logging and re-planting, have important implications for biodiversity (Thorn et al., 2016; Fritz et al., 2008) and provisioning of ecosystem services (Thom and Seidl, 2016).

Here, we combined dendroecological approaches with an analysis of current forest structure to study primary Norway spruce forests distributed across a range of forest landscapes in the Western Carpathians of Slovakia. Specifically, we reconstructed the overall regional disturbance history and those within 14 forest stands distributed over 7 different landscapes. This extended spatial scope of the analysis was chosen to capture the potentially wide range of past disturbance activity. Subsequently, we examined the effect of past disturbance activity on contemporary forest structure and composition, including current patterns of regeneration and coarse woody debris, to assess if and how past disturbance determines current forest conditions.

2. Methods

2.1. Study area

The study was conducted in the Western Carpathian Mountains in Central Europe. This area is considered to be a biodiversity hotspot within the European temperate zone, with a large number of endemic species and large remaining populations of brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), grey wolf (*Canis lupus*), and capercaillie (*Tetrao urogallus*) (Oszlányi et al., 2004; Mikoláš et al., 2015). To study landscape level disturbance dynamics, we selected stands based on the national inventory of primary forests in Slovakia, for which all forests in Slovakia were surveyed in 2009–2010 and approximately 10,000 ha of primary forests were mapped (www.pralesy.sk). Only stands in which no human activity directly affecting the tree layer were categorized as primary forest in the survey, which comprised a complex field survey, historical evidence from local experts, literature and historical military maps from the Austro-Hungarian Empire (from 1764 to 1768 and 1806 to 1869), and aerial images from 1947 to 1950. Furthermore, structural parameters (deadwood volume, natural tree species

composition, etc.) were considered in the assessment in the field. All the data and further information on the methodology of their collection are available on the official primary forest inventory web site (www.pralesy.sk). We here focused on primary forest remnants of mountain spruce forests. The study plots were situated in the core areas of the primary forest polygons. Tree species composition in the study area was dominated by Norway spruce (over 90%), while other species, such as rowan (*Sorbus aucuparia* L.), fir (*Abies alba* Mill.), beech (*Fagus sylvatica* L.), maple (*Acer pseudoplatanus* L.), larch (*Larix decidua* Mill.), pine (*Pinus* spp.), and birch (*Betula* spp.), were admixed. More detailed information about the study area is presented in [Table 1](#).

2.2. Data sampling

Seven landscapes containing 14 stands ([Table 1](#)) were selected, and within the stands 184 permanent study plots (PSP) were established using stratified random sampling. A 141.4 * 141.4-m grid was overlaid on each stand. Within each grid cell, a circular sample plot was established at a restricted random position (the inner 0.49 ha core in each 2-ha cell) using GPS (see [Svoboda et al., 2014](#) for further detail). The established PSPs were circular with an area of 1000 m² (500 m² in two cases), depending on the stand structure (with smaller sample sizes on plots that were recently disturbed and had a high density of regenerating trees). Elevation, aspect, slope, and slope position were recorded on each PSP. Furthermore, the diameter at breast height (DBH), species, and social status (non-suppressed – at least one half of the crown projection under open canopy condition; suppressed) of all trees with DBH ≥ 10 cm were recorded. The crown projection in four cardinal directions of five randomly selected trees per plot was measured. The line intersect method ([Harmon and Sexton, 1996](#)) was used to measure the amount of downed deadwood with DBH ≥ 10 cm

(CWD), using a total transect length of 100 m per plot, split into five sub-transects of 20 m each. In each PSP all individuals in the regeneration layer were recorded and classified according to three height classes (0.5–1.3 m; 1.3–2.5 m; >2.5 m and <10 cm in DBH). Data on CWD and regeneration from the Babia Hora and Poľana stands were not collected. Furthermore, 25 randomly selected, non-suppressed trees were cored at a height of 1 m above the ground (15 for 500 m² plots). One core per tree was extracted perpendicular to the slope direction and prepared by standard dendrochronological procedures. Tree-ring widths were measured with the LintabTM sliding-stage measuring device (Rinntech, Heidelberg) with a resolution of 0.01 mm. In the event that the pith was missing from the core, the estimation of missing rings was done using [Duncan's \(1989\)](#) method. The cores for which a substantial part of the sample was missing were excluded from further analyses. Finally, cores were visually cross-dated and verified using COFECHA ([Holmes, 1983](#)).

2.3. Dendrochronological analysis

Disturbance chronologies were compiled by two types of canopy accession events, as determined from radial growth patterns: (1) open canopy recruitment – rapid juvenile growth rates indicating recruitment in a former canopy gap, and (2) release – abrupt, sustained increases in tree growth indicating mortality of a former canopy ([Frelich, 2002](#)). Open canopy recruitment was defined by a threshold separating trees originating in open canopy from those found under closed canopy, based on their juvenile growth rates ([Svoboda et al., 2014](#)). Empirical data on the juvenile growth rates of sampled saplings (N = 175) growing under closed canopy and in different sizes of canopy openings were used, comparing their five-year growth rates. Thresholds were calculated using logistic regression and the intersection of specificity (an

Table 1
Characteristics of the study area.

Landscape (abbreviations)	Stands (abbreviations)	No. of plots (PSP)	Area of primary stands (hectare)	Mean elevation (m a.s.l.)	Mean annual air temperature (°C)	Mean annual precipitation (mm)	Soil Group (WRB 2014)	Bedrock
Eastern Tatras (A)	Bielovodská dolina (A1)	13	156	1340	0–2	2000–2400	Leptosols	Granitoids
	Javorová dolina (A2)	8	75	1439	0–2	1600–2000	Podzols	Granitoids
	Zadné Med'odoly (A3)	7	34	1499	0–2	1600–2000	Leptosols	Limestones, dolomites
Central Tatras (B)	Tichá dolina (B1)	14	41	1414	0–2	2000–2400	Podzols	Limestones, dolomites
	Hlinná dolina (B2)	10	63	1433	0–2	1200–1600	Podzols	Metapsammites
	Kôprová dolina (B3)	13	122	1434	0–2	2000–2400	Leptosols	Granitoids
Western Tatras (C)	Osobitá (C1)	14	110	1363	2–4	1200–1600	Leptosols	Limestones, dolomites
Low Tatras (D)	Bystrá dolina (D1)	15	88	1410	0–2	1200–1600	Podzols	Metapsammites, Granitoids
	Ďumbier (D2)	17	62	1495	0–2	1200–1600	Podzols	Granitoids
Great Fatra (E)	Jánošíkova kolkáreň (E1)	20	239	1312	2–4	1200–1600	Podzols	Granitoids
	Smrekovica (E2)	11	158	1386	2–4	1200–1600	Podzols	Granitoids
Orava Beskids (F)	Pilsko (F1)	12	431	1329	0–2	1600–2000	Podzols	Claystones, Sandstones
	Babia hora (F2)	10	249	1317	0–2	1200–1600	Podzols	Claystones, Sandstones
Poľana (G)	Zadná Poľana (G1)	20	494	1378	2–4	1000–1200	Andosols	Andesites

expression of the likelihood of false negatives) and sensitivity (likelihood of false positives) (Hosmer and Lemeshow, 2004). To obtain a conservative threshold estimate, we considered saplings with growth rates higher than 1.7 mm yr^{-1} as open canopy recruited, corresponding to gap sizes of more than 500 m^2 . For growth release detection, we used the boundary line criteria proposed by Black and Abrams (2003) and followed the approach also used by Svoboda et al. (2014). Specific boundary lines from all data of this study were constructed ($\text{PGC} = 1664.2567 * e^{(-7.1423 * \text{PG})} + 684.7334 * e^{(-0.8271 * \text{PG})}$; PGC = percent growth change, PG = prior growth following Black and Abrams (2003)). A release event was defined as any growth-change value over 20% of the boundary line. Furthermore, the post-release ring widths had to exceed the pre-event 10-year running mean for at least seven years (Fraver et al., 2009) in order to signify a release event. To minimize the overestimation of disturbance detected by mature trees already in the canopy, we used a DBH threshold for separating trees in two groups, based on the probability of their presence or absence in the canopy (Lorimer and Frelich, 1989). The threshold was estimated in the same way as that for open canopy recruitment, where the DBH distribution of canopy and sub-canopy trees was separated. The DBH threshold for Norway spruce to be classified as a canopy tree in our study was found to be 23 cm without bark, and was calculated as the intersection of specificity and sensitivity (Hosmer and Lemeshow, 2004). Norway spruce is a moderately shade-tolerant species, especially in juvenile phases of development, such that more than one disturbance may be needed for it to reach the canopy (Lorimer and Frelich, 1989). Therefore, multiple canopy accessions were allowed in deriving the disturbance chronologies.

2.4. Construction of the disturbance chronologies

Canopy accession events were summed by decade to construct disturbance chronologies at the plot level. The number of growth releases and gap recruitment events were converted to total canopy area disturbed each decade, following the approach and rationale of Lorimer and Frelich (1989). Linear regression analysis was used to predict canopy area from DBH based on the present vegetation at the PSPs (crown area = $1.1038 + 0.0517 * \text{DBH}$; $R^2 = 0.52$, $p < 0.001$). The disturbance chronologies were truncated when the percentage of canopy available in the tree ring sample fell below 10% back through time. To analyze disturbance dynamics at different spatial scales, composite disturbance chronologies were created for the overall region, as well as for the level of landscapes and stands. All the chronologies were constructed in the same way using all events indicating disturbances. Because our focus was on spatial scales of stands and beyond, our approach aggregated disturbance evidence at the plot level without any spatial resolution of the events.

Release was detected by dating the discrete event of growth change, but regenerating trees can take several years or decades to establish and grow to a height of 1 m (coring height) (Kulakowski and Veblen, 2003). To take into account such a prolonged period of tree recruitment, we calculated a 30-year running sum of the percentage of the canopy area disturbed. This approach was used for all analyses with the exception of Fig. 1. Disturbance events were dated using the peak of the local maximum of a 30-year running sum of the percentage of the canopy area disturbed. For easier visualization of the data, we used four disturbance severity classes: Low – below 20%, Moderate – between 20% and 40%, High – 40–60% and Very high – over 60% of canopy was removed. Because we are analyzing mostly regional, landscape and stand scales, some degree of generalization was needed. Our analysis disregards potential low severity disturbance events that occurred within the 30-year periods that are counted as single events. We

restricted our analysis to the period from 1790 to 1970 in each plot because in 1790 we observed a drop in the sample depth and the standard deviation (SD) of canopy area disturbed per plot with a continuously decreasing trend back through time. The upper threshold of 1970 was determined by our methodological approach (30-year running sum and missing data in recent gaps, where trees were not large enough to core). Therefore, we roughly assessed the percentage of canopy area removed in the period 1985–2010. This was done with the intersection of two GIS layers, the percentage of canopy area disturbed in the study of Griffiths et al. (2014), and the studied stand polygons delineated by the official primary forest inventory on www.pralesy.sk. This analysis likely underestimates small-scale low severity disturbance events (e.g. removal of single trees). Therefore this recent rate of canopy area removed is very conservative and serves as an illustrative example to show the difference between recent disturbances and historical disturbances.

An average disturbance return interval for each plot was calculated by dividing the number of years on record by the number of disturbance events reconstructed for that period. An average rotation period for the whole area was derived as the mean time needed for each plot to be completely disturbed.

2.5. Analysis of past disturbance influence on age pattern and current forest structure

To determine the influence of past disturbance on current forest structure, we separately analyzed five groups of stands with different disturbance histories. To focus on the role of the most severe disturbance events in the recorded history of the plots, we used the maximum value of the 30-year running sum of canopy disturbance per each plot and in some cases the date of this event to delineate different disturbance history groups. Group I (“Low severity”) was characterized by events with severity below 40%, and frequently experienced events over the entire study period. Groups II and III represented “Moderate severity” disturbance regimes, with a maximum severity between 40% and 60%. They differed in the timing of the last disturbance, with Group II experiencing the last disturbance event before 1900 and Group III after 1900. Groups IV and V represent “High severity” conditions, with past disturbances affecting more than 60% of canopy trees. As with the moderate severity groups II and III, we further distinguished between those last being disturbed in the 18th and 19th century (Group IV) and those experiencing the last high severity disturbance more recently (Group V). The influence of disturbance history on stand structure was tested with linear mixed-effects models, using stands as a random effect. The variables were individually transformed (using square root, logarithmic and power transformation), and normality and homogeneity of variance were evaluated using normal probability plots and the Shapiro-Wilk test. The analysis was performed using the R language and environment for statistical computing (R Development Core Team, 2015), specifically harnessing the library “nlme” (Pinheiro et al., 2015). All tests were performed at a pre-set significance level of 0.05.

3. Results

3.1. The historical disturbance regime of the Western Carpathian region

The disturbance chronologies reconstructed at our study sites spanned the late 18th century to the end of the 20th century (Fig. 1). Most of the tree-ring evidence of disturbance consisted of open canopy recruitment events (63% on average), indicating

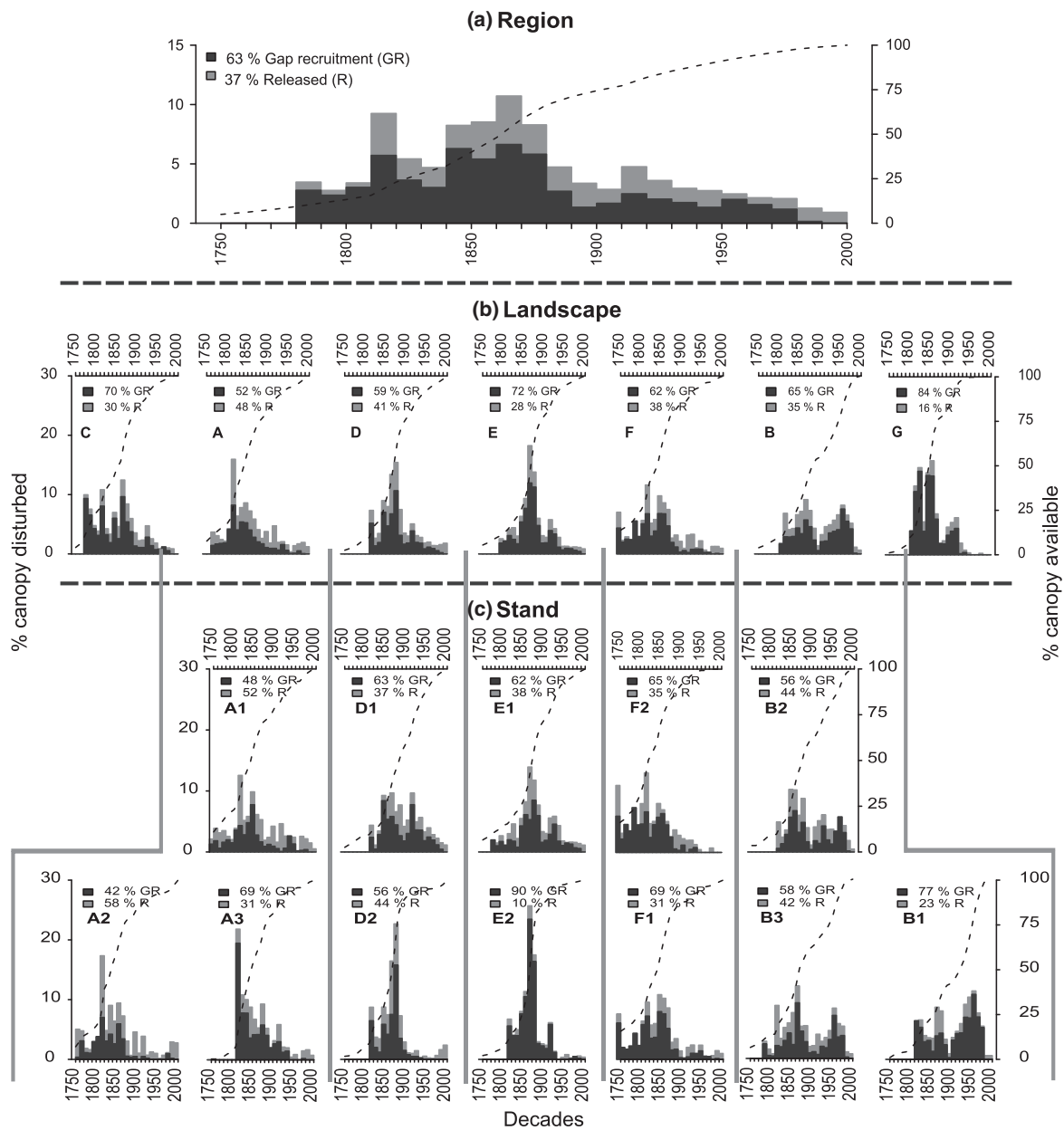


Fig. 1. Hierarchical scheme of percent canopy disturbed for the Western Carpathian region (all plots pooled) (a), the landscape scale (b), and the stand scale (c). Disturbance chronologies were derived from analyzing two types of events indicating disturbance – gap recruitment and growth release. The percentage of these two types as well as abbreviations identifying the respective stands and landscapes (cf. Table 1) are placed in the top left corner of each panel. All disturbance events in a decade were summed, and the chronologies were truncated when the percentage of canopy available (dashed black line; secondary y axis) fell below 10% of the total number of samples. The percentage of canopy available represents the cumulative portion of canopy contributing to the chronology.

growth in open canopy conditions for the entire life span of a current canopy tree; these patterns are also consistent with age distributions (Fig. Sup. 1). There was high temporal variability in disturbance patterns at both the level of landscapes (N = 7) and stands (N = 14) (Fig. 1b and c), but peaks in disturbance activity were evident in the periods 1810–1820 and 1840–1880 (Fig. 1a). At the stand scale, the temporal variation of disturbances is higher than at landscape and regional scales, and disturbance peaks are more pronounced (Fig. 1c). At this smallest scale of analysis, the distribution of canopy accession events over the reconstruction

period varied from unimodal, to bimodal and multimodal, but temporally synchronous disturbance events were evident particularly for the 1810s and 1840s–1870s across many of the stands. In the 1810s, for instance, 56.5% of the sampled stands and 7.6% of the canopy was disturbed, whereas 93.5% of the stands (34.6% of the canopy) experienced disturbance between the 1840s and 1870s. Overall, 42.2% of the canopy was disturbed within these two time windows. Spatially less extensive disturbances were also detected through more local synchronies, e.g. between the stands in the Central Tatra landscape (B) in the 1940s and 1950s. Across the

entire region, most of the canopy accession events were observed within the 19th century, except for the Central Tatra landscape (B), where a high proportion of canopy accession events was found for the 20th century.

We found that most events were characterized by low disturbance severity (65.2%), which removed only 28.1% of canopy area on average. Overall, the most canopy area was removed by events with low and moderate severity. Nonetheless, severe events (High and Very high events), despite accounting for only 14.3% of the total events, were responsible for 42.3% of the total canopy area disturbed (Table 2). The average disturbance rotation period was 242 years (SD = 59.2). On average, plots were hit by disturbance every 43 years. Disturbance frequency decreased with the severity of an event: Low severity events were most frequent (return interval of 66 years), while high severity events had an order of magnitude longer return intervals (Table 2). The distribution between different severity classes remained relatively stable over time, but high severity disturbance events were particularly prevalent in the 19th century (Fig. 2). The highest severity events occurred between 1840 and 1870, but the spatial variability across the study region was high (Fig. 3). For example, a high proportion of severe disturbances was found in the stands of the Great Fatra landscape (E1 and E2), Poľana (G1), as well as some stands of the Western, Central and Low Tatras (C1, B1, D2), whereas lower severity events characterized the Eastern Tatra landscape (A1 and A2). The spatio-temporal pattern of the most important disturbance events is summarized in Fig. 4, when in the 1810s, 32.6% of the sampled stands and 7.9% of the canopy was disturbed, whereas 89.1% of the stands (35.6% of the canopy) experienced disturbance between the 1840s–1860s. During the 1940s and 1950s 34.2% of the sampled stands and 6.9% of the canopy was disturbed. Overall, 50.3% of the canopy was disturbed within these three time windows.

3.2. The influence of past disturbance on age pattern and current forest structure

To examine the influence of the past disturbance regime on current forest structure, the study plots were split into five groups based on the timing of the major disturbance event and the maximum disturbance severity (Fig. 5). Of all plots, approximately one third (32.4%) experienced only low severity disturbance over the study period (Group I). The majority of moderate severity (Group II) and high severity (Group IV) plots were disturbed before 1900, but a smaller percentage also experienced moderate to severe disturbance within the 20th century (9.1% and 7.1% were in Groups III and V, respectively). The latter were mostly situated on northern or western slopes, but did not differ greatly from the other groups with regard to their slope inclination (Figs. Sup. 2 and Sup. 3). As expected, mean stand ages mirrored this classification, with groups experiencing moderate and high severity disturbance after 1900 (Groups III and V) being significantly younger ($p < 0.05$) than the other groups. Stand age distributions showed clear peaks corresponding to the respective periods of major disturbance events. Differences in maximum ages, on the other hand,

were not so clear among the groups: The oldest trees in the stands not disturbed mainly in the 20th century or disturbed with low severity only were between 431 and 495 years old (with the 90th percentile age between 199 and 249 years), while the oldest trees in stands disturbed mainly in the 20th century were 340 and 374 years old (with the 90th percentile age between 132 and 195 years).

Mean DBH and age were correlated ($r = 0.52$, $p < 0.05$), and DBH distributions matched the age structures within the groups well, particularly if the sampling artifact (i.e. missing tree cores from young trees < 10 DBH) is considered. Mean DBHs differed with time since disturbance, but not between severity classes (Fig. 5). Stand density was similar among the stands with different disturbance history, except for Group V (high severity disturbance after 1900), which had a significantly higher stem density than other stands ($p < 0.05$). Furthermore, downed deadwood volume and regeneration density did not differ significantly between the plots, regardless of their disturbance history. The mean CWD volume per plot ranged from 83 to 157 $m^3 ha^{-1}$. The mean regeneration density was between 806 and 1927 trees ha^{-1} , but there was substantial variation in regeneration density at the plot level within each disturbance history group (mean = 1427 trees/ha, standard deviation = 1717, range (min, max) = 20; 13,140 trees/ha, quantile (10%, 90%) = 237, 3078 trees/ha). The most common species in the regeneration layer were Norway spruce and rowan. However, 54% of the rowan were within the smallest height class. Other tree species were present, including fir, maple, beech, pine, and larch, but made up less than 1% of the total density.

4. Discussion

4.1. Disturbance history

We found the disturbance history of the mountain forests of the Western Carpathians to be characterized by a disturbance regime with high spatiotemporal variability in severity and frequency. Moderate and low severity disturbances dominated, but rare severe events were also evident in our disturbance reconstruction, and made a disproportional contribution to the overall canopy removed by disturbance. A similar mixed severity disturbance regime was also recently described for Norway spruce-dominated mountain forests in Central Europe by Trotsiuk et al. (2014), Svoboda et al. (2014), Holeksa et al., 2017 and Čada et al. (2016). Although the disturbance history in the region was temporally and spatially diverse, periods of synchrony in disturbance activity were also found. Specifically, a peak of canopy disturbance was found for the mid-19th century across the region, with the most important periods of disturbance in the 1820s and from the 1840s to the 1870s.

Interestingly, these periods also show strong disturbance signals in other mountain forest ecosystems of Central Europe (Trotsiuk et al., 2014; Čada et al., 2016; Svoboda et al., 2014; Janda et al., 2014; Zielonka et al., 2010), indicating that disturbance regimes might be synchronized across large spatial scales (Jarvis

Table 2

Characteristics of the disturbance regime of Norway spruce mountain forest ecosystems of the Western Carpathian region. Disturbance chronologies were constructed using a three-decade running sum window of the percentage of canopy area disturbed for all plots.

Events by severity class	Return interval (years)	Mean severity (% canopy removed)	Proportion of canopy area disturbed (%)	Proportion of disturbance events (%)
All events	43	20.1	1	1
0–20% Low	66	8.7	28.1	65.2
20–40% Moderate	210	29.0	29.3	20.4
40–60% High	526	47.5	19.2	8.1
Over 60% Very high	690	74.9	23.1	6.2

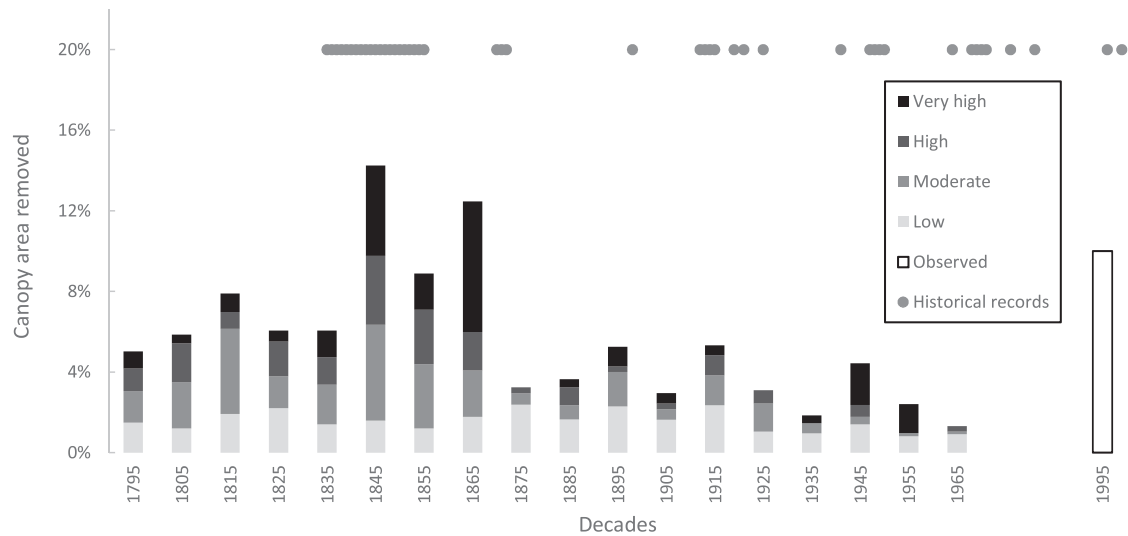


Fig. 2. The amount of canopy disturbed in the region over time, distributed over disturbance severity classes. The disturbance chronology was constructed using a three-decade running sum window of the percentage of canopy area disturbed. In the chronology we summed three decades, and the date of the events were distributed per decade (as midpoints). For easier visualization of the data, we used four disturbance severity classes: Low – below 20%, Moderate – between 20% and 40%, High – 40% to 60% and Very high – over 60% of canopy area removed. The chronology was truncated at 1790 and 1970 (see methods). Historical records of disturbance events (grey circles) are presented in the upper part of the figure (see Table Sup. 1). The observed percentage of canopy area removed was assessed by comparing the percentage of canopy area disturbed by Griffiths et al. (2014) between 1985 and 2010 with the studied stand polygons delineated by the official primary forest inventory on www.pralesy.sk.

and Kulakowski, 2015; Seidl et al., 2016a). Historical sources (Table Sup. 1) describe events during these periods as being predominately windstorm events, often combined with bark beetle outbreaks. This suggests that the past disturbance agents in the area are identical to the most common disturbance agents in these forests today (Schelhaas et al., 2003; Müller et al., 2008). However, as these are high elevation, temperature-limited ecosystems, sub-optimal temperatures and frost (Kullman and Öberg, 2009) during a cold event in the beginning of the 19th century (Büntgen et al., 2013) cannot be ruled out as a possible cause for pulses of tree mortality. Unfortunately, the methods and approaches used in this study did not allow us to distinguish between different disturbance agents (but see Zielonka et al. (2010) and Robson et al. (2015)).

The spatial patterns of the disturbance regime were highly variable, but some trends within the region could be discerned. Lower disturbance severities were, for instance, observed in the Eastern Tatras, and can be explained by the position of this particular landscape in the context of the greater Tatras mountain range, which shelters it against strong winds from predominantly westerly and northerly directions (Niedźwiedź, 1992). In contrast, landscapes exposed to these winds and without topographic sheltering were more strongly disturbed in the past, with a higher risk of severe disturbance (Cada et al., 2016). Furthermore, the region of the Central Tatras also had an elevated proportion of canopy accession events in the 20th century, suggesting an overall increased disturbance frequency. This finding is in line with the observation that this particular area is specifically influenced by strong and frequent “Bora” winds from the north (Zielonka et al., 2010; Mezei et al., 2014).

The prominent disturbance pulses of the 19th century likely also contributed to the comparatively low disturbance activity in the first part of the 20th century. The disturbance risk for the young stands originating in the mid-19th century was likely depressed for several decades, as both wind and bark beetle susceptibility increases with age in Norway spruce forests. *Ips typographus* attack primarily older and weakened trees, which are found in abundance after wind disturbance (Wermelinger, 2004; Økland

and Bjørnstad, 2006), and also wind risk increases with tree size (and hence age) (Canham et al., 2001). Furthermore, the absence of high severity disturbance after the mid-19th century could have led to a synchronous development of regenerating forest stands as well as to spatial homogenization across the landscape through increased connectivity between susceptible patches. These factors are frequently associated with increasing risk for wind disturbance and bark beetle outbreaks (Jarvis and Kulakowski, 2015; Seidl et al., 2016a), suggesting a century-scale temporal autocorrelation between disturbance episodes in these forests.

However, it should also be noted that the higher proportion of trees recruited in the 19th century could at least in part be explained by the availability of possible study sites, as we focused on remnants of primary forests, mostly in strictly protected reserves with specific topography (Figs. Supl. 1 and Supl. 2). Despite having a regional and landscape scale focus, our work was still carried out in a fragmented landscape, where only remnants of old-growth forests remained. Together with the fact that salvage logging has commonly been applied in the region during the last 50 years, unmanaged young post disturbance stands might be partly missing. Consequently, early-successional stages after recent high severity disturbance, such as described in Central Europe by Wild et al. (2014), Zeppenfeld et al. (2015) and Svoboda et al. (2014), were missing in our analysis. This decreases the utility of our disturbance reconstruction for recent decades, and suggests that the historical disturbance regime reconstructed from primary forests might not be fully representative of the entire region.

Nonetheless, our analysis suggests that the current disturbance pulse observed in several Western Carpathian mountain forests (Mezei et al., 2014) could at least in part result from past disturbance dynamics and the emerging synchrony in stand development. Additional drivers of the currently high disturbance activity might be climate change, resulting in an increasing probability of bark beetle outbreaks (Milad et al., 2011; Temperli et al., 2013) as well as increasing climatic extremes connected with damage to forests, such as drought and wind events (Dale et al., 2001; Seidl et al., 2014). Similar large-scale disturbance can also be

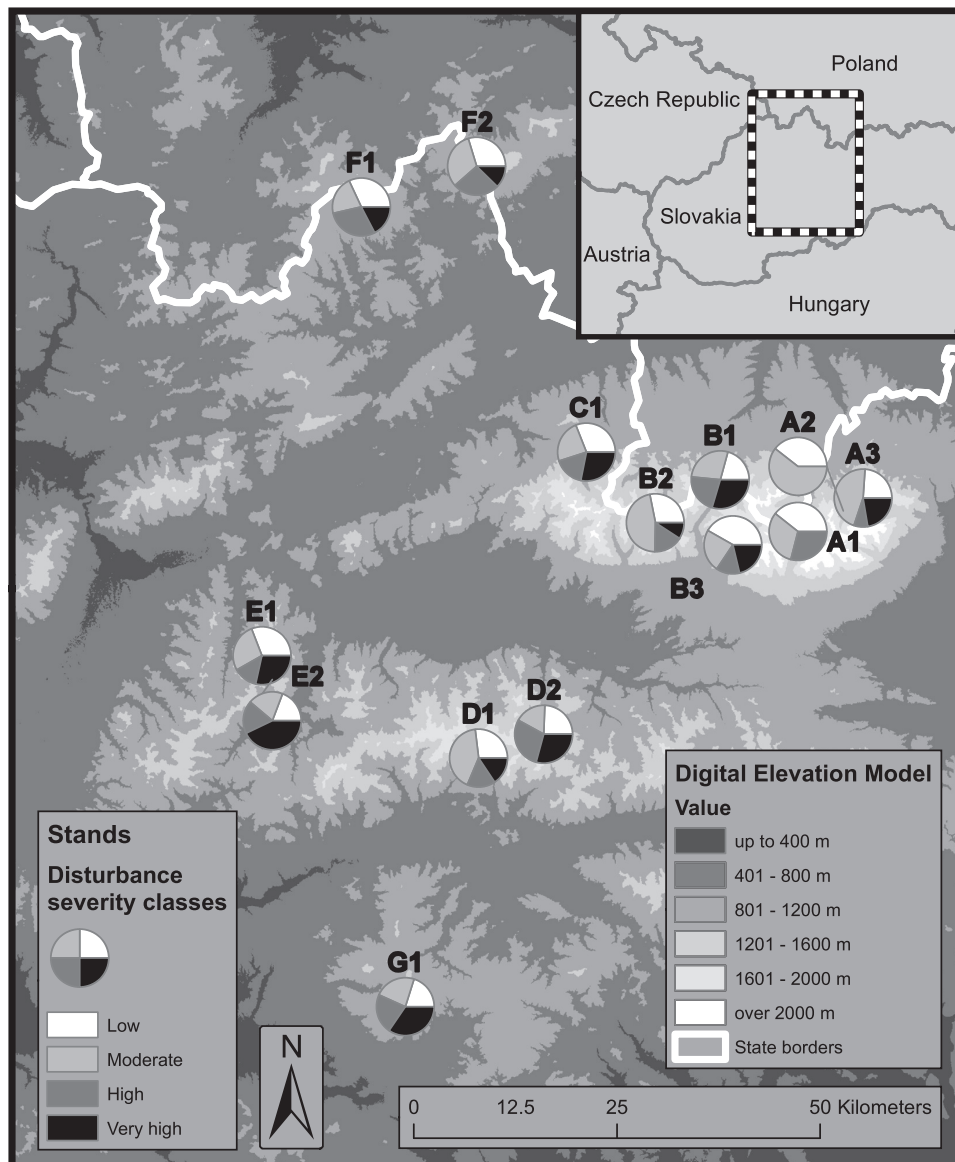


Fig. 3. The spatial distribution of stand level disturbance severity within the study region. The share of disturbance severities (canopy area disturbed) between 1790 and 1970 is shown at the stand level. Disturbance events were reconstructed using the same data as in Fig. 2 and Table 2. The abbreviations for different stands are described in Table 1.

observed in other parts of Central Europe (Čada et al., 2016; Lausch et al., 2011) or in North America (Berg et al., 2006). Thom et al. (2013), in their analysis of recent disturbances in neighboring Austria, derived a combined median disturbance rotation period for wind and beetles of 134 years, a value that suggests higher current disturbance activity compared to the historical values derived here (cf. Table 2). Furthermore, recent disturbances in Central Europe have largely been high severity events (Mezei et al., 2014; Nikolov et al., 2014; Kautz et al., 2011), suggesting that disturbance regimes might be changing in severity and frequency relative to their historical patterns (cf. Fig. 3). However, other evidence from Slovakia (Zielonka et al., 2010) and other parts of Central Europe (Svoboda et al., 2012, 2014; Čada et al., 2016; Holeksa et al., 2016; Brůna et al., 2013; Panayotov et al., 2015) suggests that large-scale severe disturbance events such as those observed recently might also have occurred in the past.

4.2. The influence of past disturbance on current forest structure

We found that the disturbance history of a stand had a significant influence on some aspects of its current structure, which is in line with previous investigations for other ecosystems (D'Amato et al., 2008; Zenner, 2005). Stand structural parameters such as DBH and stand age structure were strongly influenced by past disturbance activity. In contrast, the effect of past disturbances on parameters such as tree density, the amount of CWD, and regeneration was found to be only weak and not statistically significant. Maximum disturbance severity and time since the last substantial disturbance were both strong drivers of the DBH and age structure. Frequent low severity disturbances resulted in very wide DBH and age distributions, indicating high temporal variability in establishment and structures close to what can be expected for old-growth forest (D'Amato et al., 2008). In contrast, high severity disturbances

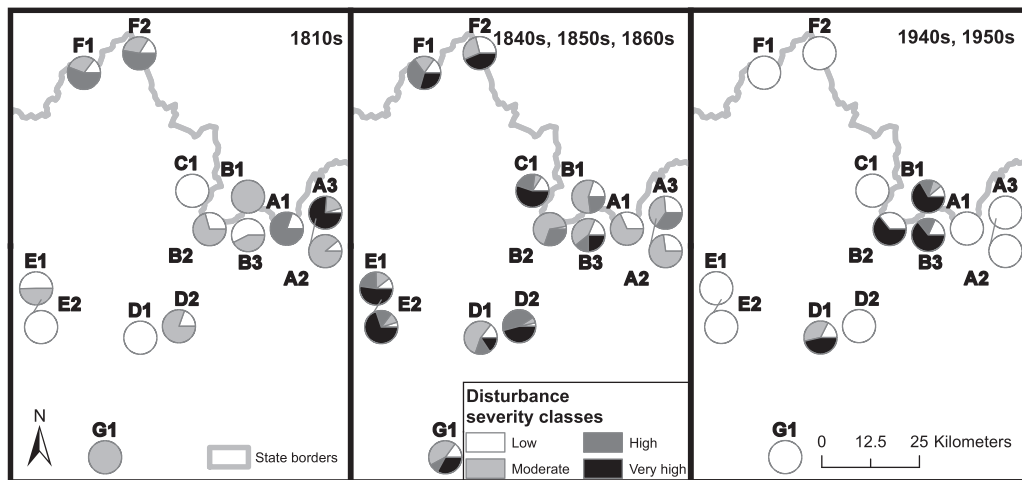


Fig. 4. The spatio-temporal distribution of stand-level disturbance severities (proportion of canopy disturbed) is shown for the three most important time periods (highest disturbance activity). Disturbance events were reconstructed using a three-decade running sum window as in Fig. 2 and Table 2.

created narrow DBH and age distributions or reverse J shaped distributions, indicating recent pulses of regeneration under an established overstorey cohort. Generally, time since disturbance had a stronger effect on current structures than past disturbance severity. Stands mainly influenced by disturbances occurring before 1900 as well as the low severity group had clear peaks in age structure between 100 and 200 years, while trees were considerably younger in more recently disturbed stands. Interestingly, we also found rather old trees in plots that were influenced by recent disturbance. This indicates the persistence of trees from previous generations surviving the last moderate or severe disturbance. This finding suggests that natural disturbances in the area were rarely complete and work selectively (Nagel et al., 2014; Šamonil et al., 2013), and that even in high severity disturbances, biological legacies in the form of surviving trees exist. Such legacy trees are very important for structural diversity in early successional development and contribute to the resilience of forest ecosystems to disturbance (Moning and Müller, 2009; Seidl et al., 2016b).

With regard to tree regeneration and CWD, on the other hand, we did not find significant effects of disturbance history on current conditions. In this context it should be noted that these two parameters are strongly linked in the high elevation Norway spruce forests of Central Europe, as CWD is a highly suitable microsite for spruce regeneration (Bačec et al., 2012). It is reasonable to expect that the amount of CWD and subsequently the abundance of regeneration would be strongly influenced by the time since disturbance, as CWD decays over a matter of decades (Zielonka, 2006). However, no such effect was evident in our data when comparing stands that were disturbed before and after 1900. This suggests that the low severity mortality events occurring with relatively high frequency throughout all sites might play an important role in maintaining CWD levels and thus providing suitable microsites for regeneration on the landscape. Overall, our findings are in line with previous assessments suggesting that the effect of disturbances persists over different time spans depending on the ecosystem property in focus (Seidl et al., 2016b).

The amount of regeneration on all study plots was on average approximately 1400 trees per hectare with a height over 0.5 m and a DBH lower than 10 cm. Similar regeneration densities were observed in other studies of mountain spruce forests (Zeppenfeld et al., 2015; Wild et al., 2014), and these levels are assumed to be sufficient to ensure continuity of forest cover. Furthermore,

there is high probability of an increasing amount of tree regeneration in the decades following large-scale dieback (Zeppenfeld et al., 2015). The overall average regeneration density was rather high across all the plots in our study, although there was considerable variation among plots. This variability contributes to high structural heterogeneity of the system at the landscape scale (Donato et al., 2012). The high densities of rowan found in the lowest height classes will probably experience high mortality, as suggested by their substantially reduced number in higher height classes. Similar trends have also recently been observed in mountain spruce forest ecosystems of the Bavarian National Park (Zeppenfeld et al., 2015).

4.3. Management implications

Extensive high severity disturbances have recently affected Central European forests, spurring a discussion among managers and policy makers as to the causes and consequences of these disturbances (Nikolov et al., 2014). An important question in this discussion has been whether such events are common, and whether these forests are adapted to these kinds of disturbances. We showed that pulses of disturbance are part of the natural disturbance regime in Norway spruce mountain forests, and that high severity disturbances have also occurred in these forest types in the past (see also Zielonka et al., 2010; Brúna et al., 2013; Svoboda et al., 2012; Čada et al., 2016). Yet, the disturbance return intervals and severity distributions estimated here suggest that recent events might be at the upper bound of the historical range of variability (HRV). This suggests that further increases in disturbance, as are expected for the region under changing climate conditions (Seidl et al., 2014), might exceed the HRV of the system. As the HRV is an important reference for understanding disturbance changes and can serve as a guideline for ecosystem-oriented management (Keane et al., 2009), future research should focus on a comprehensive comparison of the regional HRV with current activities (cf. Cyr et al., 2009), as well as on estimating the future range of variability that can be expected under global climate change (see Seidl et al., 2016b).

Our results also highlight that in assessments of future trajectories of forest ecosystems, the persistent effect of past disturbances needs to be considered. It is likely, for instance, that the temporal synchronization through the heavily disturbed period in the

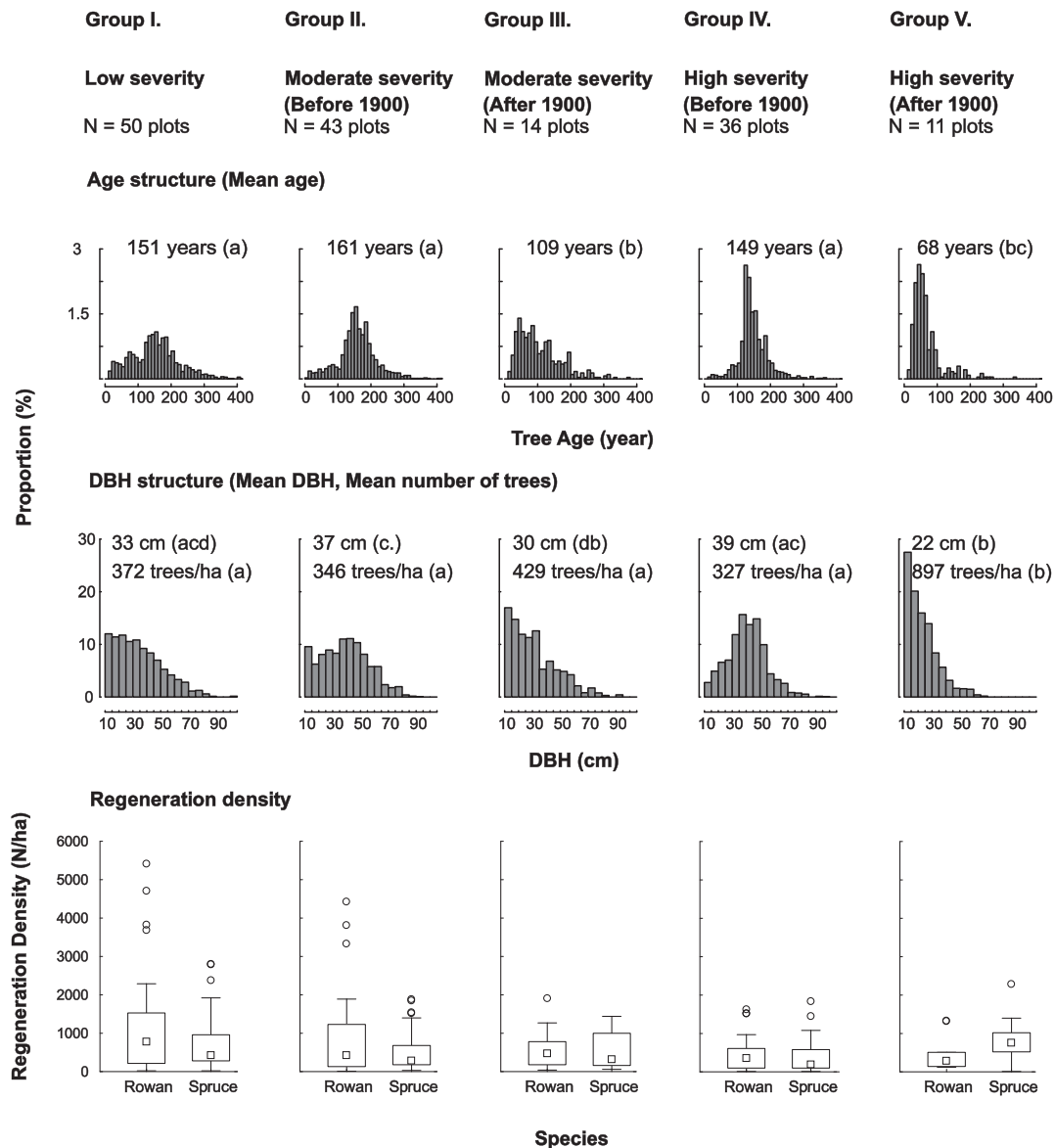


Fig. 5. The influence of disturbance history (characterized by past disturbance severity and the timing of the last major disturbance) on current stand structure and composition, with each column representing a different disturbance history group. Two stands (F2 and G1) were excluded from the analysis because of a lack of information on dead wood and regeneration. Statistical differences between mean values are indicated by lower case letters in parentheses and were tested with linear mixed-effects models, using stands as a random effect.

mid-19th century has substantially contributed to the current disturbance susceptibility of the ecosystem. Furthermore, structural parameters of the forest, such as the spread and shape of the diameter distribution, indicate a lasting effect of past disturbances. The fact that these variables are important indicators of biodiversity (Paillet et al., 2010) suggests that understanding the prevailing disturbance regime (and the potential changes therein) is crucial for conservation management. The finding that regeneration density and composition was not influenced by the disturbance regime between 40 and 220 years before the present illustrates that vastly different past disturbance histories are not likely to change the future trajectories of these forests (but see Johnstone et al., 2010). In other words, these ecosystems currently exhibit high ecological resilience to disturbance (see also Zeppenfeld et al., 2015). In conclusion, we suggest that management should recognize dis-

turbances as a natural part of ecosystem dynamics in the mountain forests of Central Europe instead of aiming to prevent them (cf. Fares et al., 2015), and should account for their stochastic occurrence in management planning (e.g. via increasing redundancies to maintain crucial ecosystem services despite disturbance, Seidl, 2014) as well as mimic their patterns (Nagel et al., 2014) to foster biodiversity in forest landscapes.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.08.014>.

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5.2.3. Neglecting legacies of past forest disturbance overstates the climate effect on current disturbances

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Author contributions:

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V.T., P.J. and M.S. conceived ideas and designed the study;

V.T., P.J., V. C., M.M. R.B., J. L. and M.S. performed the sampling;

V.T., P.J., V.C., M.M., J.L. performed the dendrochronological analyses;

J.S., V.T. and V.C. performed data and statistical analysis;

J.S., V.T., T.N., P.J., R.S., D.K., S.F., and M.S. wrote the manuscript and all authors commented on it.

Title: Neglecting legacies of past forest disturbance overstates the climate effect on current disturbances

Abstract:

Determining the climate sensitivity of forest disturbance rates remains a pressing global-change issue and the emphasis on disturbance history as a co-contributing factor has been insufficient. Large-scale forest dynamics are commonly assumed to be climate driven, but disturbance history reconstructions are rarely conducted at appropriate scales to check this assumption. We compiled multiple tree-ring based disturbance history reconstructions from primary *Picea abies* forest fragments distributed throughout five landscapes spanning the Bohemian and Carpathian mountains into a regional chronology. The chronology includes 11 595 trees spanning the years 1780 to 1990 collected from 560 inventory plots from 37 stands distributed across a 1000 km geographic gradient, amounting to the largest disturbance chronology yet constructed in Europe. Decadal disturbance rates between 1800 and 1920 were significantly above the historical mean, followed by a region-wide decline. An estimated 75% of current canopy area has recruited prior to 1900. Long-term disturbance patterns were compared to an historical drought reconstruction and disturbance history was linked to contemporary disturbance patterns derived from LANDSAT imagery. Historically, disturbance rates were weakly positively associated with drought severity, while non-synchronous landscape-scale peaks corresponded to locally documented windstorms and bark beetle outbreaks. Among stand characteristics, time since major disturbance was the best predictor of contemporary disturbance rates. Disturbance susceptibility appears to remain low during the first 100 years of development and subsequently increases. Recent disturbances were less severe in structurally heterogeneous stands and an apparent historical trend of high heterogeneity may also contribute to long-term patterns. Regional disturbance patterns suggest that high 19th century disturbance rates contributed to a reduction in disturbance susceptibility, which may have reduced the climate sensitivity of 20th century disturbance rates. Disturbance history can decouple climate-disturbance relationships and neglecting disturbance history can potentially lead

to the climate sensitivity of disturbance patterns being overstated, even at large scales.

Key Words: Dendroecology, disturbance history reconstruction, forest disturbance, Large-scale dynamics, *Picea abies*, primary forest, severity, susceptibility

Introduction

Disturbances shape forest structure and function (Attiwill 1994) and changes in the factors driving disturbance patterns are altering forest dynamics (Turner 2010, Seidl et al. 2017). In Europe, the amount of forest area affected by disturbance on an annual basis has been increasing for two centuries (Schelhass et al. 2003), with recent trends attributed to changes in both stand structure and climate (Seidl et al. 2011). These disturbance trends have largely been inferred from Europe's extensively-managed forest ecosystems; comparable patterns in primary forests have not been fully examined, even though disturbance history reconstructions in primary forests provide essential context for interpreting recent dynamics in managed or unmanaged systems (Swetnam et al. 1999; Kulakowski et al. 2017). While disturbance histories are available for several primary forest landscapes throughout Europe (e.g., Svoboda et al. 2010, Nagel et al. 2014), improving the characterization of larger-scale natural disturbance patterns remains a central research priority (Seidl et al. 2017). Increasing the spatial extent of disturbance history reconstructions is necessary to assess the range of historical variability and to partition how regional climate vs. structural dynamics influence patterns (e.g., Swetnam et al. 1999, Temperli et al. 2013).

Disturbance frequency and intensity are climate sensitive and are presumed to be increasing under climate change (e.g., Overpeck et al. 1990, Dale et al. 2001, Seidl et al. 2014). Climate exerts a temporally dynamic influence on disturbance patterns over entire regions (e.g., Swetnam and Betancourt 1998, Pederson et al. 2014, Jarvis and Kulakowski 2015), while stand dynamics, topography and inherent stochasticity contribute substantially to within-region variability (e.g., Veblen et al. 1994, Temperli et al. 2013). Identifying climate-

based regulation of disturbance patterns therefore requires compiling datasets that integrate over the variability contributed by local drivers and span the geographic extent of forest regions (Swetnam and Betancourt 1998, Pederson et al. 2014). Drought has especially been linked to wide-spread synchronization of forest dynamics, both as a direct source of tree mortality (Pederson et al. 2014) and by predisposing large areas to disturbances, such as bark beetle outbreaks in North America (Jarvis and Kulakowski 2015) and Europe (e.g., Seidl et al. 2016b, Marini et al 2017).

A forest's disturbance history influences its structural development and consequently its disturbance susceptibility, because the susceptibility of trees to various disturbance agents often depends on tree size and stem densities (e.g., Canham et al. 2001, Wermelinger 2004). Consider the susceptibility of trees to bark beetle outbreaks and wind storms, the prevailing disturbance agents in Central and Eastern Europe's temperate conifer forests (Svoboda et al. 2010): As host tree species increase in size, the availability of their cambium as a food source to bark beetles increases (Wermelinger 2004). Consequently, the potential severity of a beetle outbreak is greater for stands composed of large trees compared to stands composed of smaller trees. Wind susceptibility is similar, with stands composed of smaller trees that offer less leverage to wind being less susceptible (Foster and Boose 1992). These disturbances selectively deplete the susceptible subsets of forest populations and time is required to replenish these cohorts before a similar event can reoccur (e.g., Pickett and White 1985, Hart et al. 2015). By determining a location's susceptibility, disturbance history places an upper limit on the potential severity of a specific disturbance independent of its intensity; historical factors thus influence the apparent climate-sensitivity of disturbance rates. Neglecting history could potentially lead to climate effects being overstated if forest susceptibility increases on a large-scale independently of climate-driven disturbance intensification, which can result from a synchronization of forest dynamics by a former large-scale event (Swetnam & Betancourt 1998, Pederson et al. 2014).

Disturbances reduce canopy cover and the associated reduction in competition permits formerly suppressed trees to recruit into adult cohorts. The

disturbance history of a forest stand can therefore be reconstructed from tree recruitment dates and growth-rate anomalies, which are naturally cataloged in tree-ring series (Lorimer and Frelich 1989). A collection of five tree-ring based disturbance histories from landscapes spanning the Bohemian and Carpathian mountains (Svoboda et al. 2010, Trotsiuk et al. 2014, Čada et al. 2016, Janda et al. 2016, plus novel data) was compiled into a regional chronology to address hypotheses regarding constraints on large-scale primary *Picea abies* (L.) H. Karst. forest disturbance patterns: (1) Partitioning the relative importance of local vs. regional drivers of disturbance (Fig. 1). Synchronous occurrence of geographically distant events or trends in large-scale data implies the action of a regional driver, while misalignment of events implies independence and the importance of heterogeneous local factors. (2) The climate sensitivity of regional disturbance rates is then tested directly, by correlating mean regional disturbance rates with an historical drought reconstruction (Cook et al. 2015). Drought was targeted as a candidate climate factor due to its apparent link with beetle outbreaks throughout the region (e.g., Seidl et al. 2016b, Marini et al 2017). (3) Disturbance history and stand structure is then linked to LANDSAT-derived contemporary disturbance patterns (Hansen et al. 2013). Developmental changes in mean diameter and structural uniformity were expected to correspond with higher severity events. (4) To link relationships between stand structure and current disturbance to long-term trends and to identify how small-scale heterogeneity might influence large-scale susceptibility, we further investigate spatial structure in disturbance patterns within and among stands through time.

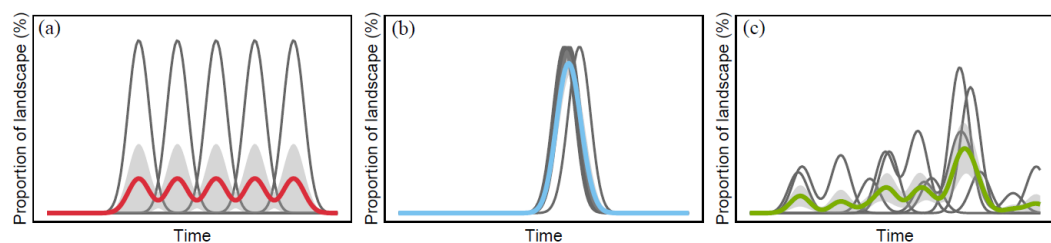


Fig 1. Hypothetical patterns in large-scale disturbance patterns indicating regional vs. local determination. (a) In absence of a regionally synchronizing disturbance agent, peaks in disturbance history will occur independently in space and through time, reflecting local drivers, and regional trends will be largely static. (b) A regional event, such as severe

drought, would induce a synchronized peak in disturbance activity. (c) A persistent increase in a regional driver (i.e. a climate change scenario) would manifest as a gradual increase in regional rates. Bold lines indicate mean disturbance rates; shaded bands indicate standard error.

Materials and Methods

Study site and data collection

Primary mountain *P. abies* forests remnants were located with assistance from managers of protected areas throughout the Bohemian mountains in the Czech Republic (Čada et al. 2013, 2016), and across the extent of the Carpathian mounts in Slovakia (Janda et al. 2016), Ukraine (Trotsiuk et al. 2014), Northern Romania (Svoboda et al. 2014) and novel data from Southern Romania, spanning 45.5° N to 51.8° N and 10.6° E to 25.5° E (Fig. 2). Within the five landscapes, we selected 37 study stands. In each stand, we placed 12-25 1000 m² (500 m² in rare cases where stem densities were > 500 stems ha⁻¹) circular plots using a stratified random design (Svoboda *et al.*, 2014) for a total of 560 plots. Plots are randomly distributed along gradients of forest age and structure, and the distribution of dendrochronology data reflects the existing distribution of disturbance histories within protected areas. In each plot, the positions, diameters, social status (Lorimer & Frelich, 1989), and species of all living trees with a diameter at breast height (DBH) >10 cm were recorded for a total of 35125 trees. We randomly selected up to 25 non-suppressed trees per plot for coring (at breast height), depending on whether there were 25 eligible trees located in the plot. Dendrochronological analyses and age estimation was conducted for 11595 trees. Detailed information on site selection, sampling, and data can be found in supplement A and the previously referenced studies.

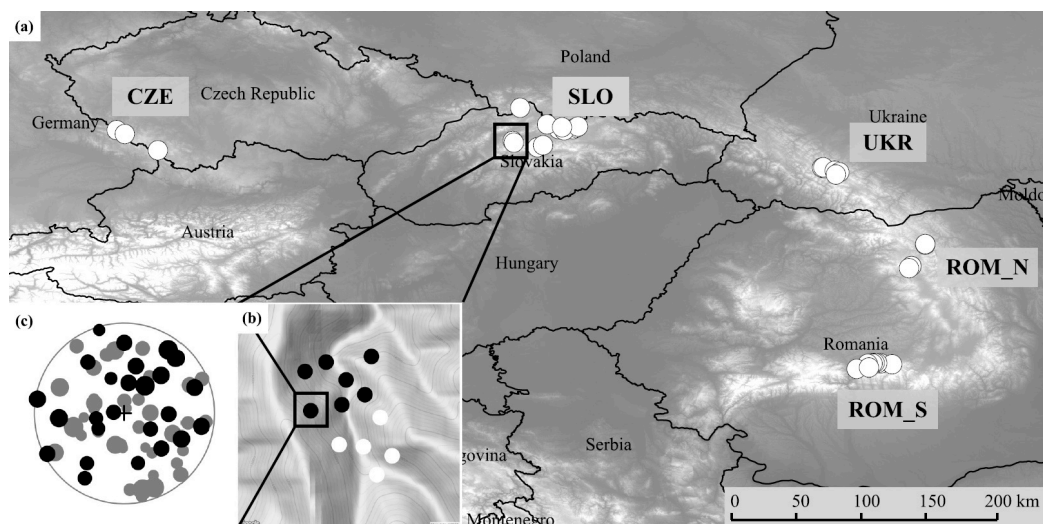


Fig. 2. (a) Geographical location of the 37 study stands with 560 plots within central Europe. (b) example of the plot distribution within a stand. Black dots represent plots that experienced a disturbance in the period 1900-1910. (c) All trees within the plot were mapped (dots) and 25 randomly selected were cored (black dots). Source of digital elevation model: <http://www.reverb.echo.nasa.gov> and Google; country boundaries: <http://www.diva-gis.org>.

Data analysis

Cores were dried, cut by a core microtome (Gärtner & Nievergelt, 2010), cross-dated, and measured following standard dendrochronological methods (Stokes & Smiley, 1968). Annual rings were measured to the nearest 0.1 mm using a stereomicroscope and Lintab™ sliding-stage measuring device in conjunction with TSAP-WIN™ software (www.rinntech.de). Cores were first visually cross-dated using the marker year approach (Yamaguchi 1991), verified with PAST4 software (www.sciem.com), and then confirmed with COFECHA software (Holmes 1983). The pith was reached in 66% of trees, and an additional 32% were within 1 cm from the pith, which allowed for age estimation as per Duncan (1989). Because cores were extracted at breast height, these ages represent recruitment ages (Fraver et al. 2009), not ages since germination.

Disturbance chronologies were reconstructed from dendrochronology data using two types of growth patterns: a) open canopy recruitment and b) growth release after suppression (Lorimer & Frelich 1989). To identify open-canopy-recruited trees, we estimated a threshold based on growth rates of individuals

growing under closed canopies and those growing in in a gradient of gap sizes (Fraver & White, 2005, Svoboda et al. 2012). Average growth rates for 5-year intervals were calculated beginning when the tree reached 4 cm DBH. The growth rates of suppressed saplings were compared with those growing in medium (ca. 500 m²) and large (1000 m² or more) gaps. Growth rate thresholds that best separated these two populations were then estimated using logistic regression (Svoboda et al. 2012). Thus, initial growth rates greater than 1.7 mm yr⁻¹, which corresponds with the change in growth rates between closed canopy and medium sized gaps, were then taken to represent individuals recruited in gaps.

Growth releases were identified by the absolute increase method (Fraver & White 2005). Running means of adjacent 10-year intervals and the differences between mean ring widths for adjacent ten year intervals were compiled. Instances where the difference between 10 year means was greater than 1.25 standard deviations from the mean difference were considered release events. Additionally, increased growth rates had to be sustained for seven years to be deemed a release event (Fraver et al. 2009). Releases were also not considered if the tree was ≥ 25 cm DBH and thus likely to already have reached the canopy (based on a logistic regression of canopy tree social status, data not shown).

Disturbance chronologies were then reconstructed by linking current crown areas of released trees to the year the detected release occurred, assuming that crown area of trees that responded to the original gap formation approximates the size of the original gap (Frelich, 2002; Svoboda *et al.*, 2014). The current tree crown areas were predicted from a statistical relationship between estimated crown areas to DBH ($R^2=0.61$, $p<0.001$). Individual tree canopy areas were then linked to the year of release, and tree-level disturbance events were summed annually and expressed as the proportion of total canopy area, resulting in a plot-level disturbance chronology. Total canopy recruited was calculated for all trees currently present in the stand. Averages over plot-level disturbance severities were produced to estimate stand-level disturbance histories.

To account for the often protracted nature of both tree growth responses and disturbance impact, especially in the case of bark beetles, we fit a kernel density function over the reconstructed disturbance histories to produce point estimates of

events that elapsed over several decades (Appendix B, Trotsiuk *et al.*, 2014). For each stand we identified the year in which the maximum proportion of the canopy area was disturbed, and from it calculated the time since last main disturbance event (TSD). The proportion of the canopy area disturbed during that event was used as maximum disturbance severity (MDS).

Statistical Analysis

Historical disturbance patterns

All analyses were done using R statistical software ver. 3.2.3 (R Development Core Team, 2012). Mean decadal disturbance rates (from 1780 – 1980) were compared among the five landscapes and among decades using a repeated measures ANOVA, conducted using the *car* package (Fox & Weisberg 2011). Stand-level disturbance rates were estimated for each decade and were treated as the unit of replication. The Greenhouse-Geisser correction was applied to the resulting p-values to account for departures from sphericity (Greenhouse & Geisser 1959). Recent canopy disturbance rates (data available from 2005 onward) on the studied landscapes were quantified from a high-resolution global map of forest cover change produced from LANDSAT imagery (Hansen *et al.* 2013). A tree-ring based reconstruction of drought throughout Europe (Cook *et al.* 2015), reported as the Palmer Drought Severity Index (PDSI) was averaged over decades, and used as a predictor of region-level decadal variability in disturbance. For the spatial analysis of disturbance patterns we use Mantel's test to evaluate the overall similarity between disturbance histories and stand geographic location. We applied Mantel's test to the stand-level disturbance chronologies with a 20-year moving window over the entire study period to detect the presence of spatial uniformity or clustering in the occurrence of disturbances.

Contemporary disturbance patterns

We then used our forest inventory data and reconstructed disturbance histories (above) to test spatial variation in contemporary disturbance patterns. Geospatial information on recent forest cover changes, extracted from LANDSAT imagery (Hansen *et al.* 2013), were aligned to plot locations using Arc-GIS

(www.esri.com). For each study plot we calculated the averaged raster values of recent cover change over a 100 m radius from plot centers for the 2005-2015 periods. Averages over plot-level estimates were then used to produce stand-level estimates. Forest inventory data was used to estimate structural attributes of each stand, including mean tree diameters and the coefficient of variation in mean diameter among plots within each stand, which was invoked as a measure of structural complexity. Disturbance history estimates (including TSD and MDS) were used to explain variability in mean tree diameters and the coefficient of variation in plot-level mean diameters. These four variables were then individually tested as potential covariates of 21st century forest cover change and a multiple linear regression was conducted simultaneously using all for variables to predict disturbance severity.

Results

Summary statistics

Mean decadal disturbance rates at the regional level were 3.9% with a standard deviation of 8.4%. At the plot level, 50% of plots experienced at least one decade with >28% canopy removal and 25% of plots were impacted by a decade of >39.7% removal. At the stand level, 50% of plots were impacted by a decade of >13.5% removal, with 25% encountered a decade of >17.6% removal. Four out of the five landscapes were subject to events that removed more than 10% of total canopy area, surpassing 15% in the case of northern Romania. The cumulative distribution of decadal disturbance rates suggests that approximately 75% of current canopy area recruited prior to 1900.

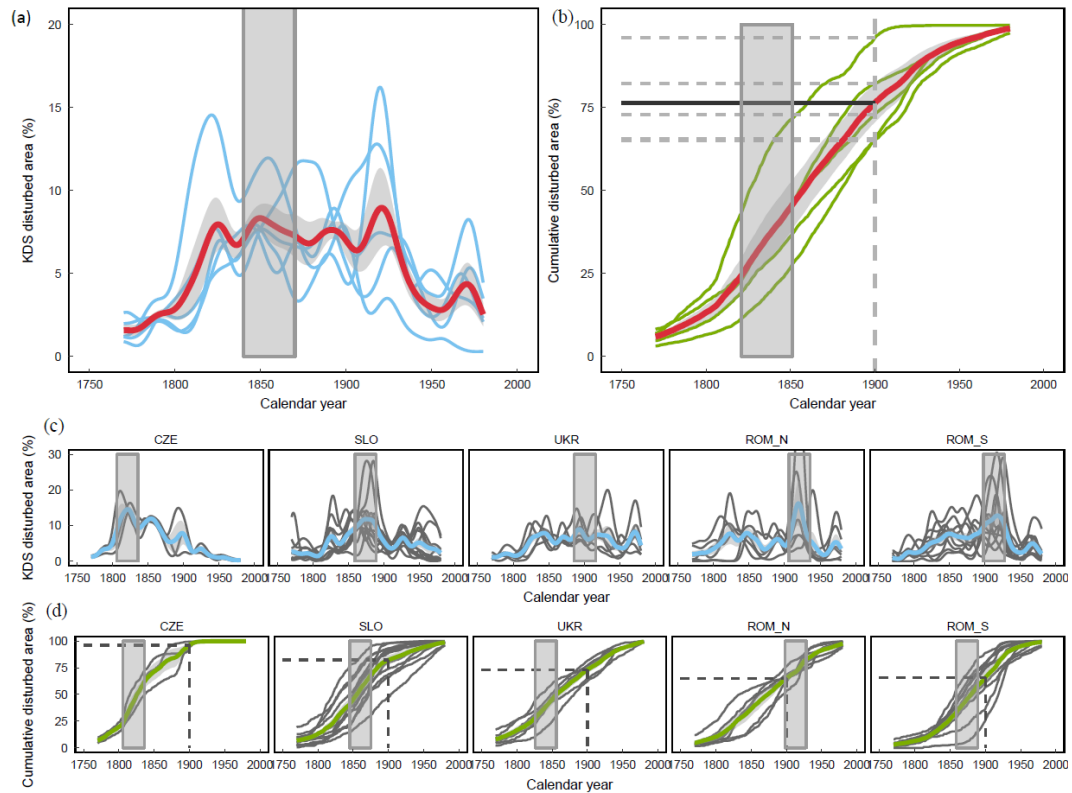


Fig. 3. Kernel density smoothed (KDS) disturbed areas and cumulative disturbance distributions. Mean regional disturbance (a, red line) with shaded standard error represents the KDS mean over each of the five landscapes (blue lines), which are each a mean over their respective stands (grey lines panel row c). These chronologies reflect a temporal range of annual rates integrated into point estimates by a Gaussian kernel. Mean cumulative disturbed area (b, red lines) reflect the mean over each landscape's cumulative sum over annual rates (d, green lines). The year 1900 is highlighted as the point when 75% of current regional canopy area has recruited before (grey dashed - landscape; grey solid - regional). Shaded rectangles indicate the consecutive 30 years when the largest proportion of canopy area was removed or the 30 year interval with the maximum recruitment rate.

Decadal time-series analyses

Mean decadal disturbance rates were compared among landscapes and among decades using a repeated measures ANOVA, treating stands as units of replication (RM-ANOVA). Decadal disturbance rates did not differ among landscapes ($F = 1.021$, $P = 0.411$). Disturbance rates did differ among decades ($F = 16.733$, $P < 0.001$). A significant interaction occurred between landscape and decades ($F = 2.3$

55, $P < 0.001$), indicating the occurrence of landscape level peaks in four out of the five compiled landscapes. Post-hoc analysis indicated that decadal rates between 1820 and 1920 were significantly above the regional historical mean decadal disturbance rate.

Mean decadal disturbance rates were regressed against mean decadal PDSI. A significant effect of PDSI on disturbance was detected ($\text{Dist} = 3.75 - 1.06 * \text{PDSI}$; $R^2 = 0.16$; $P = 0.039$). We computed autocorrelation of disturbance among decades and found that residuals were not significantly autocorrelated.

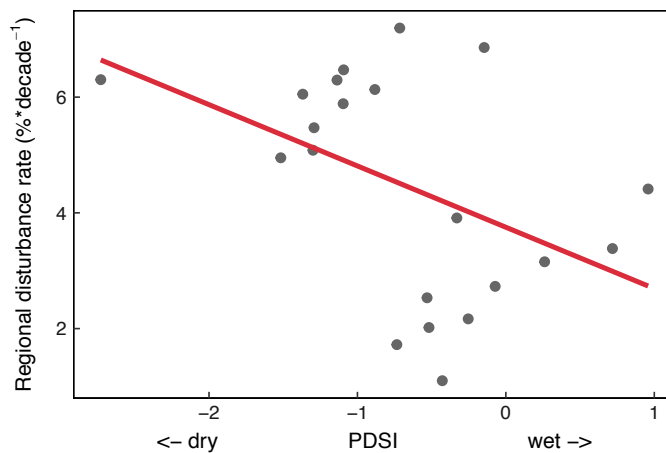


Fig 4. Decadal disturbance rates and regional drought history. Historical profiles (a) for mean regional decadal disturbance rates (black dots) and PDSI (black line) are plotted through time. Note: negative PDSI values reflect more severe drought, so a negative relationship between CA and PDSI implies a positive disturbance-drought correlation.

History, Development and Contemporary Disturbance Patterns

TSD had a significant effect on mean tree diameter (standardized effect size = 0.47, $R^2 = 0.19$, $P = 0.01$), the coefficient of variation among plot-level mean diameters (standardized effect size = -0.53, $R^2 = 0.25$, $P < 0.01$) and LANDSAT-derived contemporary disturbance severities (standardized effect size = 0.50, $R^2 = 0.22$, $P = 0.004$). MDS did not have a significant effect on mean diameter (standardized effect size = -0.31, $P = 0.09$), the coefficient of variation among plot-level mean diameters (standardized effect size = -0.31, $P = 0.09$) or contemporary disturbances (standardized effect size = -0.09, $P = 0.59$). The coefficient of variation in mean diameter (standardized effect size = -0.39, $R^2 =$

0.12, $P = 0.030$) and mean diameter (standardized effect size = 0.36, $R^2 = 0.10$, $P = 0.045$) also had a significant effect on contemporary disturbances.

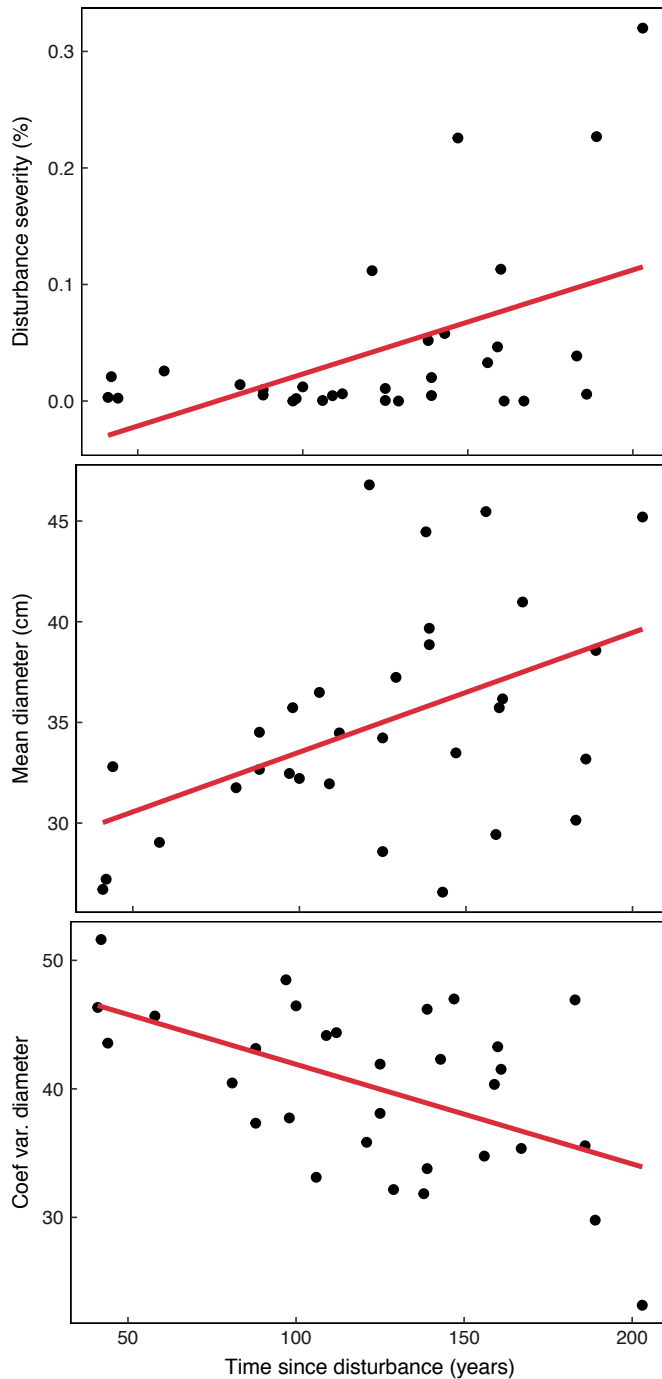


Fig. 5. Developmental patterns in forest disturbance and stand structure. TSD had a significant effect on mean tree diameter, the coefficient of variation among plot-level mean diameters and LANDSAT-derived contemporary disturbance severities (data from Hanson et al. 2013).

Spatial Analysis

A Mantel test was conducted on the smoothed disturbance severities through time. Throughout most of the time period covered, spatial pattern in disturbance activity was random (cf. Fig. 1, left panel). Stand-level disturbance activity was significantly clustered early in the 20th century (1905 and 1924) again at 1960 and 1980. Plot level disturbance rates were significantly clustered at 1900 and again in 1980 (Fig. 4).

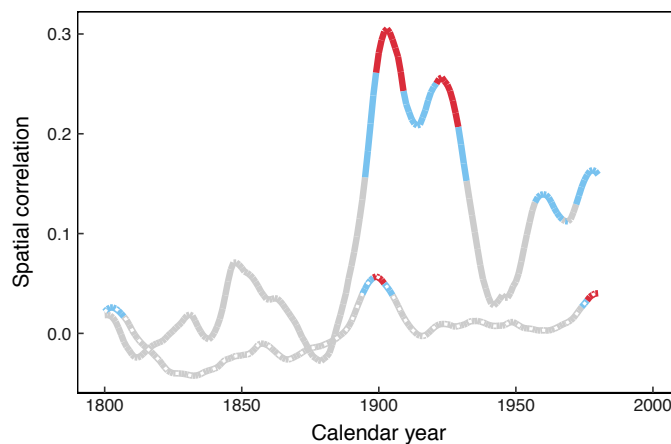


Fig. 6. Mantel test of the disturbance severity for the stand (solid) and plot (dot) level overlain by landscape scale disturbance history (solid red line). Significance of the Mantel test is expressed by red ($p < 0.01$) or blue ($0.01 < p < 0.05$) color.

Discussion

P. abies forests throughout the Bohemian and Carpathian mountains have been shaped by disturbances ranging widely in extent and severity (e.g., Svoboda et al. 2014, Čada et al. 2016, Janda et al. 2016). The general patterns in our reconstructed disturbance history, conducted at an unprecedented scale for European primary forests, provide insight into whether variation is driven by localized or regional factors (Fig 1). Mean regional disturbance rates were approximately stationary between 1800 and 1920 and declined after this interval, which implies the influence of some regionally coordinated factor. Geographic variation among the five landscapes, potentially due to topography or latitudinal gradients in local conditions, was not significant. However, four out of the five

landscapes did exhibit a detectable peak in disturbance rates between 1800 and 1920 and the independence of these major events implies localized triggers. Our results therefore suggest a mixture of regional and local factors contribute to large-scale variation (Fig. 1c). Tests for the effects of climate and stand history on disturbance are elaborated upon to interpret the specific cause of these patterns.

Detecting a time-dependent trend in mean regional disturbance suggests that an overarching regional factor is driving changes in disturbance rates, but observing a decline in disturbance rates throughout the 20th century runs counter to the general European trend of intensification (Seidl et al. 2011). The interval of elevated disturbance in our study weakly corresponds with a period of prolonged dryness, implying that changing moisture conditions might contribute to how the mean regional disturbance rate is distributed through time. We expected drought to play a role in dictating regional disturbance rates because drought-windstorm interactions have been linked to numerous high severity beetle outbreaks in Central European *P. abies* forests in recent decades (Seidl et al 2016, Marini et al. 2017, Mezei et al. 2017). Wind-storms increase deadwood volumes, which amplifies beetle population growth rates, and moisture stress has a negative effect on the production of resins used to defend against beetle infestation in the remaining live trees (Wermelinger et al. 2004, Netherer et al. 2015).

The pattern of heightened mean-regional disturbance severity between 1800 and 1920 is generated by landscape-level disturbance peaks which occurred in four out of the five landscapes during this interval. These peaks align with severe wind and bark beetle outbreaks documented by local authorities (e.g., Svoboda et al. 2014, Cada et al. 2016, Janda et al. 2016) and it is plausible that the relatively lower moisture conditions that occurred within the interval of 1800-1920 contributed to the severity of the landscape-level disturbance peaks we detected. However, the overall correlation between drought and regional disturbance rates is weak, which shifts emphasis towards considering how the consequences of disturbance history on large-scale susceptibility might be determining the sensitivity of climate-disturbance relationships. An additional point of consideration is whether preferential placement of protected areas over forests

exhibiting mature or old growth structure is acting as an inherent bias on the age structure of Europe's scarce remaining fragments of primary forest.

The disturbance peaks we detected in four different landscapes occurred stratified throughout time. Temporal alignment of spatially disjointed events suggests a common initiating factor, so stratification of peaks supports the hypothesis that local factors played a role in the independent occurrence among landscape disturbance peaks. Forest structure, specific characteristics of disturbance agents and climate interact to influence the occurrence, spatial extent and severity of disturbance events (Turner 2010). Wind-damage tends to be compartmentalized to one or several stands (Svoboda et al. 2010, Panayotov et al. 2011), which further restricts the spatial extent of an associated beetle outbreak. Compartmentalization by of beetle outbreaks is especially common at cool temperatures, because beetle outbreaks depend on wind-induced increases in deadwood volumes as a substrate to amplify population growth (e.g., Wichmann & Ravn 2001, Temperli et al. 2013). Multiple climate reconstructions throughout Central European mountain landscapes demonstrate that temperature was persistently cool during the 19th century (e.g., Popa 2009, Brazdil et al 2012). Inherent stochasticity in wind damage and low 19th century temperatures may have contributed to the compartmentalization and the consequent temporal asynchrony of the most severe events we detected. Temperature-induced tree stress can override the dependency of outbreaks on wind-induced pulses of deadwood and can thereby promote synchrony in beetle outbreaks over increasingly large areas (Temperli et al. 2013, Jarvis and Kulakowski 2015). Increased temperature throughout Central and Eastern Europe will likely promote increased synchronization of landscape-level disturbance peaks, and higher temporal variability at the regional level.

TSD was the best predictor of recent disturbance severities. The severity of recent disturbances was highest in stands with the longest TSD, implying that disturbance susceptibility increases throughout stand development, in agreement with bark beetles and wind storms preferentially removing the largest individuals from the population (e.g., Canham et al. 2001, Wermelinger et al. 2004). Following severe disturbances, a certain interval of time is required before

especially large trees are again recruited and affected forests develop into a structure that may again be susceptible to wind (e.g., Kulakowski and Veblen 2002) and outbreaks (e.g., Kulakowski et al. 2003, Hart et al. 2015). Observed disturbance severities were very low in all stands with a TDS of less than 100 years. The landscape-level peaks identified in the disturbance-history reconstructions likely removed a large portion of susceptible individuals from the respective areas, reducing susceptibility and contributing to the reduction in disturbance rates which occurred around the year 1920. Time since last major disturbance and the associated structural development, has been increasing across the region since early in the 20th century, with 75% of current canopy area having recruited since 1900, implying wide-spread increases in disturbance susceptibility.

Structural characteristics of stands were also correlated with recent disturbance severities and are more indicative of the mechanisms relating TSD to disturbance susceptibility and severity. As expected, mean canopy-tree diameter increases with stand age and is positively correlated with disturbance severity, confirming that stands with more large trees are more susceptible to wind and beetle outbreaks. We additionally detected a negative effect of within stand variability among plot-level mean diameters on severity. Structural variability following disturbance can be high in these *Picea* forests (Bace et al. 2015) and patches are expected to converge in structure as the stand develops (Kashian et al. 2005). Spatial variability in stand structure tends to compartmentalize disturbance, limiting disturbance severity at larger scales (Peterson 2002). Bark beetle outbreaks can be contained by spatial heterogeneity because their propagation depends on the presence of large susceptible trees within beetle dispersal ranges (Aukema et al. 2006, Seidl et al. 2016a). However, under optimal climatic conditions, outbreaks can erupt simultaneously from multiple epicenters, thus reducing the importance of landscape structure (Jarvis and Kulakowski 2015). Domino effects may also be reduced when wind storms impact more structurally heterogeneous stands (Everham and Brokaw 1996).

In absence of structural information through time, our analysis of historical trends in spatial variability help to bridge the gap between stand structure as a constraint on recent patterns and long-term trends. Over most of the past

centuries, the distribution of episodic canopy removal was not found to be spatially structured. The exception to this trend was a peak in positive spatial autocorrelation in disturbance corresponding with a peak in mean regional disturbance severity, induced by an especially severe windstorm that occurred in both northern and southern Romania early in the 20th century (Svoboda et al. 2014). The severe event was thus likely contained to the southern portion of the Carpathians.

Absence of any detected spatial structure in historical disturbance occurrences and severities, both within and among stands, implies that stand structure has been historically highly variable. The basis of this variability is likely also historical due to feedbacks between developmental stage and susceptibility that leads patterns in stand structure to self-replicate; as patches continuously recruit into susceptible size-cohorts, they are subsequently disturbed and thus propagate the original pattern (Peterson 2002). Variability in stand structure has potentially kept an upper limit on disturbance severity (e.g., Foster and Boose 1992, Temperli et al. 2013) and by influencing susceptibility and consequently the climate sensitivity of disturbance severity, small-scale variability in stand structure may influence large-scale patterns.

The tendency for patterns in stand structure to self-replicate also applies to homogenizing, i.e., stand-replacing events, which promote the reoccurrence of further high-severity events. For example, in the disturbance history of the Czech Republic, a landscape-level peak in disturbance severity occurred approximately 200 years ago, which aligns with documented storm activity (Čada et al. 2016). The same location has experienced extensive losses of forest cover over the last 25 years (Šumava National Park and also the Bavarian Forest National Park opposite the Czech border); approximately 12 000 ha of a potential of 19 000 ha in the Bohemian mountain spruce forest were disturbed (Čada et al. 2016). Similar development was shown for Slovakia, when peaks in disturbance history detected in the 19th century (Janda et al. 2017) were followed by extensive bark beetle and windstorm disturbance during the last 20 years (Mezei et al. 2017). Given that the most structurally uniform stands in our dataset were subject to the most severe disturbance, it seems likely that the homogenization of stand structure

resulting from the historical event predisposed the landscape to the recent high-severity event. As similar high severity events continue occurring throughout primary and managed *P. abies* forests (Seidl et al. 2016b, Marini et al. 2017, Mezei et al 2017), it is important to recognize that stand history, not just climate change, contributes to contemporary dynamics.

Conclusions

Conventional perspectives in forest landscape ecology suggest that forest dynamics should appear more stationary as spatial scale increases, but the scales at which stationarity is achieved is difficult to verify empirically. Our study constitutes the largest scale disturbance history yet reconstructed in European primary forests and has identified large-scale dynamism in forest disturbance rates. As a consequence, a large portion of Europe's protected primary forests are at an advanced and increasingly susceptible developmental stage and failure to consider disturbance history as a factor contributing to contemporary forest dynamics is likely to confound interpretations of climate-disturbance relationships. Recent high severity events (e.g., Seidl et al. 2016b, Marini et al. 2017, Mezei et al. 2017) should be reinterpreted in light of widespread increases in susceptibility during the early 20th century, not as an exclusive result of climate change *per se*. Neglecting the regional trend of increasing susceptibility will lead to an overstatement of climate effects, which is problematic because climate-change mitigation is often invoked as a justification for post-disturbance intervention strategies that typically result in an undesirable reduction in structural variability (Lindenmeyer et al. 2017). Large-scale disturbances will continue to synchronize recruitment and development across large areas and influence susceptibility to subsequent disturbances, even as climate continues to change.

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5.3. Impact of the disturbance legacies on ecosystem services

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V.T., P.J., M.M. and L.M. performed the dendrochronological analyses;

V.T. performed data and statistical analysis;

V.T. and D.F. wrote the manuscript and all authors commented on it.



The legacy of disturbance on individual tree and stand-level aboveground biomass accumulation and stocks in primary mountain *Picea abies* forests



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ABSTRACT

Disturbances, both natural and human induced, influence forest dynamics, ecosystem functioning, and ecosystem services. Here, we aim to evaluate the consequences of natural disturbances on the magnitude and dynamics of tree- and stand-level biomass accumulation from decadal to centennial scales. We use tree-ring data from 2301 trees and biometric data from 4909 trees sampled in 96 plots (each 1000 m²) to quantify the influence of mixed severity disturbance regimes on annual aboveground biomass increment (AGBI) and total aboveground biomass accumulation (AGB) across a mountainous monotypic Norway spruce (*Picea abies* (L.) Karst.) primary forest. We hypothesise that the multiple internal and external factors constraining tree growth will cause differences in tree and stand-level biomass trajectories in these natural forests.

Although we found that tree-level AGB growth increases with tree size, we also found that tree age and disturbance legacies plays a crucial role for AGB in the investigated Norway spruce forests. Importantly, while younger trees of the same diameter class have an average current AGBI rate that is ~225% higher than older trees (300–400 years), we find trees that have been suppressed for up to 120 years can respond vigorously when competition is reduced. On average, post disturbance AGBI was ~400% greater than pre-disturbance AGBI. Growth of suppressed trees, independent of their age, followed similar trajectories after canopy accession. While aboveground biomass generally increased through time, the time since disturbance and disturbance severity are important co-predictors for stand-level AGBI and AGB. These forests regained most of the above ground living biomass over short interval (~50 years) after low intensity disturbances. The highest stand-level living AGB was observed on plots that experienced >40% canopy removal 160–190 years ago, whereas the highest AGBI occurred in plots disturbed recently within the past 40–50 years.

Our results emphasize the importance of including both individual tree age and disturbance legacies to accurately characterize biomass dynamics and trajectories in forest ecosystems. Importantly, the period of time that a tree is in the canopy, and not tree age, modulates the trajectory of tree level AGBI. Growth rates begin to decline after ~30 years (tree-rings width) and ~100 years (AGBI) in the canopy. We demonstrate that even late-seral forests can rapidly regain biomass lost to low intensity disturbance.

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1. Introduction

Primary forest ecosystems constitute approximately 36% of the Earth's total forested area (Mackey et al., 2015) and are responsible for at least 10% of the global net ecosystem productivity (Luyssaert et al., 2008). Recent efforts to quantify dynamics and drivers of productivity in forested ecosystems have included comprehensive overviews of the global biomass variability among different biomes

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and climatic regions (Burrascano et al., 2013; Keith et al., 2009; Luyssaert et al., 2008), as well as the establishment of comprehensive growth models for managed forests (e.g., Weiskittel et al., 2011). Yet, much work is still needed to understand and quantify biomass dynamics and the influence of disturbances in the more remote and less well investigated primary forests (Keeton et al., 2011; Taylor et al., 2014). Most research on the impacts of disturbance on the carbon balance in primary forests has focused on stand replacing disturbances (Magnani et al., 2007; Pregitzer and Euskirchen, 2004) where forest responses have been shown to be highly analogous to those in the better investigated managed forest ecosystems (Bradford et al., 2008; Chen and Luo, 2015). This leaves many unanswered questions about the long-term biomass dynamics in primary forests characterized by complex developmental pathways and/or mixed-severity disturbance regimes (Stueve et al., 2011; Woods, 2004).

The dynamics of aboveground biomass (AGB) accumulation in forests are an aggregate of the AGB of individual trees, including the effect of competition and resource availability, and mortality (Berger et al., 2004; Coomes et al., 2014; Jucker et al., 2014; Odum, 1969). Thus, it is critical to understand the accumulation rate and carbon storage potential of trees considering their age, diameter, and competition status within a stand. In particular, interactions among tree size, tree age, tree life history, and tree lifespan require better quantification for diverse species while considering different disturbance histories (Bigler and Veblen, 2009; Johnson and Abrams, 2009). While the growth of trees as they age has classically been thought to follow an asymptotic sigmoidal curve (e.g., Weiner and Thomas, 2001), recent studies suggest that large trees continually increase their rate of carbon accumulation with increasing size (Stephenson et al., 2014). Investigations of large and/or old trees thus require particularly careful examination, firstly, owing to this interesting recent departure from conventional wisdom, and secondly, because of the disproportionately strong impact large trees have on the carbon dynamics of whole stands (Fauset et al., 2015; Slik et al., 2013).

The broad range of disturbance severities, spatial extent, timing, and return intervals makes it difficult to study and generalize disturbance impacts on forest ecosystems. Moreover, due to the stochastic nature and infrequent occurrences of natural disturbances, many traditional methods (e.g., small permanent plots, short-term remote sensing records) have limited potential to investigate long-time scale processes related to disturbance dynamics. Dendroecological methods have proven to be a useful tool in the long-term and retrospective investigations including both disturbance dynamics (Frelich, 2002; Pederson et al., 2014) and forest biomass dynamics (Babst et al., 2014a; Foster et al., 2014; Halpin and Lorimer, 2016).

In this study, we evaluate the influence of natural disturbances on the magnitude and dynamics of biomass accumulation at decadal to centennial time-scales. The high spatiotemporal variability and wide range of disturbance severities represented in our extensive sampling allow us to draw conclusions on interactions between disturbance characteristics and forest productivity. In particular, we assess: (i) individual tree AGB increment (AGBI) trends, and (ii) living AGB and AGBI in forest stands in relation to past disturbance. Our study aims to advance understanding of biomass accumulation dynamics from the individual tree to stand-level in primary forest ecosystems. We hypothesize that the tree sizes, tree ages, and disturbance legacies will cause differences in tree and stand-level biomass trajectories. We test this hypothesis in primary forests dominated by Norway spruce in the Carpathians Mountains. Our work is broadly applicable to montane coniferous forest systems in similar temperate and boreal regions.

2. Materials and methods

2.1. Study site and data collection

We conducted our study in upper elevation, monotypic primary forests of *Picea abies* (L.) Karst. in the Ukrainian Carpathian mountains. Using remote sensing data, a review of scientific and popular literature, and visual inspections, we selected six stands that ranged from ~15 to 30 ha. Stands were situated between 1200 and 1500 m a.s.l., and had no evidence of human disturbance. These stands are protected from selective logging or grazing by poor access and the steep and rocky slopes (for details see Trotsiuk et al., 2014). The mean monthly temperature of the warmest month (July) is +16.4 °C, and of the coldest (January) is –7.6 °C. Precipitation in the region varies from 850 to 1000 mm/year, peaking in June and July. Leptosols and albic podzols predominate on sandstone bedrock (Chernyavskyy and Shpylychak, 2011; Valtera et al., 2013).

In each stand, we placed 15–20, 1000 m² (or 500 m² if the density was >800 trees/ha, $N = 8$) circular plots using a stratified random design (Svoboda et al., 2014) for a total of 96 plots (Fig. 1). We recorded the positions and diameters of all living trees with a DBH >10 cm in each plot for a total of 4909 trees. A single increment core from each of 23–25 randomly selected canopy trees in each stand was collected ($N = 2396$). We ensured that the retained increment cores hit or were close to the pith: 49% of all cores hit the pith, 41% were within 0.5 cm of pith, and 10% within 1.5 cm of pith. All tree cores were dried and the surfaces were prepared with a core microtome (Gärtner and Nievergelt, 2010). Ring widths were measured and cross-dated following standard techniques (Stokes and Smiley, 1968) using TSAP-Win™ software (Rinntech, Heidelberg, Germany) and verified with COFECHA software (Holmes, 1983).

2.2. Tree ring analysis

We classified canopy accession events into two primary groups: (i) rapid early growth rate and (ii) abrupt, sustained increase in tree growth (Appendix A; Frelich and Lorimer, 1991; Svoboda et al., 2014). Tree recruitment was characterized as open canopy if average annual radial growth for the first 15 years was >1.3 mm or under a closed canopy for growth rates below that threshold (Fraver and White, 2005; Trotsiuk et al., 2014). We used the boundary line approach to detect release events from tree-ring width series of individual trees (Black and Abrams, 2004, 2003). Release was defined as any growth change in excess of 20% of the boundary line (Black and Abrams, 2003) that was sustained for at least 7 years (Fraver et al., 2009). Tree responses were converted to the proportion of canopy area disturbed in each plot. This served to scale the evidence of disturbance according to each tree's current crown area (Lorimer and Frelich, 1989). Current crown areas were predicted from DBH based on a linear regression fitted to the 485 measured trees (5 per plot). A plot level disturbance chronology was compiled from the annually-resolved percent canopy disturbed area. A kernel density estimation function was fit to the plot level distribution of canopy accession events, with the maximum peak of each density function used to classify the main disturbance event. As a measure of severity, we calculated the percentage of canopy removed during the main disturbance event for each plot (Lorimer and Frelich, 1989). The study sites are characterized by variability in disturbance histories in terms of timing and magnitude (Figs. A1 and A2), with these forests characterized with a prevailing mixed severity disturbance regime. We divided all plots into three groups based on their maximum disturbance severity: low (20–40%, $N = 36$), moderate (40–60%, $N = 34$),

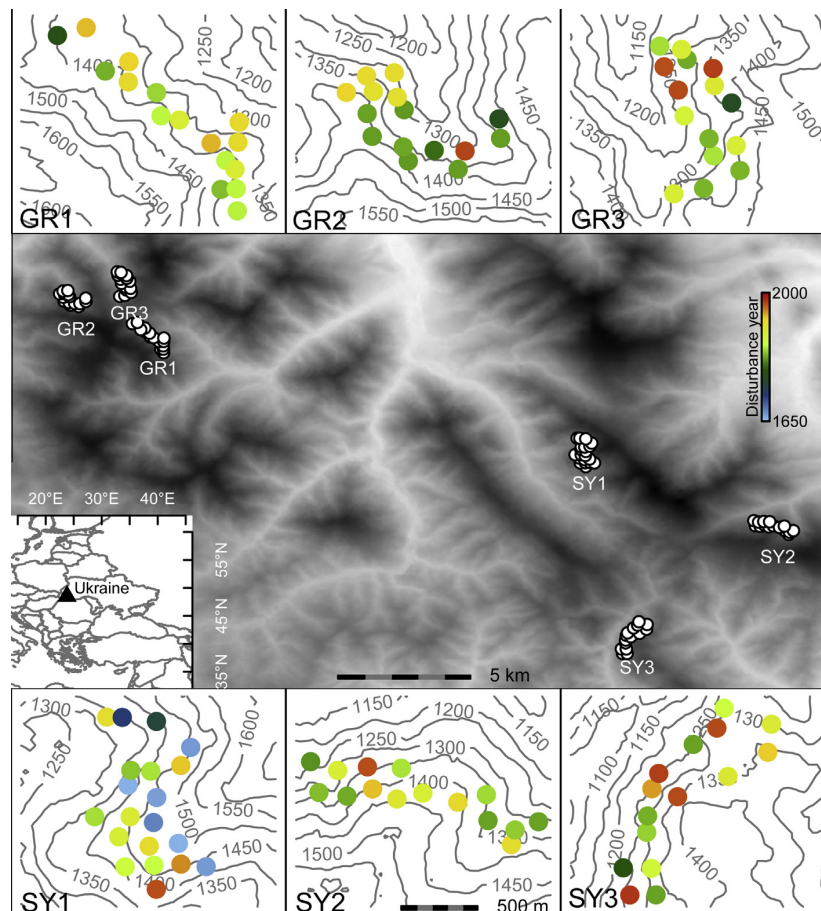


Fig. 1. Geographical location and period of occurrence of maximum disturbance severity (colour gradient) of the 96 study plots (0.1 ha each). The reconstructed disturbance history is based on the growth pattern of 23–25 randomly selected trees per plot. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.) Source of digital elevation model: <http://www.reverb.echo.nasa.gov>; country boundaries: <http://www.diva-gis.org>. Updated from Trotsiuk et al. (2014).

and high (60–100%, $N = 27$). More information on sampling and site conditions can be found in Trotsiuk et al. (2014).

2.3. Aboveground biomass and its increment calculation

To estimate biomass based on a trees' DBH, we considered allometric equations for spruce based upon output parameters (AGB in kg), the species and diameter range used to develop the equation, as well as the geographical location of the allometric study site. The equation developed for the Czech Republic spruce forest (Zianis et al., 2005) was found to be the closest match to our study region. Individual tree diameters were reconstructed back in time based upon the method of Bakker (2005). Using these reconstructed diameters, we then computed the historical AGB and AGBI for each tree and year (Babst et al., 2014b). Stand-level AGB and AGBI were calculated as a sum of AGB and AGBI of all living trees on each plot. We define current AGBI as the average growth rate of the last 10 years. AGBI of non-cored trees was derived from the allometric equation fitted to the trees with available AGBI that had a similar DBH and average plot level increment ($r^2 = 0.51$, $RMSE = 0.039$ Mg, $P < 0.001$). This calculation implies some uncertainties due to unknown ages of trees. Cored trees composed on average 71% of the plot level AGB, and the percentage was

higher on plots with low severity events, while on recently disturbed plots we lack higher number of small even-aged trees.

2.4. Analysis

We fitted a generalized additive mixed model (GAMM) with a linear combination of smooth functions of DBH and tree age and their interaction as explanatory variables on AGBI, considering random effects (Tree). The pertinence of the random effect and interaction effect was determined by comparing the different models using the Akaike Information Criterion (AIC) value (Burnham and Anderson, 2002). We calculated significance of the explanatory variables and the overall variance explained by the model. Note, that the size (or age) of a tree in a given year is not independent from the trees previous state. While this still allows for accurate estimates in mean predictions, an underestimation of uncertainty may occur if conventional error analyses are applied. Model fitting and calculations were done using 'mgvc' package (Wood, 2011) in the R software (R Development Core Team, 2012). The specific model applied was:

$$\log(\mu_{ij}) = \beta_0 + b_i + s_{DBH}(DBH_{ij}) + s_{Age}(Age_{ij}) + s_{DBH \times Age}(DBH_{ij}, Age_{ij})$$

$$b_i \sim N(0, \sigma^2)$$

where

- μ_{ij} is the AGBI of tree i at year j
- b_i are (independent) random effects of individual tree (i)
- S_{DBH} , S_{Age} , $S_{DBH \cdot Age}$ are smooth functions to be estimated (penalized splines are used here)
- S_{DBH} reflects the (smooth) marginal effect of tree DBH
- S_{Age} reflects the (smooth) marginal effect of tree Age
- $S_{DBH \cdot Age}$ reflects the (smooth) interaction of tree DBH and Age (obtained as a tensor product spline).

To describe the trends in stand level AGB and AGBI, we fitted logarithmic regressions with time since main disturbance as the explanatory variable for three levels of disturbance severity (20–40%, 40–60%, and 60–100%). Time since main disturbance and disturbance severity class significantly correlate with stand level AGB and AGBI ($p < 0.05$). We assessed the impact of different disturbance severity classes on stand level AGB and AGBI trajectories.

3. Results

3.1. Tree level

Age, DBH, and their interaction had significant effects on the tree level aboveground biomass increment (AGBI) (Table 1). AGBI

Table 1
Results of GAMM for influence of DBH and age and their interaction on tree AGBI.

Response variable	Explanatory variable	Estimated degree of freedom	Chi. sq	p-value
AGBI	($r^2 = 0.83$)	Random effect of tree	2305.4	36
<0.0001	Smooth main effect of DBH	4.0	1646	<0.0001
	Smooth main effect of age	4.0	473	<0.0001
	Interaction between main effects	16.0	847	<0.0001

varied significantly among trees from different size and age classes (Fig. 2). For a given size, the absolute AGBI is generally largest for younger spruce trees (Fig. 2a and b). Similarly, for a given age, AGBI is higher for larger trees (Fig. 2a and c). Only 40% of the trees showed a positive increase in growth after their diameter exceeded 30 cm. Long-lived individuals had lower biomass growth rates over their entire lifespan. Even though these long-lived trees were large, their annual biomass accumulation is rather low. On average, trees younger than 100 years and with a 30–40 cm DBH, have an AGBI that is ~225% higher than 300–399 year old trees with the same DBH.

Legacies of disturbance strongly influenced the growth patterns and AGBI of the trees (Fig. 3), yet growth followed similar trajectories after the main canopy accession event (Fig. 3b and d). To quantify the legacy of disturbances, we divided all trees based on their duration of suppression into 10-year bins (Fig. 3a and b); more than half (~60%) of the trees originated in open canopy conditions. For those that did not originate in open canopy, long periods of suppression were regularly observed. Seventeen percent of our sampled trees experienced suppression for 50 or more years, with suppression exceeding 100 years in 6% of all cases. Notably, the increase in radial growth after suppression was similarly high, but independent of the duration of suppression period or tree age (Fig. 3c). The average in radial growth after suppression is ~1 mm, but with some differences at the individual site (explored below). Even after a prolonged period of suppression (>50 years), spruce trees can abruptly increase radial growth. The AGBI of individual spruce trees peaked approximately 100 years after canopy accession and experienced relatively stable AGBI thereafter (Fig. 3b), indicating a rather constant tree growth behaviour after canopy accession.

3.2. Stand-level

Both the severity and timing of disturbance strongly influenced the stand AGB and AGBI (Fig. 4, $p < 0.01$). The pools of living stand level AGB increased continuously for at least 200 years following

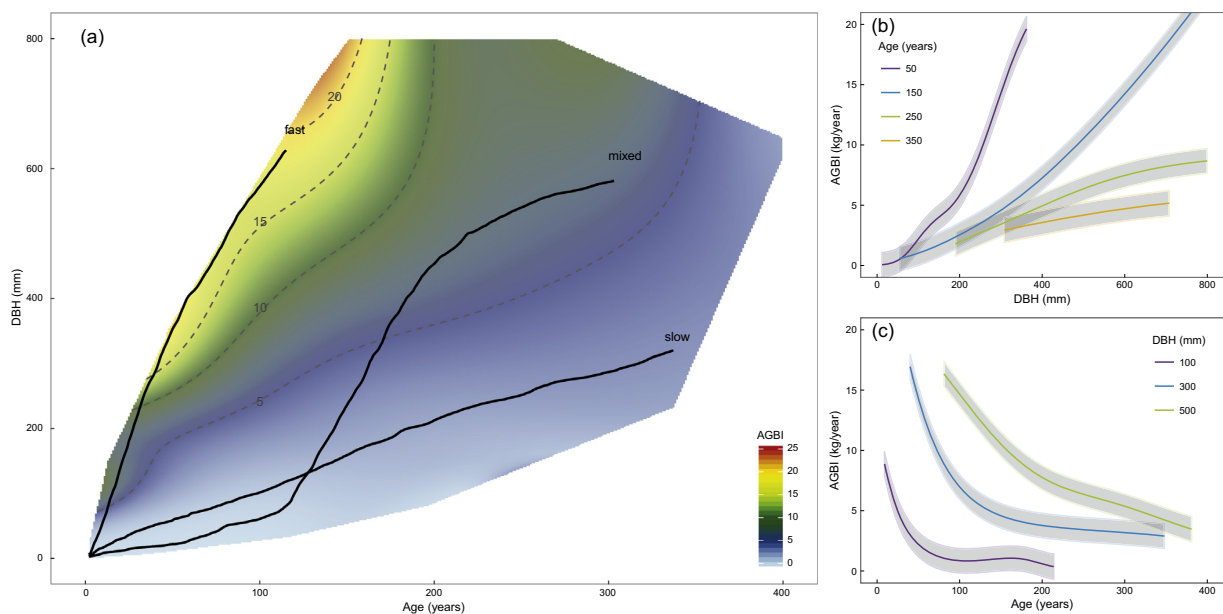


Fig. 2. Predicted aboveground biomass increment (AGBI) from generalized additive mixed model based on the ca. 342,000 yearly resolved tree DBH, Age and their interaction (a). Black lines show examples of growth trajectories and change in AGBI during lifespan for selected trees. AGBI is significantly higher for younger trees within same DBH class (b), and larger trees within same Age class (c).

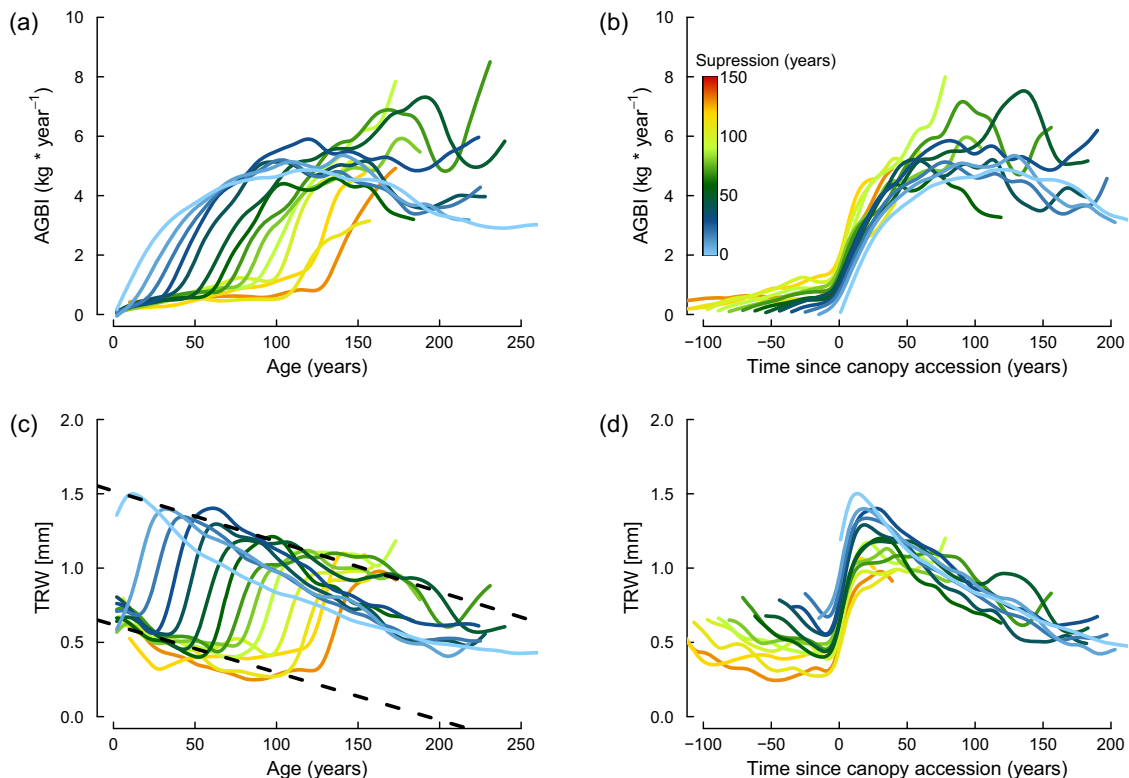


Fig. 3. Tree-level aboveground biomass increment (AGBI) and ring-width increment (TRW) in relation to age (a, c) and time since main canopy accession event (b, d). All trees were grouped based on the duration of suppression period into 10 years step classes (colour gradient) and the average chronology was truncated when the sample depth drops below 15 individuals. Trees show similar growth trends in both AGBI and tree-ring increment after main canopy accession event (b, d). Dashed lines (c) were fitted to the TRW values shortly before and after the canopy accession event from each curve, and show a steady potential for growth increase over tree age. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

disturbance (Fig. 4a). The rate of AGB increase slowed in time and appeared to become roughly constant about 200–350 year after disturbance. However, we note abilities to accurately assess the trajectory more than 200 years after disturbance are limited in this dataset due to decreases in sample size. Greater percentages of canopy removal (60–100%) were associated with steeper increases in AGB compared to low severity disturbance (20–40%, $p < 0.05$). Concomitantly, the rate of AGBI decreased as AGB increased (Fig. 4b). Minor changes in AGBI were observed for the plots that experienced low severity disturbance (20–40% canopy removed) and were significantly lower ($p < 0.01$) compared to moderate and high severity disturbances (40–60% and 60–100% canopy removed).

Across the entire sites, stand-level living AGB ranged from 141 to 399 Mg ha⁻¹ (average 267 Mg ha⁻¹), and the current AGBI between 1.5 and 6.1 Mg ha⁻¹ year⁻¹ (average 3.1 Mg ha⁻¹ year⁻¹). The highest AGB (top 10%) was observed on plots where more than 40% of the canopy was estimated to have been removed 120–190 years ago (median = 176 years). In comparison to more lightly disturbed plots (<40% canopy removal), plots with a higher disturbance severities (>40% of the canopy removed) show 16% greater living AGB 150 years after disturbance and up to 30% higher AGBI 50 years after the disturbance. Much of the AGB (90% of the maximum from fitted regression Fig. 4) in plots influenced by low percentage canopy removal can be regained within a short period (50 years). In more highly disturbed plots, and despite their greater AGBI, this level of recovery takes approximately 110–125 years (Fig. 4).

4. Discussion

A deeper knowledge of disturbance legacy effects is needed to improve our understanding about the patterns and processes driving biomass development and the fate of primary forest ecosystems. Here we show the importance of simultaneously considering tree-level and stand-level dynamics to draw an improved picture of development and biomass accumulation over time in the investigated *Picea abies* (L.) Karst. forest ecosystems. We found that prolonged suppression did not reduce trees' potential to attain high growth rates after disturbance. Such trees, independently of their age, can thus follow high trajectories of AGBI after a reduction in competition/canopy accession. Young, large spruce trees had greater rates than older trees of comparable size. At the stand level, sites that experienced minor canopy removal recovered 90% pre-disturbance AGB approximately twice as fast as those stands that experienced major canopy removal. While aboveground biomass generally increased through time, we found that both the time since disturbance and disturbance severity are important co-predictors for stand-level biomass accumulation rate and biomass pool size.

4.1. Tree growth trends and biomass increment

Individual tree AGBI data are required to better understand and model stand and ecosystem level AGBI. Yet key uncertainties remain on the relevant tree-level biomass growth dynamics. Stephenson et al. (2014) emphasized the potential of large trees

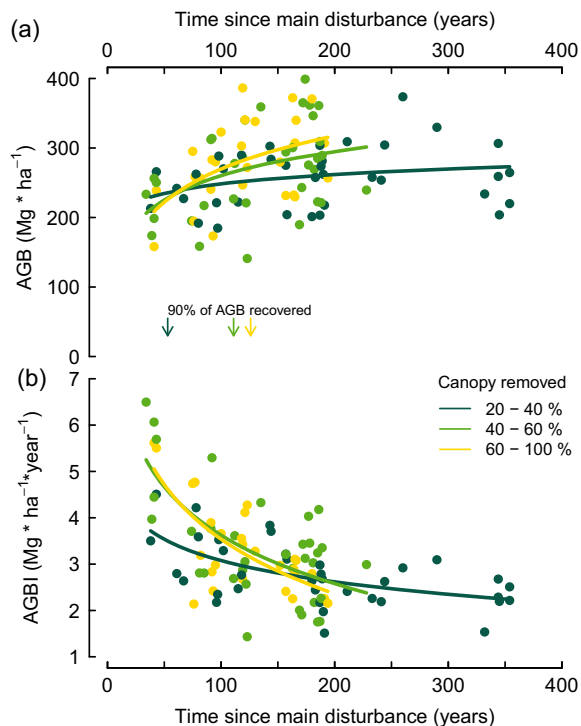


Fig. 4. Living aboveground biomass (AGB) and current aboveground biomass increment (AGBI) expressed by the time since main disturbance and severity of the main disturbance event (% of canopy removed, as colour of points/lines). Majority of the AGB (90% from the level at 200 years, indicated by arrows) can be recovered within ca. 50 or 120–130 years after respectively moderate or heavy/extreme disturbances. Solid lines show logarithmic models fit [$y = a * \ln(x) - b$] for the different disturbance severities.

to continuously increase carbon accumulation rates with increasing size. They detailed, for example, how a single large tree can accumulate as much biomass in one year as the total biomass of one mid-sized tree in a stand. This notion, however, contradicts (i) the hypothesis that the growth of organisms will always be constrained by some factor and follow a sigmoidal curve (Weiner and Thomas, 2001), and (ii) various widely applied physiological growth models (Berger et al., 2004; Odum, 1969).

In our investigation of montane monotypic primary Norway spruce forests, we could partially support and partially refine the conclusions from Stephenson et al. (2014). While we found that mid-sized trees tended to have larger AGBI, we also found that the age of the tree, a potential constraint of tree growth not factored in Stephenson et al. (2014), strongly influences AGBI for a given tree size (Fig. 2). Considering growth trends of individual trees separately, fewer than half of the trees showed a positive slope in AGBI after their DBH exceeded 30 cm. Furthermore, for those trees displaying a positive slope in AGBI, the slope was only 23% of that observed for small individuals (DBH < 20 cm). So, while we found growth increases in big spruce trees in these monotypic stands, the rate of growth increase was far lower than that observed for smaller trees.

Various lines of evidence provide insights and some explanations for these apparent contradictions. Some elements to consider include: individual tree growth peculiarities and crown architecture (Pretzsch and Schütze, 2005); biases in inferring dynamical processes from inventory snapshots (Bowman et al., 2013; Nehrbaas-Ahles et al., 2014); and the potential influence of climate

change (Andreu-Hayles et al., 2011; Cole et al., 2009). The rate of tree biomass accumulation is partially dependent on the photosynthetic rate as a function of the crown structure and light use efficiency (Binkley et al., 2010). Norway spruce have a limited ability to laterally expand their crowns and occupy canopy space after entry into the upper canopy layer (Pretzsch and Schütze, 2005). Therefore, spruce trees face constraints to increase their photosynthetic capacity and theoretically have a “predefined” sigmoidal growth after canopy accession (Fig. 3b and d). In comparison to a more diverse stand, competition in a monotypic stands would limit niche space as individuals will mostly compete for a narrow range of resources. In contrast, other tree species have higher ability to expand their crown as they gain better canopy position (Pretzsch and Schütze, 2005; Sillett et al., 2015). The extent to which such tendencies are related to phylogenetic controls beyond the level of individual species (e.g., early versus late successional or angiosperm versus gymnosperm) requires investigation.

Second, while physiological models are mainly generated for the growth of individual trees, biased assessments will be obtained if population snapshots are assumed to represent the growth dynamics of individuals (Bowman et al., 2013). This is a notable pitfall as it is convenient to assume that, for example, the height-diameter relationships obtained in a single site visit to a forest stand represents the growth trajectories of the individual trees within the stand (Sumida et al., 2013). Shortly, substituting time by space (Wolkovich et al., 2014). This pitfall may especially be true for trees with the ability to persist in the understory from decades to centuries before reaching a canopy position. Tracing the growth dynamics of individual trees would in reality either require a multi-decade, if not multi-centennial, monitoring campaign or laborious sectioning of a tree (Pensa et al., 2005). The few such (long-term) measurements that are available indeed show the individual growth trajectories are not well represented by population structure (Bowman et al., 2013).

Third, the potential influence of on-going environmental change on tree growth (Andreu-Hayles et al., 2011; Cole et al., 2009; Marshall, 1927) and site conditions change (Boyer, 2001; Monserud et al., 2008) should also be considered. The environmental variation experienced during the past decades includes some monotonic and/or low-frequency variations that can impact tree growth (e.g., CO₂ concentration, increasing temperatures, anthropogenic aerosols, sulphur emissions), but may be difficult to differentiate from contemporaneous trends caused by tree age, size, or changing competitive status and canopy position. Such diverse and contemporaneous growth influencing factors might have influenced patterns observed in existing data and contributed to different conclusions in literature.

Importantly, we found in this study, tree age, which is not always collected in long-term monitoring campaigns, plays an important role in individual tree AGBI estimation in montane Norway spruce. Our work reveals that the amount of time a tree spent in the canopy is important factor in understanding tree level AGBI rates. Omitting tree age in the AGBI modelling of montane Norway spruce in monotypic stands can lead to high uncertainties on the tree-level and thus also on any subsequent up-scaling. A significant part of the forest carbon sequestration models are based on the country level forest inventories data, which often do not include tree age information (Tomppo et al., 2009). More routine and extensive collection of tree cores in forest inventories might greatly improve the models parameterization and AGBI estimation. This is likely especially important in forests with greater species diversity and structural complexity.

4.2. Stand-level living aboveground biomass dynamics

Here we used a primary spruce forest to describe natural pathways of the AGB and AGBI dynamics based not only on time since disturbance, but also disturbance severity. We demonstrated that both the timing and severity of disturbance events influence pathways of AGB and AGBI in the primary mountain spruce forest (Fig. 4). Higher disturbance event severity (>40% canopy removal) leads to greater AGBI for approximately 100 years after disturbances and a longer recovery time for living AGB. Such trends of the biomass dynamics are similar to those created by forest management systems oriented towards even-aged stands. Recovery time after severe disturbance events (defined here as regaining 90% of the maximum from fitted regression) fits well with the rotation period for even-aged managed forests in the study region (90–120 years). In addition, our study indicates, that 40–50 years is sufficient for the forest to recover 90% AGB from a simultaneous loss of 20–40% of the canopy, as in group selection forest management (Misson et al., 2003; Nilsen and Strand, 2008).

It is important to separate semi even-aged stands that experienced severe disturbances from those with complex stand and age structure driven by mixed severity disturbances when investigating forest development and biomass dynamics. In this study we could evaluate tree and stand level AGB and AGBI from annual to multi-centennial time-scales. Although we observed a trend of increasing AGB and decreasing AGBI after disturbances, we could not confirm (or refute) that late-seral (old-growth) forest have any trend in AGB at the late developmental stages. Such long-term trends, if present, were below the detection limits in our study. We stress that further discussion on increasing or decreasing of AGB in the old growth forest based upon chronosequences of highly spatially distributed sample units with different stand development history should take into account the past disturbance history as an important element in explaining AGB and AGBI trends.

5. Conclusion

Legacies of disturbance history influence both tree and stand-level biomass dynamics by changing local environmental conditions and levels of inter-tree competition. Trees growing in monotypic spruce forests followed a similar sigmoidal trajectory after canopy accession, regardless of age or prior duration of suppression. This finding supports physiological theories and suggests that trees in these types of forest structures might be competing for similar limiting factors. Tree-level AGBI differ between individuals within the same size class demonstrating that both DBH and age data are required for precise tree-level AGBI estimations. While stand characteristics (e.g., time since disturbance, existing biomass, etc.) can explain much of the variability in tree and stand-level AGBI (Coomes et al., 2014; Michaletz et al., 2014), inclusion of the direct and indirect interactions with climatic and physiological factors, together with disturbance regimes, will be required for predictive models of biomass dynamics. Application of the sampling and analytical methods employed herein for other species and in other primary forest ecosystems and biomes will be crucial to refine our knowledge between mixed severity disturbances and long-term terrestrial carbon dynamics.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.04.038>.

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L.Z. and M.S. conceived ideas and designed the study;

All co-authors performed the sampling;

V.T. and M.M. performed the dendrochronological analyses;

L.Z., V.T. and R.B performed data and statistical analysis;

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Old trees as a key source of epiphytic lichen persistence and spatial distribution in mountain Norway spruce forests

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Abstract Habitat loss and fragmentation can negatively impact the persistence of dispersal-limited lichen species with narrow niches. Rapid change in microclimate due to canopy dieback exposes species to additional stressors that may limit their capacity to survive and colonize. We studied the importance of old trees as micro-refuges and microclimate stability in maintaining lichen survival and diversity. The study was situated in mountain Norway spruce (*Picea abies*) forests of the Gorgany Mountains of the Ukrainian Carpathian mountain belt. Lichens were collected on 13 circular study plots (1000 m²). Dendrochronological methods were used to reconstruct age structure and maximum disturbance event history. A linear mixed effects model and general additive models were used to explain patterns and variability of lichens based on stand age and disturbance history for each plot. Tree age was the strongest variable influencing lichen diversity and composition. Recent (<80 years ago) severely disturbed plots were colonized only by the most common species, however, old trees (>200 years old) that survived the disturbances served as microrefuges for the habitat-specialized and/or dispersal limited species, thus epiphytic lichen biodiversity was markedly higher on those plots in comparison to plots without any old trees. Most species were able to survive microclimatic change after disturbances, or recolonize disturbed patches from surrounding old-growth forests. We concluded that the survival of old trees after disturbances could maintain and/or recover large portions of epiphytic lichen biodiversity even in altered microclimates.

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Introduction

The role of natural disturbances and predictions of increased frequency and severity of disturbances with changing environmental conditions is an increasingly important subject of research (Schelhaas et al. 2003). The area of old-growth temperate forests has been decreasing over the past century due to intensive management pressure (e.g., Knorn et al. 2013). Old-growth forest remnants often provide services, habitat, and biodiversity uncommon in many landscapes, but they too are subject to disturbances of varying severity; thus, uncertainties abound regarding the long-term persistence of many species after disturbances (Johansson 2008), particularly large-scale windthrow events and bark-beetle outbreaks.

If habitat heterogeneity is increased by natural disturbances, the effect on species diversity would be positive (Beudert et al. 2014), but it may also result in the loss of habitat and consequent fragmentation for certain species (Johansson et al. 2006). According to the metapopulation theory (Hanski 1999), a network of habitat fragments must satisfy certain necessary conditions in terms of number, size, and spatial configuration of fragments to allow for long-term persistence of the focal species (Hanski and Ovaskainen 2003). The capacity of individual species to persist and recolonize adjacent areas after disturbances can help us to understand the processes and value of old-growth forests to preserve rare species in altered landscapes.

Epiphytes are long-lived sessile organisms that persist on trees until tree fall; other threats to local extinction are relatively minor, and it is unlikely to go extinct locally until the tree dies (Johansson et al. 2012; Snäll et al. 2003). Species with a narrow ecological niche and large dispersal propagules have lower colonization rates than species with a wide niche and small, easily dispersed propagules (Johansson et al. 2012; Löbel et al. 2006). Colonization rates are substantially higher when habitat connectivity is high (Fedrowitz et al. 2012; Johansson et al. 2012; Löbel et al. 2006), in accordance with the metapopulation theory (Hanski 1999). Isolation of subpopulations in fragmented landscapes greatly increases the risk of future extinction at a landscape scale despite survival of subpopulations (Berglund and Jonsson 2005; Johansson et al. 2013), described by Tilman et al. (1994) as extinction debt.

Lichens with limited dispersal ability may be restricted to survive in metapopulations in dispersed remnant old-growth forest fragments (Johansson et al. 2013; Jonsson et al. 2005; Snäll et al. 2005). Hypothetically, long-lived epiphytic lichens could survive on trees for several hundred years, thereby reducing the risk of extinction with longer time frames to allow for the creation of suitable conditions for colonization in the surrounding landscape (Johansson et al. 2013).

In disturbed landscapes, residual individual or small groups of older trees that survive severe disturbance events could serve as micro-refuges until surrounding trees become suitable for colonization (e.g., develop suitable bark structure for the capture of vegetative propagules, presence of compatible photobiont for fungus spores). However, lichen species must be able to survive on micro-refuges in altered microclimatic conditions related to the surrounding canopy dieback (Gauslaa et al. 2007; Johansson et al. 2006); however, despite

the possible existence of micro-refuges after disturbance, subpopulations of some species could disappear immediately after the disturbance. Lichens are poikilohydric organisms, thus their relationship to microclimate is strongly dependent on their symbiotic photobiont (Aptroot and van Herk 2007; Ellis and Coppins 2006; Marini et al. 2011; Peksa and Škaloud 2011) or could be regulated by some secondary metabolites (Gauslaa et al. 2008). Microclimatic sensitivity in combination with low colonization rates would be crucial determinants for species surviving in disturbed woodlands.

We studied the occurrence and biodiversity of epiphytic lichen flora in severely disturbed subalpine primary *Picea abies* forests of the Ukrainian Gorgany Mountains. We analysed the effect of tree level variables (age, stem diameter) and the influence of continuity. Age has been demonstrated to have a positive influence on lichen biodiversity (Boudreault et al. 2008; Fritz et al. 2008; Lie et al. 2009; Marmor et al. 2011; Nascimbene et al. 2009). Continuity has typically been estimated by the arbitrary minimum ages of old-growth forests (Marmor et al. 2011; Dittrich et al. 2013; Nascimbene et al. 2010) without detailed information about age structure and disturbance history. To our knowledge, no studies have examined the role of microclimatic continuity in lichen persistence. We evaluated continuity as both the age of the oldest tree on the plot as a potential micro-refuge for lichens, and as the minimum time needed to disturb 80% of the canopy (see Materials and methods) to estimate microclimatic continuity within plots.

We addressed the following three questions: (i) is the presence of old trees (>200 years) on plots important for epiphytic lichen biodiversity in areas of high severity disturbances? (ii) If so, how important is the microclimatic continuity? (iii) What is the threshold of tree age for maintaining epiphytic lichens biodiversity in the studied forests?

Materials and methods

Study area

The study was conducted in the primeval subalpine spruce forest remnants in Gorgany Mountains (Ivano-Frankivsk region, Ukraine), one of the largest primeval spruce forest preserves in Central Europe. Two localities, approximately 20 km apart, were selected: north and east slopes of Grofa Mountain (altitude range of 1320–1409 m, 48°34'N, 24°03'E) and east slopes of Syvulya Mountain (altitude range of 1306–1364 m, 48°32'N, 24°07'E). Both localities represent the same forest type with long-term continuity of *P. abies* as the dominant species, followed by *Pinus cembra*, *Sorbus aucuparia*, *Betula* spp., and scattered *Acer pseudoplatanus* and *Fagus sylvatica*. Bedrock was formed by sandstone with leptosols and albic podzols. The mean monthly temperature varies between 16.4 °C in July and −7.6 °C in January, and annual precipitation ranges between 853 mm and 1007 mm, peaking during June and July.

Disturbance histories of both localities are characterized by mixed severity disturbances and spatiotemporal patterns of disturbance severity were highly heterogeneous (Trotsiuk et al. 2014). Extreme disturbances (>60% canopy removal for a single event) did not exceed areas of 1 or 2 ha, and plots with continuous development were about 250 m from the disturbed areas.

Data collection

Data were collected on 13 (Grofa, $n = 9$; Syvulya, $n = 4$) 1000 m² circular plots (diameter = 17.83 m) in August 2012. Plots were stratified by their historical maximum severity disturbance event: (i) two plots with extreme disturbance (>60% canopy removal in a single event) about 80 to 90 years ago with no older trees (>90 years); (ii) two plots with heavy disturbances (>40 and ≤60% canopy removal in a single event) about 80 to 90 years ago, in which several old trees survived (current ages of 200–280 years old), (iii) two plots with moderate disturbances (>20% and ≤40% canopy removal in a single event) with trees 200 and 340 years old; and (iv) seven plots with light disturbance (≤20% canopy removal in a single event), in which age of the oldest trees were between 260 and 390 years (for details see Table 1). Current plot structures were representative of forest interiors with no signs of recent disturbance.

Geographical coordinates, elevation, orientation, and slope gradient were recorded for each plot. Crown cover was calculated as the mean value of six hemispherical photos taken at plot centre and at 5 points situated 12.10 m from plot centre (at azimuths of 0°, 72°, 144°, 216° and 288°) according to the pixels classification method (WinScanopy 2012a, © Regent Instruments Canada Inc.).

In each plot, at least 25 Norway spruce trees with diameter at breast height (DBH) >10 cm were cored at 1.3 m from the base of the tree. Tree age was determined from the number of tree rings. Coordinated increases in ring increment sizes among trees within plots indicated changes in canopy cover, which was used to reconstruct plot disturbance history, as detailed in Trotsiuk et al. (2014). Detected releases were converted to the percentage of canopy area disturbed in each plot based on each tree's current crown area (see Trotsiuk et al. 2014 for a more detailed explanation). Canopy time was calculated as the minimum sum of subsequent years to remove 80% of the canopy.

We selected ten of the cored trees from different DBH classes per plot to evaluate lichen presence by size classes. Of the 130 trees sampled, six were excluded from the analysis because accurate age estimates were not possible because the pith was not present. Lichen species were recorded as either present or absent for each stem up to a height of 1.8 m. Branches were not accessible in many cases, therefore only stems were sampled. Species we could not adequately identify in the field were collected and determined microscopically in the laboratory using spot reaction tests and also thin layer chromatography in cases of *Usnea* spp., *Lepraria* spp., and some sterile crustose lichens, such as *Ochrolechia* spp. Lichen nomenclature used in this study follows Liška and Palice (2010) with some newly accepted changes: *Lecanora mughosphagneti* Poelt and Vězda, *Lecidea nylanderii* (Anzi) Th. Fr., and *Lepraria finkii* (de Lesd.) R. C. Harris.

Data analysis

All analyses were performed in R statistical software (R Development Core Team, 2012). Number of species per tree were analysed using the following explanatory variables: Age (age of tree), DBH (diameter of tree at 1.3 m height), MaxAge (age of the oldest tree sampled on the plot according to Fritz et al. 2008), CanTime (number of subsequent years to remove 80% of canopy as specified above), CanOpen (canopy openness calculated from hemispherical photos), and Locality (Grofa and Syvulya). We recognize the potential effect of elevation, slope, and orientation, but we did not test their effects because of their relatively narrow range of values.

Table 1 Individual plot values of measured variables

Loc	MaxAge (years)	CanTime (years)	CanOpen (%)	DistSev	Age (years)	BH (cm)	No. of trees	Species per tree	Species per plot
Gr	203	14	8.1	Heavy	146 ± 46	45 ± 13	10	7.9 ± 1.2	16
Gr	82	12	7.0	Extreme	66 ± 11	28 ± 8	10	3.5 ± 1.1	10
Gr	337	65	11.9	Moderate	131 ± 13	31 ± 14	8	8.1 ± 1.9	17
Gr	198	62	11.3	Moderate	151 ± 41	39 ± 12	10	5.4 ± 3.4	14
Gr	87	7	7.4	Extreme	77 ± 3	35 ± 7	9	5.8 ± 1.6	13
Gr	256	102	16.8	Light	174 ± 32	33 ± 12	9	9.3 ± 1.7	17
Gr	271	148	20.5	Light	202 ± 38	56 ± 16	10	11.3 ± 1.6	24
Gr	282	187	11.9	Light	190 ± 73	43 ± 14	8	8.4 ± 4.3	18
Gr	289	95	12.5	Light	156 ± 99	41 ± 19	10	8.1 ± 2.6	19
Sy	393	144	10.6	Light	179 ± 72	35 ± 14	10	11.8 ± 3.3	28
Sy	331	209	12.8	Light	233 ± 88	36 ± 12	10	13.0 ± 3.2	29
Sy	305	112	12.1	Light	175 ± 60	48 ± 15	10	10.5 ± 2.8	25
Sy	273	30	10.0	Heavy	111 ± 13	50 ± 13	10	11.2 ± 2.1	27

Columns from left to right: 1. Loc—plot locality (Gr Grofa, Sy Syvulya); MaxAge age of the oldest tree on the plot; CanTime—time to removal of 80% of the plot canopy; CanOpen—canopy openness, calculated by Pixels Classification Method; DistSev—disturbance severity classified according to Trotsiuk et al. (2014); Age—average age of sampled trees (± standard deviations); DBH—average stem diameter of sampled trees (± standard deviations); No. of trees—number of sampled trees on the plot; Species per tree—average number of species on each tree of plot (±SD); Species per plot—total number of species recorded

Table 2 Correlation matrix of relevant plot variables, including: age—average age of sampled trees; DBH—average stem diameter of sampled trees; MaxAge—age of the oldest tree on the plot; CanTime—time to removal of 80% of the plot canopy; CanOpen—canopy openness, calculated by Pixels Classification Method

	Age	DBH	MaxAge	CanTime
DBH	0.43			
MaxAge	0.39	−0.02		
CanTime	0.57	−0.01	0.61	
CanOpen	0.47	0.23	0.47	0.57

Individual plot values of tested variables and Pearson correlations of variables are shown in Tables 1 and 2, respectively. The number of species per tree was normally distributed, as tested using the Shapiro–Wilk normality test. We used a linear mixed-effects model (LMER) from the ‘lme4’ package (Bates et al. 2014); plot was considered a random effect. Explanatory variables were centred by means before analysis to reduce correlations between fixed factors. Forward manual selection was used, and variables were added to the model in order of the strongest explanatory power. Every new model was compared to the previous simpler model with the maximum likelihood method from the likelihood-ratio test.

We analysed individual species relationships to tree age and presence of old trees at the plot level in comparison to microclimate change. We used general additive models (GAM) from the ‘mgcv’ package (Wood 2016) with binomial distribution and with Plot as a random effect to test the influence of age variables (Age and MaxAge) and microclimatic change, simplified to two categories, high (extreme and heavy disturbance) and low severity (light and moderate); for high severity events, we assumed substantial microclimatic changes existed in historical development of the canopy. We compared our results with relevant studies (including Bradtka et al. 2010; Holien 1997; Hedenås and Ericson 2000; Marmor et al. 2011; Meier et al. 2005; Nascimbene et al. 2010; Nilsson et al. 2001; Sætersdal et al. 2005) and their rarity in the studied region (Makarevych et al. 1982) as well as adjacent Carpathian regions (Cieśliński et al. 2006; Pišút et al. 2001). Species information was summarized in Table 4. To approximate the minimum threshold for successful colonization of the individual species, we used the lowest values of the tree plot variable Age and the plot variables MaxAge and disturbance severity (high and low).

Results

A total of 43 lichen species were recorded, including some very rare species, such as *Alectoria sarmentosa*, *Cyphelium inquinans*, and *Lecanora mughosphagneti* (for a complete list of species and their abundances, see Fig. 2 and Table 4). The median number of species recorded per tree was 9, with a minimum of 0 and maximum of 17 species. The highest number of species on a plot, 28, was found in a plot with a light disturbance history; however, a comparable number of species, 27, was recorded in a heavily disturbed plot with tree older than 270 years. The lowest number of species in a plot was 10, which occurred on the youngest extremely disturbed plot. Plot estimates of the mean number of species per tree and total number of species are provided in Table 1.

The LMER indicated a significant effect for tree age and stem diameter at the individual tree level, MaxAge at the plot level, and Locality also had a significant effect. Plots in Syvulya had on average about two more species than plots in Grofa. To increase the average number of species in Grofa to a level comparable to that found in Syvulya, it would require 100 years of additional tree age, 200 years of additional MaxAge, or 40 cm of diameter growth (for coefficients see Table 3). CanTime and CanOpen had no significant effects on species richness. The effect of Age by MaxAge and DBH was evident, with older trees generally having higher species richness (Fig. 1); species richness increased with increasing Tree Age, regardless of MaxAge, and it increased by DBH for younger trees (trees <150 years old), but older trees (trees >150 years old) had only a weak positive relationship of species richness to increased DBH.

Figure 2 shows that the vast majority of lichen species (except species with the lowest frequency) were able to colonize trees within 100 years or less after disturbance. The most

Table 3 Relationship of species richness to tree level and plot level variables (Var.); results of linear mixed effects model (LMER) with plot as a random effect are shown with average coefficient estimates (Est.) and significance levels (Sign.; ***p < 0.001, ** p < 0.01, * p < 0.05, n. s. not significant)

Level	Var.	Est.	Sign.
	Intercept	8.45	
Tree level	Age	0.02	***
	DBH	0.05	**
Plot level	MaxAge	0.01	**
	CanTime	–	n.s.
	CanOpen	–	n.s.
Locality	Syvulya	2.31	***

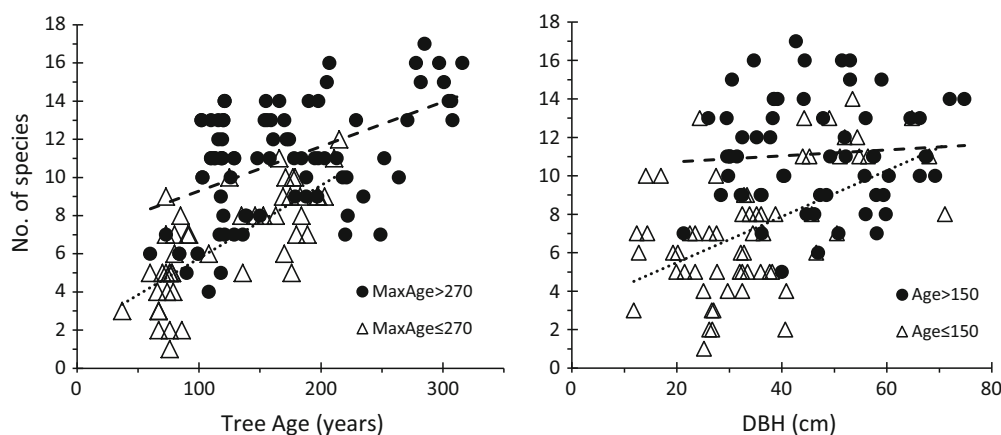
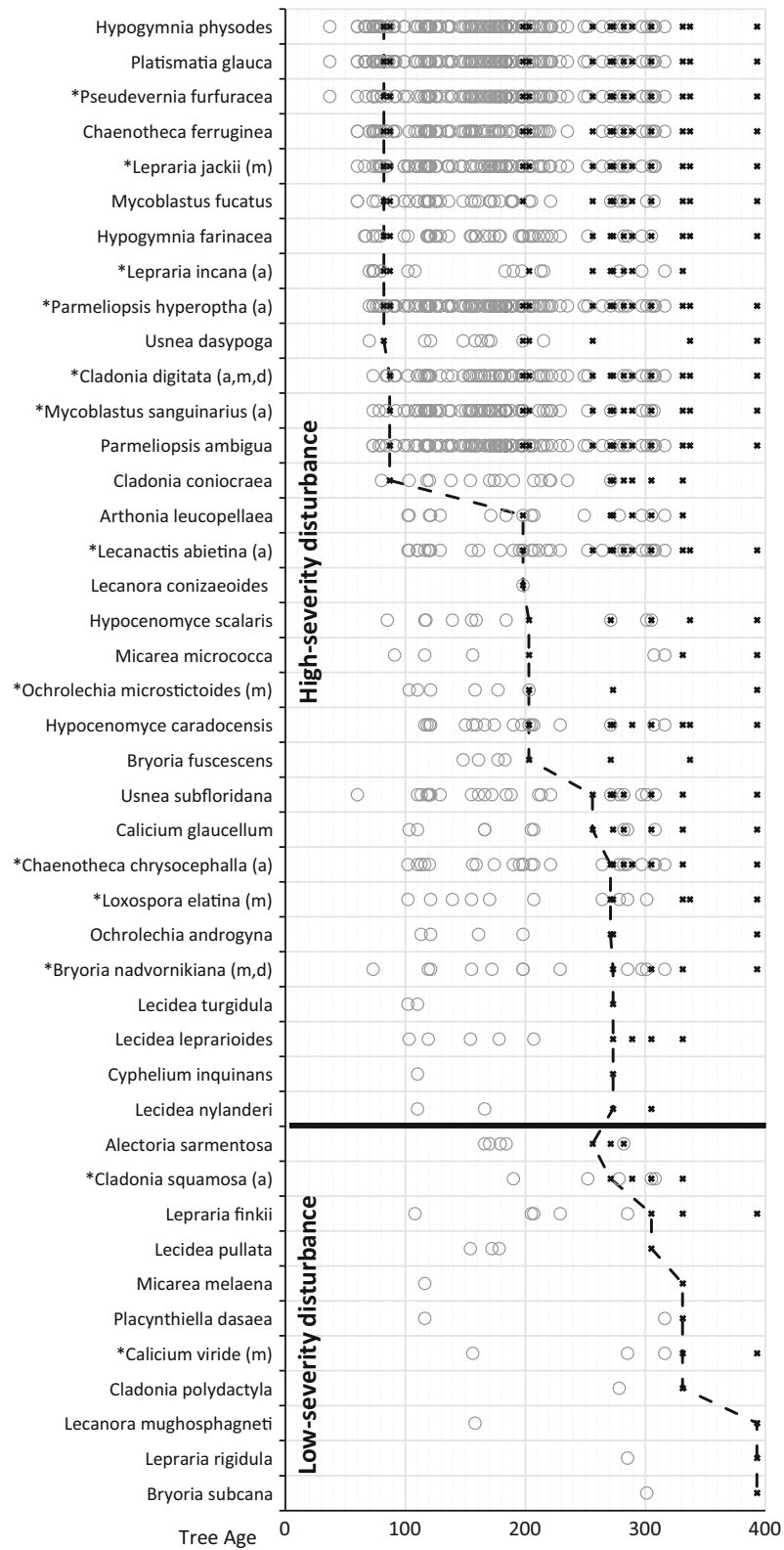


Fig. 1 Relation between the number of lichen species and individual tree age, age of the oldest tree per plot, and tree diameter (DBH); *left panel* number of species per tree (y-axis) along tree age gradient (x-axis) split into two intervals of MaxAge (*empty triangles* trees from plots in which the oldest tree was younger than 270 years, *black points* trees from plots in which the oldest tree was older than 270 years); *right panel* number of species per tree (y-axis) along stem diameter (DBH, x-axis, *empty triangles* trees younger than 150 years, *black points* trees older than 150 years); linear trendlines were added (*dotted line* MaxAge ≤ 270 years in *first panel* and age ≤ 150 years in *second panel*, *dashed line* MaxAge > 270 years in *first panel* and age > 150 years in *second panel*)



◀ **Fig. 2** Species chronology along tree age and plot-level maximum tree age gradients; species are ordered by the lowest MaxAge, *top to bottom*, and grouped by plot disturbance severity (high, which includes extreme and heavy disturbances, are *above the solid black line*, and low, which includes moderate and light disturbances, are *below the solid black line* (these groups are intended to represent differences in microclimatic continuity). Host tree ages are indicated by the empty grey circles (x-axis); MaxAges are indicated by *black crosses* (x-axis); the lowest MaxAge of the plot on which each species occurred is indicated by the *dashed line*. Species with significant response to any of the variables are indicated by *asterisk* and accompanied by an abbreviation of the significant variable (*a* age, *m* MaxAge, *d* low disturbance severity); for more details about species traits see Table 4

remarkable difference in lichen species number and composition is apparent between extremely disturbed plots without any trees older than 80 years and heavily disturbed plots, where some trees older than 200 years survived. Based on this observed pattern, we tested relationships of individual species to Age, MaxAge, and disturbance severity, expressed as 2 categories: high (extreme and heavy disturbance) and low (moderate and light disturbance). A significant positive relationship to Age was found in *Chaenotheca chrysocephala*, *Cladonia digitata*, *Cladonia squamosa*, *Lecanactis abietina*, *Lepraria incana*, *Mycoblastus sanguinari*, *Parmeliopsis hyperoptha*, and *Pseudevernia furfuracea*; however, we also observed weaker, marginally significant effects in *Bryoria nadvornikiana*, *Calicium glaucellum*, *Calicium viride*, and *Usnea subfloridana*. Age of the oldest tree (MaxAge) had significant positive effect on *Bryoria nadvornikiana*, *Calicium viride*, *Cladonia digitata*, *Lepraria jackii*, *Loxospora elatina* and *Ochrolechia microstictoides*. Low disturbance severity was significantly preferred by *Bryoria nadvornikiana* and *Cladonia digitata*, while *Ochrolechia microstictoides* had higher frequency on heavily disturbed plots.

Discussion

Old trees as micro-refuges

We observed a strong relationship between lichen species richness and composition with both individual tree age and maximum tree age on a plot. Species richness increased linearly with tree age (see Fig. 1), which was augmented by the presence of old trees as micro-refuges for species colonization of surrounding trees. Nascimbene et al. (2009) observed species composition turnover on over-mature spruce trees. In our study, species colonizing relatively young trees were also able to survive on very old trees (see Fig. 2), which demonstrates accumulation of species over time and it underlines the critical role of age as a function of time for species colonization. Plots that had experienced extreme severity disturbances with no surviving trees and were currently dominated by young trees (~80 years) were colonized only by the most common lichen species. The highest frequency of species was usually epiphytes that are non-selective with regards to host trees, those growing on other substrata, or those with frequent sexual dispersal or producing many small soredia, which is consistent with the findings of Johansson et al. (2012) and Jürjado et al. (2006). However, even some of the most common species, such as *Cladonia digitata*, *Parmeliopsis hyperoptha*, and *Pseudevernia furfuracea*, displayed increasing frequency with tree age.

Although *Mycoblastus sanguinari* is considered to be an old-growth mountain spruce forest indicator (Holien 1997; Marmor et al. 2011), it was able to colonize extreme disturbance patches from surrounding old-growth forest over distances of approximately

Table 4 List of species and their important traits

Species	Morph.	Repr.	Ind.	Ukr. Carp.	SK	PL	Freq.	Age	MaxAge	Dist
<i>Alectoria sarmentosa</i>	ale	v (s)	Continuity (Bradtka et al. 2010; Holien 1997; Hedenås and Ericson 2000); old trees (Nilsson et al. 2001)	Not rare	CR	EN	5			
<i>Arthonia leucopellaea</i>	cru	s	Continuity (Marmor et al. 2011)	Very rare	CR	VU	15			
<i>Bryoria fuscescens</i>	ale	v (s)		Not rare	VU	VU	4			
<i>Bryoria nadvornikiana</i>	ale	v	Continuity (Bradtka et al. 2010)	Not listed	CR	EN	12	–	*	*
<i>Bryoria subcana</i>	ale	v		Scattered	CR	CR	1			
<i>Calicium glaucellum</i>	cal	s	Forests older than 120 years (Nascimbene et al. 2010)	Not specified	CR	VU	9	–		–
<i>Calicium viride</i>	cal	s	Continuity (Marmor et al. 2011)	Scattered	EN	VU	3	–	*	*
<i>Chaenotheca chrysocephala</i>	cal	s	Old forests (Meier et al. 2005)	Fairly frequent	VU		23	*		
<i>Chaenotheca ferruginea</i>	cal	s		Not specified			82			
<i>Cladonia coniocraea</i>	cla	sv		Very frequent			16			
<i>Caldonia digitata</i>	cla	sv	Older trees (Marmor et al. 2011)	Very frequent			62	**	**	*
<i>Cladonia polydactyla</i>	cla	sv		Not specified			1			
<i>Cladonia squamosa</i>	cla	v (s)		Frequent			5	*		
<i>Cyphelium inquinans</i>	cal	s	Forests older than 200 years (Nascimbene et al. 2010)	Very rare	CR	CR	1			
<i>Hypocenomyce caradocensis</i>	squ	sv		Not listed			18			
<i>Hypocenomyce scalaris</i>	squ	sv		Rare			10			
<i>Hypogymnia farinacea</i>	fol	sv	Old pinus forests (Marmor et al. 2011)	Not listed	VU	VU	42			
<i>Hypogymnia physodes</i>	fol	v		Very common			114			
<i>Lecanactis abietina</i>	cru	asv	Continuity (Bradtka et al. 2010; Marmor et al. 2011)	Rare	CR	EN	33	***		
<i>Lecanora conizaeoides</i>	cru	s		Not listed			1			
<i>Lecanora mughosphagneti</i>	cru	v		Not listed			1			
<i>Lecidea leprarioides</i>	cru	sv		Not listed			5			
<i>Lecidea nylanderi</i>	cru	v	Older trees (Marmor et al. 2011)	Not listed			2			
<i>Lecidea pullata</i>	cru	v		Not listed			3			

Table 4 continued

Species	Morph.	Repr.	Ind.	Ukr. Carp.	SK	PL	Freq.	Age	MaxAge	Dist
<i>Lecidea turgidula</i>	cru	s		Rare		VU	2			
<i>Lepraria incana</i>	lep	v		Not listed			16	*	–	
<i>Lepraria jackii</i>	lep	v		Not listed			82		*	
<i>Lepraria finckii</i>	lep	v		Not listed			5			
<i>Loxospora elatina</i>	cru	v (s)		Rare	NT	CR	10		*	
<i>Micarea melana</i>	cru	s		Very rare		NT	1			
<i>Micarea micrococca</i>	cru	s		Not listed			5			
<i>Mycoblastus fucatus</i>	cru	sv		Not listed			39			–
<i>Mycoblastus sanguinarius</i>	cru	as	Continuity (Holien 1997); old forests (Marmor et al. 2011)	Fairly rare	CR	VU	64	*		
<i>Ochrolechia androgyna</i>	cru	v (s)		Very rare		VU	4			
<i>Ochrolechia microstictoides</i>	cru	v		Not listed			6		*	
<i>Parmeliopsis ambigua</i>	fol	v		Frequent			88			
<i>Parmeliopsis hyperoptha</i>	fol	v	Forests older than 200 years (Nascimbene et al. 2010); old pinus forests (Meier et al. 2005)	Fairly frequent	VU	VU	98	**		
<i>Placynthiella dasatea</i>	squ	v (s)		Not listed			2			
<i>Platismattia glauca</i>	fol	v		Frequent	NT		113			
<i>Pseudevernia furfuracea</i>	fru	v		Very common	NT		94	*		
<i>Usnea dasypoga</i>	ale	v		Not rare	CR	VU	10			
<i>Usnea subfloridana</i>	ale	v(s)	Indicator of high biodiversity (Sætersdal et al. 2005)	Not rare	CR	EN	23	–		

Columns from left to right include: Species—species name; Morph.—growth form (*ale* alectoroid, *cal* calicioid, *cl* Cladonia species with dimorphic thallus, *cru* crustose, *fol* foliose, *fru* fruticose, *squ* squamulose); Repr.—dominant reproduction mode (*a* asexual with pycnidia, *s* sexual with apothecia, *v* vegetative with soredia, *iz* izidia or thallus fragments, rarely occurred modes are in brackets); Ind.—indicator value of species from literature; Ukr. Carp.—distribution of species in Ukrainian Carpathians in accordance with Makarevych et al. (1982); SK—Red List category in Slovakia (Pišút et al. 2001), PL—Red List category in Poland (Cieślinski et al. 2006); CR—critically endangered, EN—endangered, VU—vulnerable, NT—near threatened), Freq.—frequency of species on trees (n = 124); Age—relationship of the species to individual tree age; MaxAge—relationship of the species to age of the oldest tree at the plot level; Dist—relationship of the species to low disturbance level (last three columns are results of Generalized Additive Models on individual species; tests of significance are shown—*** p < 0.001, ** p < 0.01, * p < 0.05., marginally significant)

250 m, which could be explained by frequent production of apothecia and pycnidia and its relatively good dispersal ability. The probability of *M. sanguinarius* occurrence significantly increased with tree age, as did *Lecanactis abietina*, another old-growth forest indicator species (Bradtka et al. 2010; Marmor et al. 2011). Calicioid lichens generally are considered indicators of forest continuity (Bradtka et al. 2010; Holien 1997; Löhmus 2003). We found a significant relationship of tree age for *Chaenotheca chrysocephala*, and a marginally significant effect also on *Calicium glaucellum* and *Calicium viride*, which displayed a significant relationship to MaxAge. In contrast, *Chaenotheca ferruginea* was one of the most common species; it occupied about 66% of the sampled trees, including trees on extremely disturbed patches, and it did not show any relationship to forest age, in accordance with Marmor et al. (2011). Calicioid old-growth forest indicator, *Cyphelium inquinans* was extremely rare (Nascimbene et al. 2010), thus we could not verify its associations.

Heavy disturbances with survival of some trees were represented by events dating to approximately 100 years ago in this study. Although the vast majority of species were able to colonize trees about 100 years old, approximately two-thirds of the species occurred only in plots with trees 200 years and older present (see Fig. 2). This is consistent with Johansson et al. (2013), who observed that 100-years old post-disturbance trees had become suitable for colonization by lichens from surrounding old trees in disturbed oak (*Quercus*) forests. In general, many crustose lichens are slow colonizers relative to foliose and fruticose lichens (Jüriado et al. 2006; Nimis et al. 2002), and rapidity of colonization is strongly dependent on habitat connectivity. We found a significant relationship to age of the oldest tree in *Bryoria nadvornikiana*, an alectorioid lichen that has vegetative dispersal, as well as in crustose lichens reproducing occasionally by soredia, such as *Loxospora elatina*, *Ochrolechia microstictoides*, and *Lepraria jackii*, which implies that the existence of old-trees as micro-refuges at the plot level are especially critical for species lacking sexual dispersal. We could not reliably test this hypothesis for extremely rare species, however, on the basis of their observed low colonization rate, we assume this pattern also in other crustose lichens with vegetative dispersal, such as *Lecanora mughosphagneti*, *Lecidea nylanderii*, and *Ochrolechia androgyna*.

Microclimatic continuity

The main difference between heavily disturbed plots with persistent old trees as potential micro-refuges and lightly disturbed plots is that less disturbed plots provide long-term microclimatic stability below the largely intact canopy. Low colonization rates in clear-cut and young forest stands has been observed in alectorioid lichens (Johansson 2008). Most species of this morphological group, such as *Usnea dasypoga*, *Usnea subfloridana*, *Bryoria fuscescens*, and *Bryoria nadvornikiana*, were able to colonize heavily disturbed plots. Although we observed higher frequency of *Bryoria nadvornikiana* and *Cladonia digitata* in lightly disturbed patches, microclimatic continuity apparently would not be limiting for their occurrence. Only two species, *Bryoria subcana* and *Alectoria sarmentosa*, were restricted to plots with microclimatic continuity, however, their rare occurrence was not sufficient to confirm this pattern.

Many of the oceanic species are old-growth forest indicators in suboptimal climatic conditions (Ellis et al. 2009), such as in the Carpathian Mountains of central Europe. Although oceanic species were sparse in this study, some, such as *Alectoria sarmentosa*, are sensitive to forest edges (Esseen 2006) and are strongly associated with forest continuity (Holien 1997; Hedenås and Ericson 2000). *Alectoria sarmentosa* displayed an

association with old trees, as it colonized trees ranging from 166 to 282 years old, which implies a limited capacity to colonize younger, highly disturbed sites, as Nilsson et al. (2001) also observed; their continual presence in forests characterized by low severity disturbances has been previously observed (Benson and Coxson 2002).

Recommended threshold for biodiversity maintenance

Svoboda and Pouska (2008) proposed that even secondary forests achieve old-growth forest structure approximately 200 years after large-scale disturbances. Whether this is sufficient time for various habitat-dependent groups of organisms is an unresolved and rarely studied question (Johansson 2008). In *P. abies* forests of the Harz Mountains of Germany, Dittrich et al. (2013) concluded that within a natural landscape matrix that includes old-growth forests, 200 years of secondary forest development is a sufficient time period to become saturated by all the regional lichen species. In *P. abies* forests of the Alps, lichen species compositions in old-growth forests older than 200 years were similar to mature managed forests younger than 180 years. However, caution is advised in making direct comparisons to those studies due to a reduced regional epiphytic lichen flora as a result of atmospheric pollution in Harz (Dittrich et al. 2013), and higher biodiversity related to a more oceanic climate in the Alps (Nascimbene et al. 2010).

In our study, plots with trees from 200 to 300 years old that served as micro-refuges were saturated by most of the obligate, habitat-specialized epiphytes without requiring microclimatic continuity (see Fig. 2). In plots with microclimatic continuity in which the age of the oldest tree was above 300 years, a random pattern of facultative epiphytes associated with various substrata (e.g., dead wood) occurred (Fig. 2). The time accessible for random colonization on old trees or their favourable bark characteristics (e.g., pH, moisture retention capacity) could increase the probability of further colonization. However, microclimatic continuity could be crucial at least for rare alectorioid lichens, such as *Alectoria sarmentosa*, some *Bryoria* species, and *Usnea longissima*, which is listed within the Gorgany Mountains (Makarevych et al. 1982). For this reason, the mixed severity disturbance regime with undisturbed areas, which is typical of these old-growth forests, should ensure their survival in natural landscapes.

Conclusions

Old-growth forests constitute a tiny fraction of the contemporary landscape in temperate zones and they provide the last refuges for many endangered species (Parviainen et al. 2000; Wesolowski 2005). However, old-growth Carpathian forests remnants have been substantially diminished and fragmented by forest management, particularly large-scale clear-cutting and salvage logging (Mikoláš et al. 2016). Previous studies have demonstrated that natural disturbances create a mosaic of different successional stages and structural complexity across varying spatial scales (Trotsiuk et al. 2014; Svoboda et al. 2014), and these diverse forest landscapes host many rare and endangered lichens, which are likely extinct in many regions (e.g. Dittrich et al. 2013). Persistence of old trees as micro-refuges after disturbances could help increase species biodiversity of many specialized epiphytic species, even in altered microclimates. We recommend the preservation of old-growth forest fragments in Europe without any post-disturbance management

interventions; these areas would preserve existing habitats for uncommon lichen species and also act as a source to colonize surrounding forests.

Long-term microclimatic stability could be necessary for alectorioid lichens, which may be threatened by large-scale disturbances due to its weak dispersal ability and microclimatic sensitivity. However, mixed severity disturbance regimes should preserve and promote its survival in old-growth forests. Pristine forests and protected old-growth forests should be maintained to preserve all stages of forest development to spatiotemporal dispersal of species throughout the various stages of forest development. In addition, forest management in adjacent forests should replicate important structural features of old-growth forests, such as retention of at least 10 trees per hectare that are older than 200 years or maintaining trees that survive disturbances, as they will help to potentially act as source populations and preserve rare lichen species.

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6. Discussion

6.1. Dendroecological methods for reconstruction disturbance dynamic

We found that each of the four tree-ring based methods demonstrated efficacy in reconstructing canopy disturbance events as more often than not each method identified the correct number of expected growth releases in the hurricane experiment data; however, the performance of each method varied under different forest conditions. In the forest with a relatively low rate of canopy disturbance (Lyford plots), there is little separation between methods and all methods performed better compared to the hurricane pulldown experiment forest. In fact, no method produced false negatives in the Lyford plots. While high temporal precision in the detection of past disturbance is found for all methods, greater uncertainty is found when using the boundary line and time series methods. These findings highlight that the timing of the detected events can vary significantly depending on which method is used (Copenheaver et al., 2014; see also Fraver and White, 2005). The ability of a method's temporal precision can have a strong impact on the reconstruction of disturbance history.

A significant constraint of the boundary line and absolute increase methods is the amount of pre-required data for reliable analysis and expert knowledge needed. Given the dependence on the species and site condition necessary for the application of these two methods, they are primarily limited to the large datasets from one species or location (Black and Abrams, 2003; Fraver and White, 2005; Ziaco et al., 2012). We view the need for large data sets, a large amount of a priori information regarding species, or expert knowledge a substantial limitation for studies in forests with high tree species diversity or with short windows to conduct disturbance research.

Important weakness is observed across methods in reconstructing the intensity of canopy disturbance. Radial-growth averaging and absolute increase methods estimated disturbance intensity of about 60-65%, while boundary line and time series method only of ca. 20-25%, comparing with 80% canopy damage on the hurricane experimental pulldown. While each method might detect the same number of trees showing a release around the time of known disturbance event, the subsequent estimation of disturbance intensity of that event ranges by nearly

30% as the result of the temporal precision. It is clear that temporal accuracy of the various methods needs to be considered carefully when estimating disturbance intensity. Despite limitations in estimating disturbance intensity, time series is the only method that has a single series-specific disturbance threshold and considers the variation within a series giving it the ability to overcome the limitations for the boundary line and absolute increase methods. The time series method also has the ability to provide quantitative reconstructions of the magnitude and duration of a tree's response to a disturbance event as disturbance-growth index.

6.2. Disturbance dynamic in the natural forest landscapes

Primary montane spruce forests in the study regions were shaped by a disturbance regime with high spatiotemporal variability in severity and frequency. Moderate and low severity disturbances dominated, but rare severe events were also evident in our disturbance reconstruction, and made a disproportional contribution to the overall canopy removed by disturbance. A similar mixed severity disturbance regime was also recently described for Norway spruce-dominated mountain forests in Central Europe. Although the disturbance history in the study landscapes was temporally and spatially diverse, periods of synchrony in disturbance activity were also found.

Such mixed patterns of disturbance, which fit neither the small-scale patch dynamics nor the large-scale catastrophic disturbance models, have recently been described as mixed severity (a.k.a. moderate, intermediate) disturbances (Hanson and Lorimer, 2007; Stueve et al., 2011; Woods, 2004). Such disturbances may create patchy but severe or widely dispersed yet moderate canopy damage. While mixed severity disturbances of forest ecosystems were mostly discussed in fire communities (Perry et al., 2011) they are more rare in the scientific literature on forests driven by other disturbance agents and there is still no clear definition of what constitutes a mixed severity disturbances regime, common characteristics include variability in patch size and number and broad ranges in the amount of canopy removed (Greenberg and McNab, 1998; Hanson and Lorimer, 2007; Nagel et al., 2006; Stueve et al., 2011; Woods, 2004). This may arise from a single disturbance hitting a large area with variable intensity and

extent within the landscape, or from a combination of numerous disturbance events occurring in different parts of the landscape that may be driven by different disturbance agents. Importantly, the consequences of both are read in the spatiotemporal heterogeneity and complexity of forest structure. Nevertheless, mixed severity disturbances are often an important link that is missing in the discussion between fine scale patch dynamics and large infrequent disturbances.

While the spatial patterns of the disturbance regime were highly variable, some trends within the region could be still discerned. Lower disturbance severities were, for instance, observed in Ukraine, and can be explained by the position and physiography of this particular landscape (more Trotsiuk et al., 2014). In contrast, landscapes exposed to these winds and without topographic sheltering were more strongly disturbed in the past, with a higher risk of severe disturbance (Čada et al., 2016).

The prominent disturbance pulses of the 19th century likely also contributed to the comparatively low disturbance activity in the first part of the 20th century. The disturbance risk for the young stands originating in the mid-19th century was likely depressed for several decades, as both wind and bark beetle susceptibility increases with age in Norway spruce forests. *Ips typographus* attack primarily older and weakened trees, which are found in abundance after wind disturbance (Wermelinger, 2004), and also wind risk increases with tree size (and hence age) (Canham et al., 2001). Furthermore, the absence of high severity disturbance after the mid-19th century could have led to a synchronous development of regenerating forest stands as well as to spatial homogenization across the landscape through increased connectivity between susceptible patches. These factors are frequently associated with increasing risk for wind disturbance and bark beetle outbreaks (Jarvis and Kulakowski, 2015), suggesting a century-scale temporal autocorrelation between disturbance episodes in these forests.

However, it should also be noted that the higher proportion of trees recruited in the 19th century could at least in part be explained by the availability of possible study sites, as we focused on remnants of primary forests, mostly in strictly protected reserves with specific topography. Despite having a regional and

landscape scale focus, our work was still carried out in a fragmented landscape, where only remnants of old-growth forests remained. Together with the fact that salvage logging has commonly been applied in the region during the last 50 years, unmanaged young post disturbance stands might be partly missing. Consequently, early-successional stages after recent high severity disturbance, such as described in Central Europe by Wild et al. (2014), Zeppendorf et al. (2015) and Svoboda et al. (2014), were missing in our analysis. This decreases the utility of our disturbance reconstruction for recent decades, and suggests that the historical disturbance regime reconstructed from primary forests might not be fully representative of the entire region.

Nonetheless, our analysis suggests that the current disturbance pulse observed in several Carpathian mountain forests (Mezei et al., 2014) could at least in part result from past disturbance dynamics and the emerging synchrony in stand development. Additional drivers of the currently high disturbance activity might be climate change, resulting in an increasing probability of bark beetle outbreaks (Temperli et al., 2015, 2013) as well as increasing climatic extremes connected with damage to forests, such as drought and wind events (Dale et al., 2001; Seidl et al., 2014b). Similar large-scale disturbance were also observed in other parts of Central Europe (Lausch et al., 2011) or in North America (Berg et al., 2006). Recent disturbances in Central Europe have largely been high severity events (Kautz et al., 2011; Mezei et al., 2014), suggesting that disturbance regimes might be changing in severity and frequency relative to their historical patterns. However, other evidence from Central and Eastern Europe (Čada et al., 2016; Holeksa et al., 2016; Panayotov et al., 2011; Svoboda et al., 2014; Zielonka et al., 2010) suggests that large-scale severe disturbance events such as those observed recently might also have occurred in the past.

Primary forest is not a simple functioning ecosystem, but rather has a complex hierarchical structure (Mori, 2011). Interpreting landscape dynamics based on single plot-level data is thus inappropriate (White and Jentsch, 2001), making it impossible to evaluate disturbance history at local, stand and landscape scales based on small sampling datasets or preferential selection. While interpreting the disturbance regime, the area of observations must therefore be

taken into account. The results from this thesis showed high variability of disturbance severities on the plot-level, but greater balance at the stand level. If only a subset of the plots had been used for the analysis, the overall picture of the disturbance histories would have been incomplete and may have given inappropriate results. For example, if the sample had only observed plots with high and extreme severity, we would have concluded that high severity disturbances were prevailing in this forest. Or conversely, if the sample had only observed plots with light disturbances, the conclusion would have been that a patch disturbance regime prevailed. Therefore, our data support the conclusion that an extensive and balanced sampling design can better uncover the true complexity of the disturbance history of a forest.

Every new disturbance event overrides the evidence of the previous one, and therefore it is difficult to conduct retrospective studies of disturbance. The individual plots may have experienced a different severity in previous disturbance events, but we can only interpret the last most important event, which likely overrode the evidence of previous once (by killing trees), especially for recent heavy disturbances. These limitations should be taken into greater consideration during retrospective analysis of disturbance histories. However, it is difficult to interpret the main disturbance event of plots that only experienced light disturbances. Due to frequent singletree mortality, a single main event cannot be identified. Moreover, the area affected by past events is even more difficult to estimate (Shimatani and Kubota, 2011).

6.3. Impact of the disturbance legacies on ecosystem services

A deeper knowledge of disturbance legacy effects is needed to improve our understanding about the patterns and processes driving biomass development and the fate of primary forest ecosystems. Here we show the importance of simultaneously considering tree-level and stand-level dynamics to draw an improved picture of development and biomass accumulation over time in the investigated *Picea abies* (L.) Karst. forest ecosystems. We found that prolonged suppression did not reduce trees' potential to attain high growth rates after disturbance. Such trees, independently of their age, can thus follow high

trajectories of AGBI after a reduction in competition/canopy accession. Young, large spruce trees had greater rates than older trees of comparable size. At the stand level, sites that experienced minor canopy removal recovered 90% pre-disturbance AGB approximately twice as fast as those stands that experienced major canopy removal. While aboveground biomass generally increased through time, we found that both the time since disturbance and disturbance severity are important co-predictors for stand-level biomass accumulation rate and biomass pool size.

In our investigation of montane monotypic primary Norway spruce forests, we could partially support and partially refine the conclusions from Stephenson et al. (2014). While we found that mid-sized trees tended to have larger AGBI, we also found that the age of the tree, a potential constraint of tree growth not factored in Stephenson et al. (2014), strongly influences AGBI for a given tree size. Considering growth trends of individual trees separately, fewer than half of the trees showed a positive slope in AGBI after their DBH exceeded 30 cm. Furthermore, for those trees displaying a positive slope in AGBI, the slope was only 23% of that observed for small individuals (DBH < 20 cm). So, while we found growth increases in big spruce trees in these monotypic stands, the rate of growth increase was far lower than that observed for smaller trees.

We used a primary spruce forest to describe natural pathways of the AGB and AGBI dynamics based not only on time since disturbance, but also disturbance severity. We demonstrated that both the timing and severity of disturbance events influence pathways of AGB and AGBI in the primary mountain spruce forest. Higher disturbance event severity (>40% canopy removal) leads to greater AGBI for approximately 100 years after disturbances and a longer recovery time for living AGB. Such trends of the biomass dynamics are similar to those created by forest management systems oriented towards even-aged stands. Recovery time after severe disturbance events (defined here as regaining 90% of the maximum from fitted regression) fits well with the rotation period for even-aged managed forests in the study region (90–120 years). In addition, our study indicates, that 40–50 years is sufficient for the forest to

recover 90% AGB from a simultaneous loss of 20–40% of the canopy, as in group selection forest management (Misson et al., 2003; Nilsen and Strand, 2008).

We observed a strong relationship between lichen species richness and composition with both individual tree age and maximum tree age on a plot. Species richness increased linearly with tree age, which was augmented by the presence of old trees as micro-refuges for species colonization of surrounding trees. Nascimbene et al. (2010) observed species composition turnover on over-mature spruce trees. In our study, species colonizing relatively young trees were also able to survive on very old trees, which demonstrates accumulation of species over time and it underlines the critical role of age as a function of time for species colonization. Plots that had experienced extreme severity disturbances with no surviving trees and were currently by young trees (~ 80 years) were colonized only by the most common lichen species. The highest frequency of species was usually epiphytes that are non-selective with regards to host trees, those growing on other substrata, or those with frequent sexual dispersal or producing many small soredia, which is consistent with the findings of Johansson et al. (2012) and Juriado et al. (2006). However, even some of the most common species also displayed increasing frequency with tree age.

Heavy disturbances with survival of some trees were represented by events dating to approximately 100 years ago in this study. Although the vast majority of species were able to colonize trees about 100 years old, approximately two-thirds of the species occurred only in plots trees 200 years and older present. This is consistent with Johansson et al. (2013), who observed that 100-years old post-disturbance trees had become suitable for colonization by lichens from surrounding old trees in disturbed oak (*Quercus*) forests. We found a significant relationship to age of the oldest tree in *Bryoria nadvornikiana*, as well as *Loxospora elatina*, *Ochrolechia microstictoides*, and *Lepraria jackii*, which implies that the existence of old-trees as micro-refuges at the plot level are especially critical for species lacking sexual dispersal. We could not reliably test this hypothesis for extremely rare species, however, on the basis of their observed low colonization rate.

7. Conclusions

Findings in this thesis contribute to the scientific understanding of the past disturbance dynamic in the montane Norway spruce forests and impact of its legacies on ecosystem services. This thesis presents a comprehensive picture with particular emphasis on: i) efficacy of four dendroecological methods, ii) spatiotemporal dynamics of past disturbances, iii) impact of disturbances on aboveground biomass development and lichen diversity.

Our comparison of four commonly used methods of disturbance detection based on the analysis of tree-ring width series of trees from forests with well-documented disturbance events leads to three main considerations. First, we find that the temporal uncertainties produced when determining the date of growth release at the tree level create large uncertainties when reconstructing disturbance at the stand level. Second, parameter settings are among the most critical and still widely discussed issues in the disturbance detection methods analysed, as they can lead to the over- or underestimation of the disturbance events (Bouriaud and Popa, 2007; Copenheaver et al., 2014; Pederson et al., 2014; Rubino and McCarthy, 2004). Finally, our results indicate that a yearly binning approach to canopy disturbance could improve reconstructions of forest history and a better understanding of forest dynamics.

Central and Eastern Europe mountain spruce forest has been affected by series of mixed severity disturbances; especially during the 19th century. Disturbance legacies affect forest structure, development pathways and consequently susceptibility to new events. Those forests are under high probability to be disturbed in the near future, as a consequence of past disturbances and not only current climate change.

We observed remarkable spatiotemporal complexity in natural disturbances, which is likely impossible to precisely mimic through anthropogenic perturbations (Kuuluvainen, 2009). Nonetheless, mimicking natural disturbances through management can be used successfully in forests where species diversity and structural heterogeneity are the primary objectives. Heterogeneity on the plot-level is created through single disturbances while heterogeneity at the stand level is a result of a combination of different plot-level disturbances. Forest

management can thus model disturbances at the forest compartment level. Forest management compartments, which are commonly used by forestry enterprises, can represent the units affected by a single disturbance within the range of natural disturbance severities (Hanson and Lorimer, 2007; Seymour et al., 2002). In those units, management could be oriented to have a range of disturbance severities, targeting moderate canopy disturbances (Woods, 2004). If those compartments were spatially and temporally distributed, disturbance conditions approximating a mixed severity disturbance regime could be achieved.

Legacies of disturbance history influence both tree and stand-level biomass dynamics by changing local environmental conditions and levels of inter-tree competition. Trees growing in monotypic spruce forests followed a similar sigmoidal trajectory after canopy accession, regardless of age or prior duration of suppression. This finding supports physiological theories and suggests that trees in these types of forest structures might be competing for similar limiting factors. While stand characteristics (e.g., time since disturbance, existing biomass, etc.) can explain much of the variability in tree and stand-level aboveground biomass increment (AGBI) (Coomes et al., 2014; Michaletz et al., 2014), inclusion of the direct and indirect interactions with climatic and physiological factors, together with disturbance regimes, will be required for predictive models of biomass dynamics.

Persistence of old trees as micro-refuges after disturbances could help increase species biodiversity of many specialized epiphytic species, even in altered microclimates. We recommend the preservation of old-growth forest fragments in Europe without any post-disturbance management interventions; these areas would preserve existing habitats for uncommon lichen species and also act as a source to colonize surrounding forests.

8. Literature

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