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More ways than one: Mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways

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ABSTRACT

Mixed-severity disturbance regimes are prevalent in temperate forests worldwide, but key uncertainties remain regarding the variability of disturbance-mediated structural development pathways. This study investigates the influence of disturbance history on current structure in primary, unmanaged Norway spruce (*Picea abies*) forests throughout the Carpathian Mountains of central and eastern Europe, where windstorms and native bark beetle outbreaks are the dominant natural disturbances. We inventoried forest structure on 453 plots (0.1 ha) spanning a large geographical gradient (> 1,000 km), coring 15–25 canopy trees per plot for disturbance history reconstruction (tree core total n = 11,309). Our specific objectives were to: (1) classify sub-hectare-scale disturbance history based on disturbance timing and severity; (2) classify current forest structure based on tree size distributions (live, dead, standing, downed); (3) characterize structural development pathways as revealed by the association between disturbance history and current forest structural complexity. We used hierarchical cluster analysis for the first two objectives and indicator analysis for the third. The disturbance-based cluster analysis yielded six groups associated with three levels of disturbance severity (low, moderate, and high canopy loss) and two levels of timing (old, recent) over the past 200 years. The structure-based cluster analysis yielded three groups along a gradient of increasing structural complexity. A large majority of plots exhibited relatively high (53%) or very high (26%) structural complexity, indicated by abundant large live trees, standing and downed dead trees, and spruce regeneration. Consistent with conventional models of structural development, some disturbance history groups were associated with specific structural complexity groups, particularly low-severity/recent (very high complexity) and high-severity/recent (moderate complexity) disturbances. In other cases, however, the distribution of plots among disturbance history and structural complexity groups indicated either divergent or convergent pathways. For example, multiple disturbance history groups were significantly associated with the high complexity group, demonstrating structural convergence. These results illustrate that complex forest structure – including features nominally associated with old-growth – can be associated as much with disturbance severity as it is with conventional notions of forest age. Because wind and bark beetles are natural disturbance processes that can induce relatively high levels of tree mortality while simultaneously contributing to structural complexity and heterogeneity, we suggest that forest management plans allow for the stochastic occurrence of disturbance and variable post-disturbance development trajectories. Such applications are especially appropriate in conservation areas where biodiversity and forest resilience are management objectives, particularly given projections of increasing disturbance activity under global change.

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1. Introduction

Forest ecosystems are inherently dynamic, shaped by natural and anthropogenic disturbances operating at multiple scales across space and time (*e.g.,* Kashian et al., 2005; Lorimer and Halpin, 2014). Recognizing the importance of managing for change, contemporary forest management activities increasingly seek to emulate natural disturbance regimes and promote structural complexity (Drever et al., 2006; North and Keeton, 2008; Bauhus et al., 2009). Quantifying the patterns and processes of natural disturbances thus is vital for conserving biodiversity and ecosystem services, particularly given projections of increasing disturbance frequency and/or severity under global change (*e.g.,* Dale et al., 2001; Turner, 2010; Kulakowski et al., 2017). Recent research has highlighted the importance of mixed-severity disturbance regimes in temperate forests (Halofsky et al., 2011; Perry et al., 2011; Reilly and Spies, 2015), but the degree to which disturbance severity and timing contribute to divergence or convergence in forest structure over time remains unclear (Kashian et al., 2005). This study investigates the influence of disturbance history on contemporary forest structure in a mountainous landscape shaped by a mixed-severity disturbance regime, the Carpathian Mountains of central and eastern Europe.

Rather than traditional binary classifications of infrequent, stand-replacing versus frequent, gap-forming disturbances (Seymour, 2005), recent studies and management initiatives have focused on the full continuum of disturbance timing and severity, particularly intermediate-severity disturbance in temperate and boreal forests (Woods, 2004; Hanson and Lorimer, 2007; Stueve et al., 2011; Tepley et al., 2013; Nagel et al., 2014; Čada et al., 2016). These mixed-severity systems are characterized by high temporal and spatial variability of disturbance extent, frequency, and severity (e.g., tree mortality), which collectively influence forest structure and function in complex ways (Perry et al., 2011; Tepley et al., 2013; Nagel et al., 2017; Reilly et al., 2017). Such complexity poses significant hurdles for forest ecosystem management aimed at emulating natural dynamics. Because much of the recent literature on mixed-severity disturbance comes from ecosystems dominated by fire disturbances (*e.g.,* Hjelmfelt, 2010; Halofsky et al., 2011; Dunn and Bailey, 2016; Johnston et al., 2016), this challenge is particularly acute for relatively mesic forests where windstorms and insect outbreaks are more prevalent. Primary Norway spruce [*Picea abies* (L.) Karst.] forests of the Carpathian Mountains, a region affected by stand-replacing fire to a lesser degree than other temperate regions (Feurdean et al., 2017), represent an excellent opportunity to elucidate general properties of mixed-severity disturbance regimes, particularly in the context of structural development and complexity.

Indeed, although structural complexity has emerged recently as a key objective of sustainable forest management (McElhinny et al., 2005; Keeton, 2006; Bauhus et al., 2009), conventional conceptual frameworks of forest structural development do not address complexity explicitly, nor do they encompass the full gradient of disturbance variability. Instead, conventional frameworks typically invoke time since stand-replacing disturbance and depict the development of uniform, high-density stands into structurally complex stands driven by gap-dynamics (*e.g.,* Oliver and Larson, 1996; Franklin et al., 2002) (Fig. 1). In addition, previous studies have suggested that long time periods are required to increase structural complexity in temperate forests, including key elements like large trees (Lutz et al., 2012), diversity of gap sizes (Seymour et al., 2002), vertical diversification of canopy layers (Franklin and Van Pelt, 2004), and large deadwood of variable decay stage (Spies et al., 1988) (Fig. 1). More recent studies have emphasized early emergence of structural complexity and heterogeneity (Donato et al., 2012) and multiple, nonlinear pathways of structural development and resilience (*e.g.,* Lorimer and Halpin, 2014; Reilly and Spies, 2015; Halpin and Lorimer, 2016). However, key uncertainties remain regarding the influence of variable disturbance severity and timing on forest structural complexity, particularly in mixed-severity systems (Svoboda et al., 2014). Importantly, non-stand-replacing disturbances of moderate or low severity can accelerate key processes of structural development (Abrams and Scott, 1989). For example a single event could compress decades' worth of endogenous tree mortality, generating dead wood, opening forest canopies, and releasing understory vegetation sooner than would otherwise have occurred. Alternatively, disturbances can produce fundamentally different pathways and structural outcomes, or even reverse structural development if sufficiently frequent or severe (Frelich and Lorimer, 1991b; Halpin and Lorimer, 2016). Moreover, feedbacks between disturbance patterns and forest structure can have persistent effects on forest development and ecosystem memory across multiple scales (Johnstone et al., 2016; Jõgiste et al., 2017). Forest managers may benefit from new conceptual frameworks articulating natural disturbance effects on structural complexity across a broader range of disturbance timing and severity.

In recent decades, windstorms have affected Norway spruce forests throughout Europe (Schelhaas et al., 2003), and outbreaks of the native European spruce bark beetle (*Ips typographus*) often have followed (Schelhaas et al., 2003; Janda et al., 2017). An apparent trend towards increasing disturbance severity highlights the need to understand the consequences of disturbance variability for forest structural development (Seidl et al., 2011; Kulakowski et al., 2017). Although Carpathian spruce forests traditionally have been characterized as relatively low-severity, canopy gap driven systems (*e.g.,* Korpel', 1995), recent research highlights the predominance of mixed-severity disturbance regimes exhibiting variable disturbance timing, severity, and pulsed regeneration (Svoboda et al., 2014; Trotsiuk et al., 2014; Janda et al., 2017). Wide variation in disturbance severity, coupled with the essentially monospecific composition of these forests, provides an ideal setting for analyzing relationships between disturbance and structure without the potentially confounding effect of interspecific competition (Coomes et al., 2012). This study focuses on remote, remnant primary Norway spruce forests, leveraging extensive inventory plots and intensive dendroecological analyses. Building on prior studies that quantify mixed-severity disturbance regimes at broader spatiotemporal scales (Svoboda et al., 2014; Trotsiuk et al., 2014; Janda et al., 2017), we assess the influence of localized (sub-hectare) disturbance severity and timing on the development of structural complexity. Our specific objectives were to: (1) classify sub-hectare scale disturbance history based on natural disturbance timing and severity; (2) classify current forest structure based on tree size distributions (live and dead, standing and downed); (3) characterize structural development pathways as revealed by the association between disturbance history and current forest structural complexity. We used hierarchical cluster analysis for the first two objectives and indicator analysis for the third. We hypothesized that: (1) some forests would exhibit a structural development pathway consistent with *conventional* models (*i.e.,* more severely/recently disturbed plots associated with lower structural complexity due to reduction of large trees and other late successional elements) and (2) other forests would exhibit *divergent* pathways (a given disturbance history associated with multiple current structures) or *convergent* pathways (multiple disturbance histories associated with a given current structure).

2. Methods

2.1. Study area

The study area spans the Carpathian Mountain Range in central and eastern Europe, encompassing a broad range of latitude (45–50°N) and longitude (19–25°E) (Fig. 2). The region is characterized by a temperate continental climate, with increasingly continental climate conditions from west to east. Mean annual precipitation ranges from ~800 mm at lower elevations to ~2,000 mm at higher elevations, and mean annual temperature is approximately 3 °C at mid-elevations (UNEP, 2007;