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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 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.

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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., this issue). 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 (Frelich, 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., this issue; 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; Szewczyk 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

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