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

Self-report on dissertation thesis

PRAGUE

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It is possible to read the dissertation thesis at the department of Science and Research, Faculty of Forestry and Wood Sciences, CULS Prague.

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 4.1); then ii) access spatiotemporal characteristics of disturbance regime on the plot, stand, landscape, and region level (section 4.2); and finally iii) evaluate the influence of natural disturbances on the magnitude and dynamics of biomass accumulation and maintaining lichen survival and diversity (section 4.3). 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 founding 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 4.1.1).

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 4.2.1 & 4.2.2). 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 feature (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 4.3.1). 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 4.3.2).

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.

Table of Contents

1. Introduction

Climate change is expected to alter disturbance regimes around the globe (Seidl et al., 2014). 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. 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 allow to advance 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 4.1.1).
2. Reconstruct the spatiotemporal pattern of past disturbances at different scales (plot, stand, and landscape) for Central (Slovakia) and Eastern (Ukraine) Europe (section 4.2.1. and 4.2.2).
3. Access 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 4.3.1).
5. Evaluate the importance of old trees as micro-refuges and microclimate stability in maintaining lichen survival and diversity (section 4.3.2).

3. Methods

3.1. Study area and data collection

Study was conducted in two distinct regions: New England, USA (section 4.1) and Carpathian mountain range (all other results).

3.1.1. 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 (Foster, 1988; Rowlands, 1941) 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 $\geq$ 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 $\geq$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 4.1.

3.1.2. 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. 3.1). 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 crystalinic (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 m^2 (500 m^2 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 4.2 and 4.3.

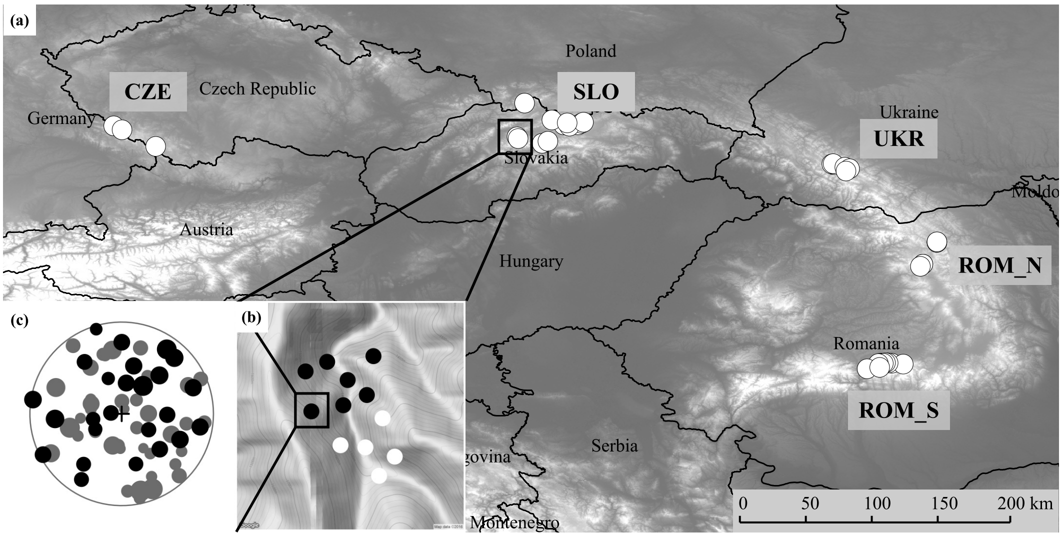

Fig. 3.1 Geographical location of the 37 study stand with 560 plots (0.1 ha each). B: example of the plot distribution within a stand. Black dots represent plots that experienced a disturbance event in the period 1900-1910. C: All trees within the plot were mapped (grey dots) and 25 randomly selected were cored (black dots). Source of digital elevation model: http://www.reverb.echo.nasa.gov and Google; country boundaries: http://www.diva-gis.org.

3.2. Data analysis

3.2.1. 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 jacknifed 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.

3.2.2. 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. 3.2): 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 4.1).

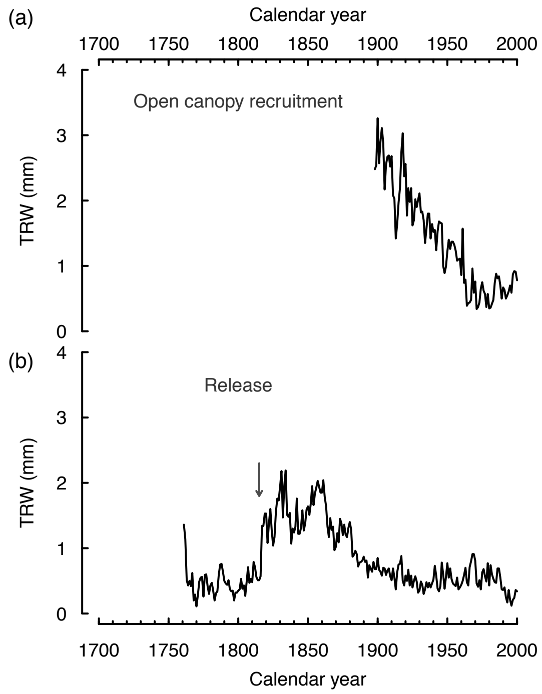

Fig. 3.2 Examples of trees categorized as recruited in the gap (a) and having a release after suppression (b). Release after suppression was identified using absolute increase method.

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. 3.3), 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).

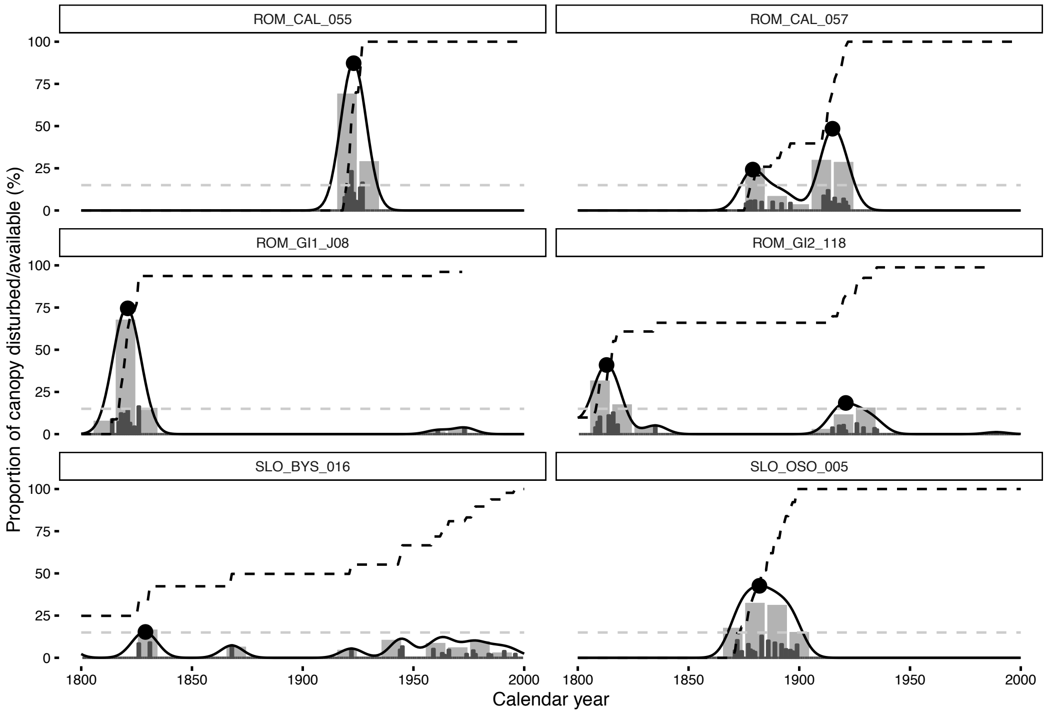

Fig. 3.3 Plot level disturbance history represented as proportion of the trees canopy area responded to disturbances binned by year (black bars) or decade (grey bars). Peaks of disturbances (solid circles) were identified based on the standardized density function (black line) for events with more than 15% of intensity. The dashed grey line shows available tree canopy area.

3.2.3. 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., 2014). 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.

4. 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 4.1). The second part aims at analysis the spatiotemporal dynamic of disturbances on the plot, stand, landscape and region levels (section 4.2). The third part presents an assessment of the impact of disturbance legacies on ecosystem services (section 4.3).

4.1. Dendroecological methods for reconstruction disturbance dynamic

4.1.1. 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.

Abstract:

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.

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.

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 ($p<0.001$).

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.

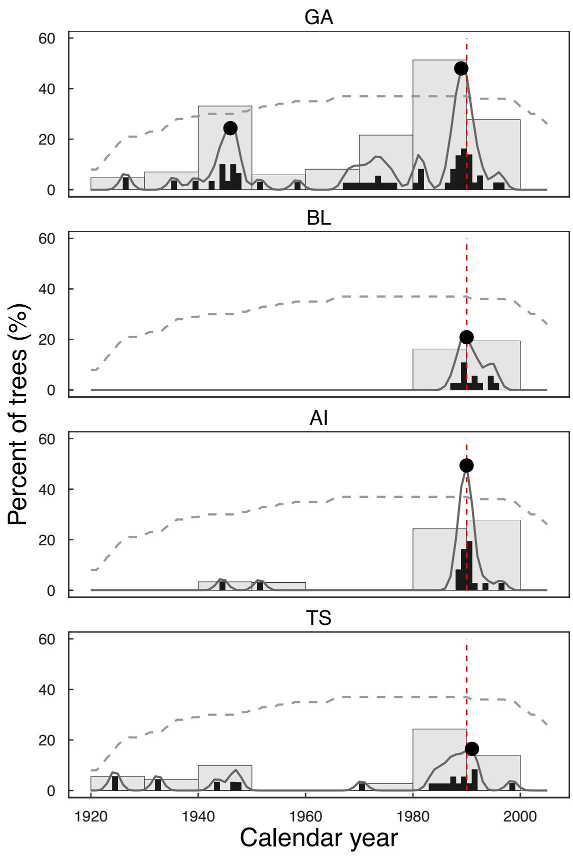

Fig. 4.1 Plot-level disturbance history in response to a simulated hurricane in 1990 (represented by the red line) at the hurricane pulldown experiment. The proportion of trees responding to disturbances is binned by year (black bars) and decade (grey bars).

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.

4.2. Disturbance dynamic in the natural forest landscapes

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

Published as:

Trotsiuk, V., Svoboda, M., Janda, P., Mikolas, M., Bace, R., Rejzek, J., Samonil, P., Chaskovskyy, O., Korol, M., Myklush, S., 2014. A mixed severity disturbance regime in the primary Picea abies (L.) Karst. forests of the Ukrainian Carpathians. Forest Ecology Management 334, 144–153.

Author contributions:

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.

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.

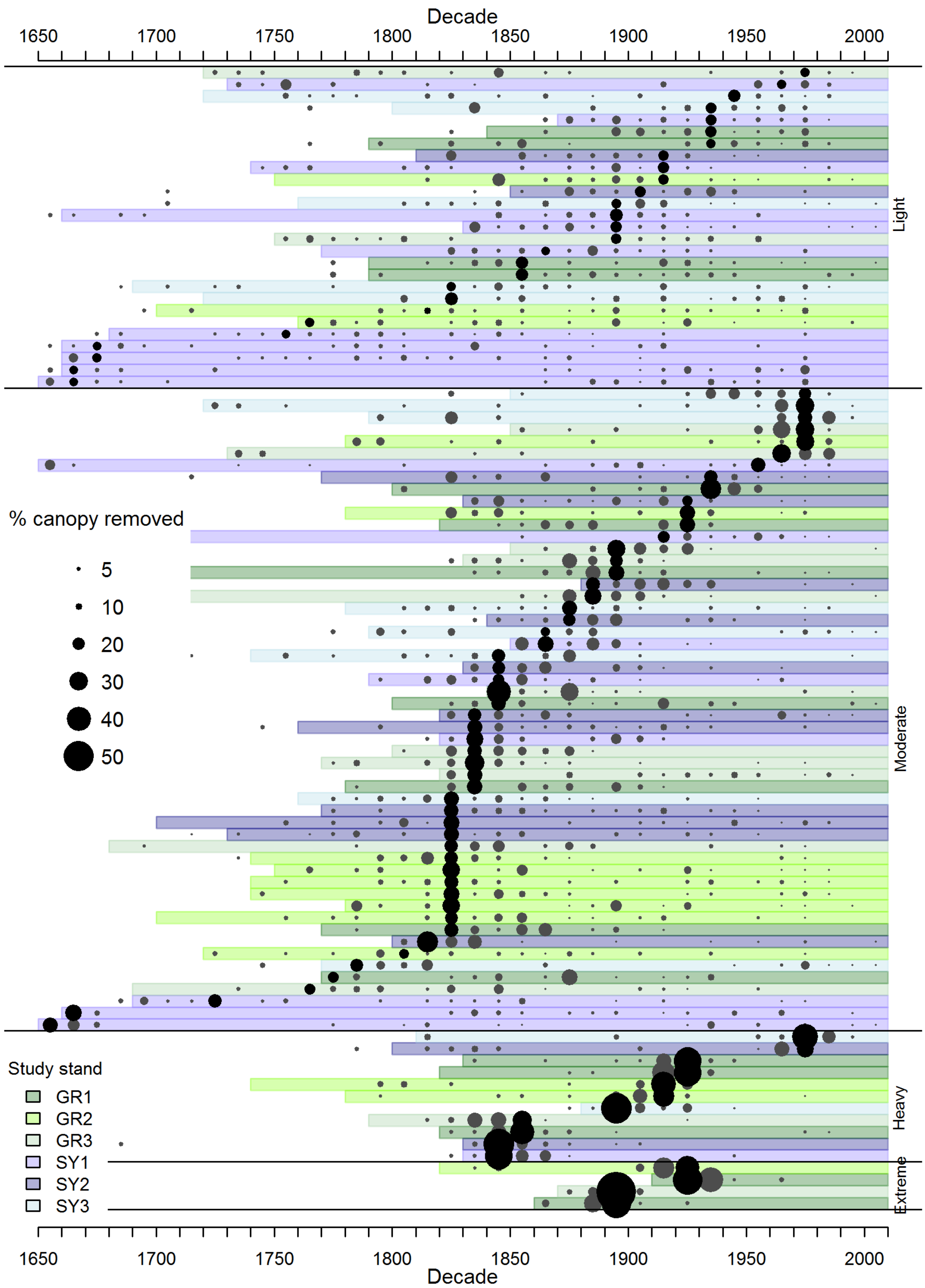

Fig. 4.2 Plot-level disturbance chronology. Each horizontal bar corresponds to one study plot, with the color of the studied stand. Size of the point represents the proportion (%) of the canopy area removed per decade. Black point show the midpoint of the decade in which each MDS event occurred. Plots are ordered by the time of the main disturbance event and horizontal bars were truncated when the percent of available canopy dropped below 10%.

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

Published as:

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

Author contributions:

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

P.J., V.T., M.M. M.J., J.V., H.M, J.L., L.M., and M.S. performed the sampling;

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

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.

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 m^2) 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.

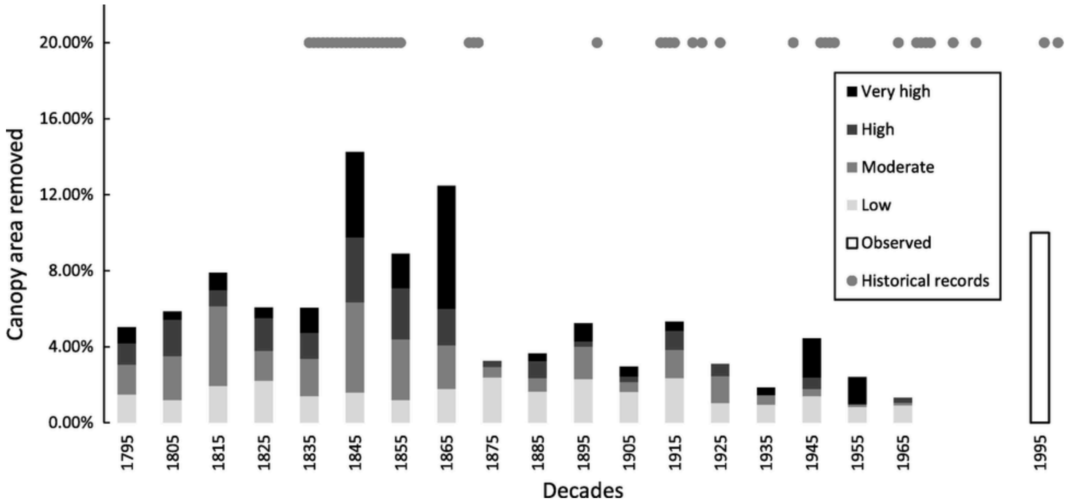

Fig. 4.3 The amount of canopy disturbed in the region over time, distributed over disturbance severity classes. The disturbance chronology was constructed using a three-decade running sum window of the percentage of canopy area disturbed. In the chronology we summed three decades, and the date of the 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. 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.

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

Submitted as:

Schurman, J. S.*, Trotsiuk, V.*, Bace R., Cada V., Fraver S., Janda P., Kulakowski D., Labusova J., Mikolas M., Nagel T., Seidl R., Svoboda M., Neglecting legacies of past forest disturbance overstates the climate effect on current disturbances. Global Change Biology

Author contributions:

* - both authors contributed equally (ordered by name);

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.

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.

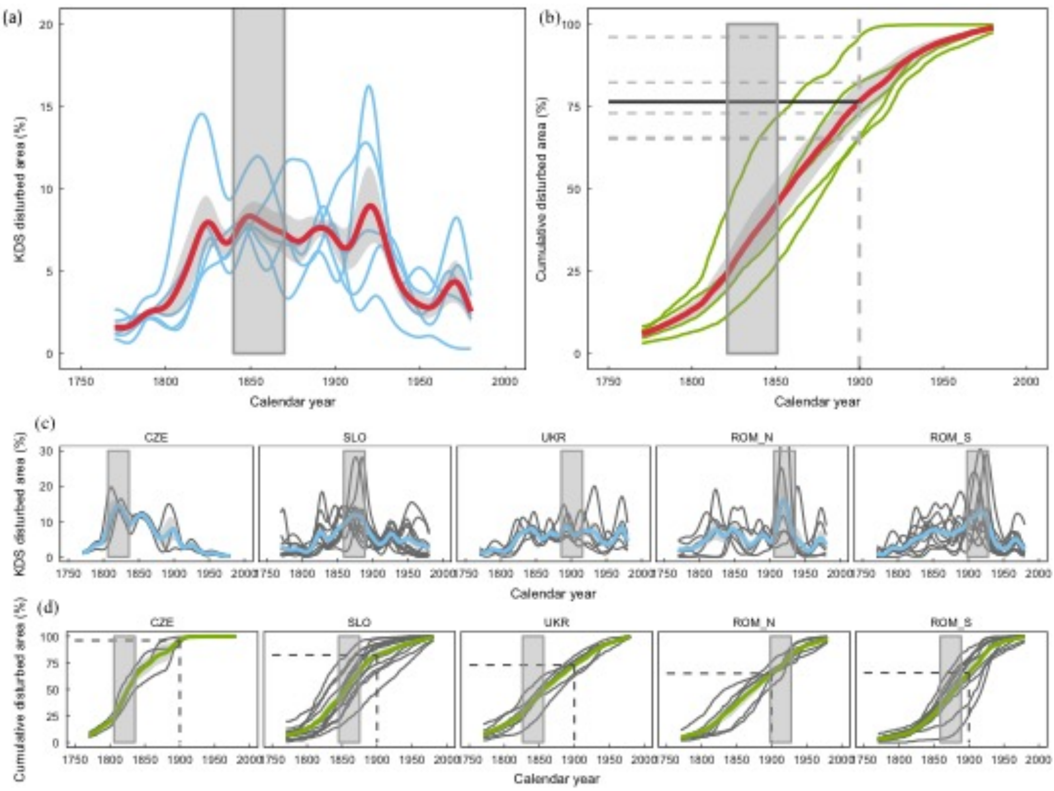

Fig. 4.4 Kernel density smoothed (KDS) disturbed areas and cumulative disturbance distributions. Mean regional disturbance (a, red line) with shaded standard error represents the KDS mean over each of the five landscapes (blue lines), which are each a mean over their respective stands (grey lines panel 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.

4.3. Impact of the disturbance legacies on ecosystem services

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

Published as:

Trotsiuk, V., Svoboda, M., Weber, P., Pederson, N., Klesse, S., Janda, P., Martin-Benito, D., Mikolas, M., Seedre, M., Bace, R., Mateju, L., Frank, D., 2016. The legacy of disturbance on individual tree and stand-level aboveground biomass accumulation and stocks in primary mountain Picea abies forests. Forest Ecology Management 373, 108–115

Author contributions:

V.T., M.S., P.W., and D.F. conceived ideas and designed the study;

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

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.

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 m^2) 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 hypothesize 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 rv225% 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 ca. 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.

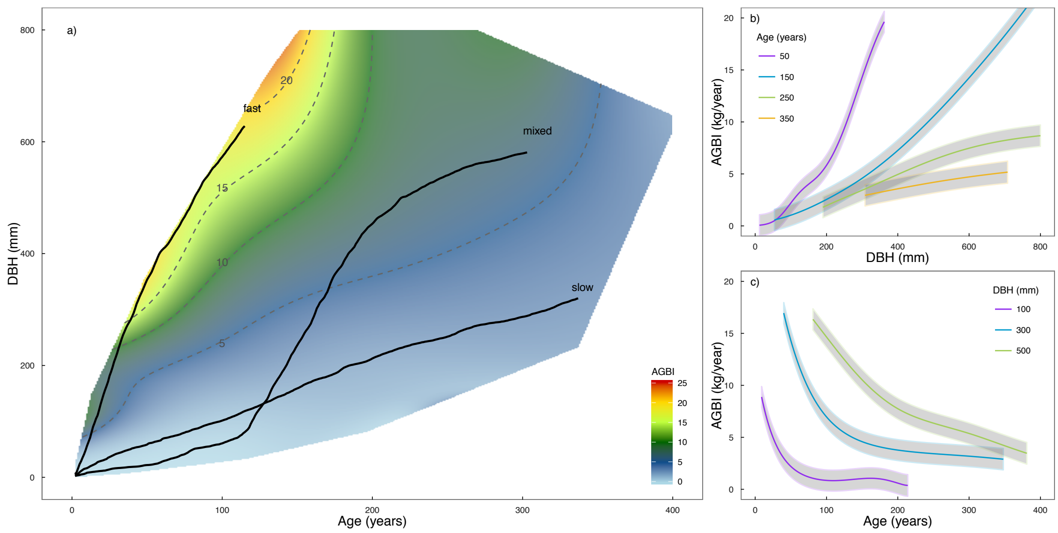

Fig. 4.5 Predicted aboveground biomass increment (AGBI) from generalized additive mixed model based on the ca. 342,000 yearly resolved tree DBH, Age and their interaction (a). Black lines show examples of growth trajectories and change in AGBI during lifespan for selected trees. AGBI is significantly higher for younger trees within same DBH class (b), and larger trees within same Age class (c).

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

Published as:

Zemanova, L., Trotsiuk, V., Morrisey, R.C., Bače, R., Mikoláš, M., Svoboda, M., 2017. Old trees as a key source of epiphytic lichen persistence and spatial distribution in mountain Norway spruce forests. Biodiversity and Conservation.

Author contributions:

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;

L.Z. and M.S. wrote the manuscript and all authors commented on it.

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* (L.) Karst.) forests of the Gorgany Mountains of the Ukrainian Carpathian mountain belt. Lichens were collected on 13 circular study plots (1000 m^2).

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.

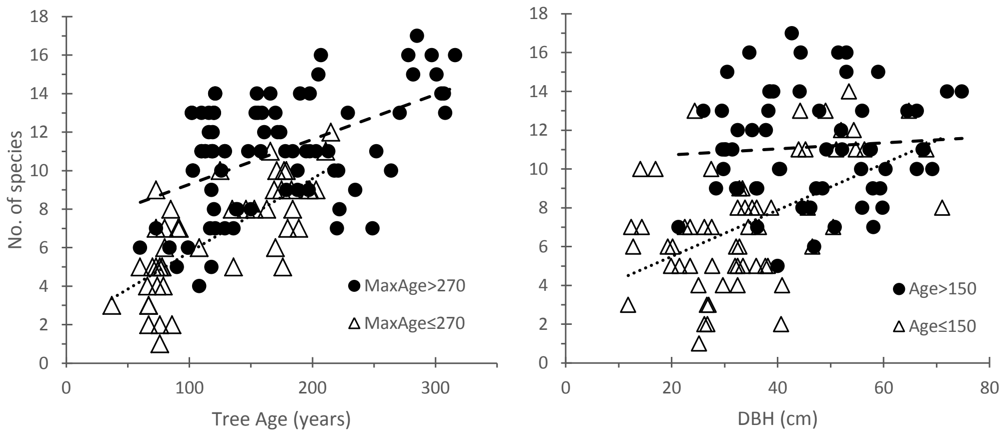

Fig. 4.6 Relation between the number of lichen species and individual tree age, age of the oldest tree per plot, and tree diameter (DBH); left panel – number of species per tree (y-axis) along tree age gradient (x-axis) split into two intervals of MaxAge (empty triangles – trees from plots in which the 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).

5. 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 feature, 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.

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7. Curriculum Vitae

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Education:

- *October 2013 – September 2017.* PhD student, Czech University of Life Science, Prague.
- *September 2009 – February 2011.* MSc with honors in Forestry. National Forestry University in Ukraine. Master thesis: "Age structure of beech dominated forest in the Uholka-Shyrokuy Lyh massif Carpathian biosphere reserve".
- *September 2009 – June 2010.* Attended MSc course in Sustainable Forest and Nature Management (Euroforester program), Swedish University of Agricultural Science, Sweden.
- *2005-2009.* BSc with honours in Forestry, Garden and Park service. National Forestry University, Ukraine.

International fellowship and training:

- *September-October 2015.* Research fellow in Harvard Forest University, USA.
- *September 2013 – August 2014.* SCIEX fellowship, Swiss Federal Institute of Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland.
- *July 2011 – January 2012.* Internship in dendrochronological methods and analysis. Swiss Federal Institute of Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland.
- *March 2011 – June 2011.* Scientific guest at Swiss Federal Institute of Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland.
- *March 2011.* Course on writing scientific English, Swiss Federal Institute of Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland.
- *October-December 2010.* Training in dendrochronological analysis and it applications. Swiss Federal Institute of Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland.

Projects:

- *2016.* Spatiotemporal synchrony in episodic disturbances in Primary Norway spruce forest across Europe: legacies and consequences, Scientific Excellence FFWS CULS.
- *2015-2017.* Mixed severity disturbances as drivers of structural variability, carbon dynamics, and biodiversity at the stand and landscape levels in primary Picea abies (L.) Karst. forests in Central and Eastern Europe, CAGR P504/10/1644.
- *2015-2017.* Dynamics, structure and biodiversity in mountain spruce (Picea abies (L.) Karst.) forests in Central and Eastern Europe, CIGA 20154316.

- *2015.* Unifying tree-ring methods for reconstructing disturbance dynamics, NOVUS 2015.
- *2015-2016.* Dynamika biomasy a růstu na úrovni buňky, stromu a porostu ve vztahu k historii disturbancí a podmínkám prostředí, IGA B02/15.
- *2013-2014.* Life history of Fagus sylvatica and Picea abies: exploring and testing dendroecological methods (TreeLife), SCIEX-NMS 12.255.

Awards:

- *2014-2016.* Czech University of Life Sciences. Rector award for the best student publication performance (second, fifth and fourteen places).

Teaching:

- *January-February 2015 & 2016.* An introduction to R and R-studio. Czech University of Life Science, Prague.
- *May 19-20 2014.* Scientific visualization using R, Swiss Federal Institute of Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland. Course leading by Jan Wunder.

8. Publications

WOS (due to 07.2017)**:** publications – 14; h-index – 4; citations – 112

Google Scholar (due to 07.2017)**:** publications – 16; h-index – 8; citations – 230

- **Publications with Impact factor** (due to 07.2017, in alphabetical order)**:**

1. Anderegg, W.R.L., Martinez-Vilalta, J., Cailleret, M., Camarero, J.J., Ewers, B.E., Galbraith, D., Gessler, A., Grote, R., Huang, C.-Y., Levick, S.R., Powell, T.L., Rowland, L., Sánchez-Salguero, R., Trotsiuk, V. When a Tree Dies in the Forest: Scaling Climate-Driven Tree Mortality to Ecosystem Water and Carbon Fluxes (2016) Ecosystems, 19 (6), pp. 1133-1147.
2. Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Čada, V., Camarero, J.J., Cherubini, P., Cochard, H., Coyea, M.R., Čufar, K., Das, A.J., Davi, H., Delzon, S., Dorman, M., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hartmann, H., Hereş, A.-M., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Kramer, K., Lens, F., Levanic, T., Linares Calderon, J.C., Lloret, F., Lobo-Do-Vale, R., Lombardi, F., López Rodríguez, R., Mäkinen, H., Mayr, S., Mészáros, I., Metsaranta, J.M., Minunno, F., Oberhuber, W., Papadopoulos, A., Peltoniemi, M., Petritan, A.M., Rohner, B., Sangüesa-Barreda, G., Sarris, D., Smith, J.M., Stan, A.B., Sterck, F., Stojanović, D.B., Suarez, M.L., Svoboda, M., Tognetti, R., Torres-Ruiz, J.M., Trotsiuk, V., Villalba, R., Vodde, F., Westwood, A.R., Wyckoff, P.H., Zafirov, N., Martínez-Vilalta, J. A synthesis of radial growth patterns preceding tree mortality (2017) Global Change Biology, 23 (4), pp. 1675-1690.
3. Janda, P., Trotsiuk, V., Mikoláš, M., Bače, R., Nagel, T.A., Seidl, R., Seedre, M., Morrissey, R.C., Kucbel, S., Jaloviar, P., Jasík, M., Vysoký, J., Šamonil, P., Čada, V., Mrhalová, H., Lábusová, J., Nováková, M.H., Rydval, M., Matějů, L., Svoboda, M. The historical disturbance regime of mountain Norway spruce forests in the Western Carpathians and its influence on current forest structure and composition (2017) Forest Ecology and Management, 388, pp. 67-78.
4. Mikoláš, M., Svoboda, M., Pouska, V., Morrissey, R.C., Donato, D.C., Keeton, W.S., Nagel, T.A., Popescu, V.D., Müller, J., Bässler, C., Knorn, J., Rozylowicz, L., Enescu, C.M., Trotsiuk, V., Janda, P., Mrhalová, H., Michalová, Z., Krumm, F., Kraus, D. Comment on "opinion paper: Forest management and biodiversity": The role of protected areas is greater than the sum of its number of species (2014) Web Ecology, 14 (1), pp. 61-64.
5. Novák, J., Trotsiuk, V., Sýkora, O., Svoboda, M., Chytrý, M. Ecology of Tilia sibirica in a continental hemiboreal forest, southern Siberia: An analogue of a glacial refugium of broad-leaved temperate trees? (2014) Holocene, 24 (8), pp. 908-918.
6. Primicia, I., Camarero, J.J., Janda, P., Čada, V., Morrissey, R.C., Trotsiuk, V., Bače, R., Teodosiu, M., Svoboda, M. Age, competition, disturbance and elevation effects on tree and stand growth response of primary Picea abies forest to climate (2015) Forest Ecology and Management, 354, pp. 77-86.

7. Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyer, C.P.O. Forest disturbances under climate change (2017) Nature Climate Change, 7 (6), pp. 395-402.
8. Svoboda, M., Janda, P., Bače, R., Fraver, S., Nagel, T.A., Rejzek, J., Mikoláš, M., Douda, J., Boublík, K., Šamonil, P., Čada, V., Trotsiuk, V., Teodosiu, M., Bouriaud, O., Biriş, A.I., Sýkora, O., Uzel, P., Zelenka, J., Sedlák, V., Lehejček, J. Landscape-level variability in historical disturbance in primary Picea abies mountain forests of the Eastern Carpathians, Romania (2014) Journal of Vegetation Science, 25 (2), pp. 386-401.
9. Trotsiuk, V., Svoboda, M., Weber, P., Pederson, N., Klesse, S., Janda, P., Martin-Benito, D., Mikolas, M., Seedre, M., Bace, R., Mateju, L., Frank, D. The legacy of disturbance on individual tree and stand-level aboveground biomass accumulation and stocks in primary mountain Picea abies forests (2016) Forest Ecology and Management, 373, pp. 108-115.
10. Trotsiuk, V., Svoboda, M., Janda, P., Mikolas, M., Bace, R., Rejzek, J., Samonil, P., Chaskovskyy, O., Korol, M., Myklush, S. A mixed severity disturbance regime in the primary Picea abies (L.) Karst. forests of the Ukrainian Carpathians (2014) Forest Ecology and Management, 334, pp. 144-153.
11. Trotsiuk, V., Hobi, M.L., Commarmot, B. Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians) (2012) Forest Ecology and Management, 265, pp. 181-190.
12. Zemanová, L., Trotsiuk, V., Morrissey, R.C., Bače, R., Mikoláš, M., Svoboda, M. Old trees as a key source of epiphytic lichen persistence and spatial distribution in mountain Norway spruce forests (2017) Biodiversity and Conservation, 26 (8), pp. 1943-1958.

- **Publications in Scopus data base** (due to 07.2017, in alphabetical order)**:**

13. Cook, E.R., Seager, R., Kushnir, Y., Briffa, K.R., Büntgen, U., Frank, D., Krusic, P.J., Tegel, W., van der Schrier, G., Andreu-Hayles, L., Baillie, M., Baittinger, C., Bleicher, N., Bonde, N., Brown, D., Carrer, M., Cooper, R., Čufar, K., Dittmar, C., Esper, J., Griggs, C., Gunnarson, B., Günther, B., Gutierrez, E., Haneca, K., Helama, S., Herzig, F., Heussner, K.-U., Hofmann, J., Janda, P., Kontic, R., Köse, N., Kyncl, T., Levanič, T., Linderholm, H., Manning, S., Melvin, T.M., Miles, D., Neuwirth, B., Nicolussi, K., Nola, P., Panayotov, M., Popa, I., Rothe, A., Seftigen, K., Seim, A., Svarva, H., Svoboda, M., Thun, T., Timonen, M., Touchan, R., Trotsiuk, V., Trouet, V., Walder, F., Ważny, T., Wilson, R., Zang, C., 2015. Old World megadroughts and pluvials during the Common Era. Sci. Adv. 1. doi:10.1126/sciadv.1500561
14. Mrhalová, H., Trotsiuk, V., Svoboda, M., Janda, P., Bače, R., Cada, V., Mikoláš, M. Canopy accession strategies of norway spruce (Picea abies (L.) Karst.) in primeval mountain forests of Calimani and Giumalau, Romania [Strategie dosažení horního stromového patra smrku ztepilého (Picea abies (L.) Karst.) v přirozených lesích Rumunska] (2015) Zpravy Lesnickeho Vyzkumu, 60 (3), pp. 211-217.

15. Weber, P., Heiri, C., Lévesque, M., Sanders, T., Trotsiuk, V., Walthert, L. Growth potential and climate sensitivity of tree species in the ecogram for the colline and sub montane zone [Zuwachs und Klimasensitivität von Baumarten im Ökogramm der kollinen und submontanen Stufe] (2015) Schweizerische Zeitschrift fur Forstwesen, 166 (6), pp. 380-388.