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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;

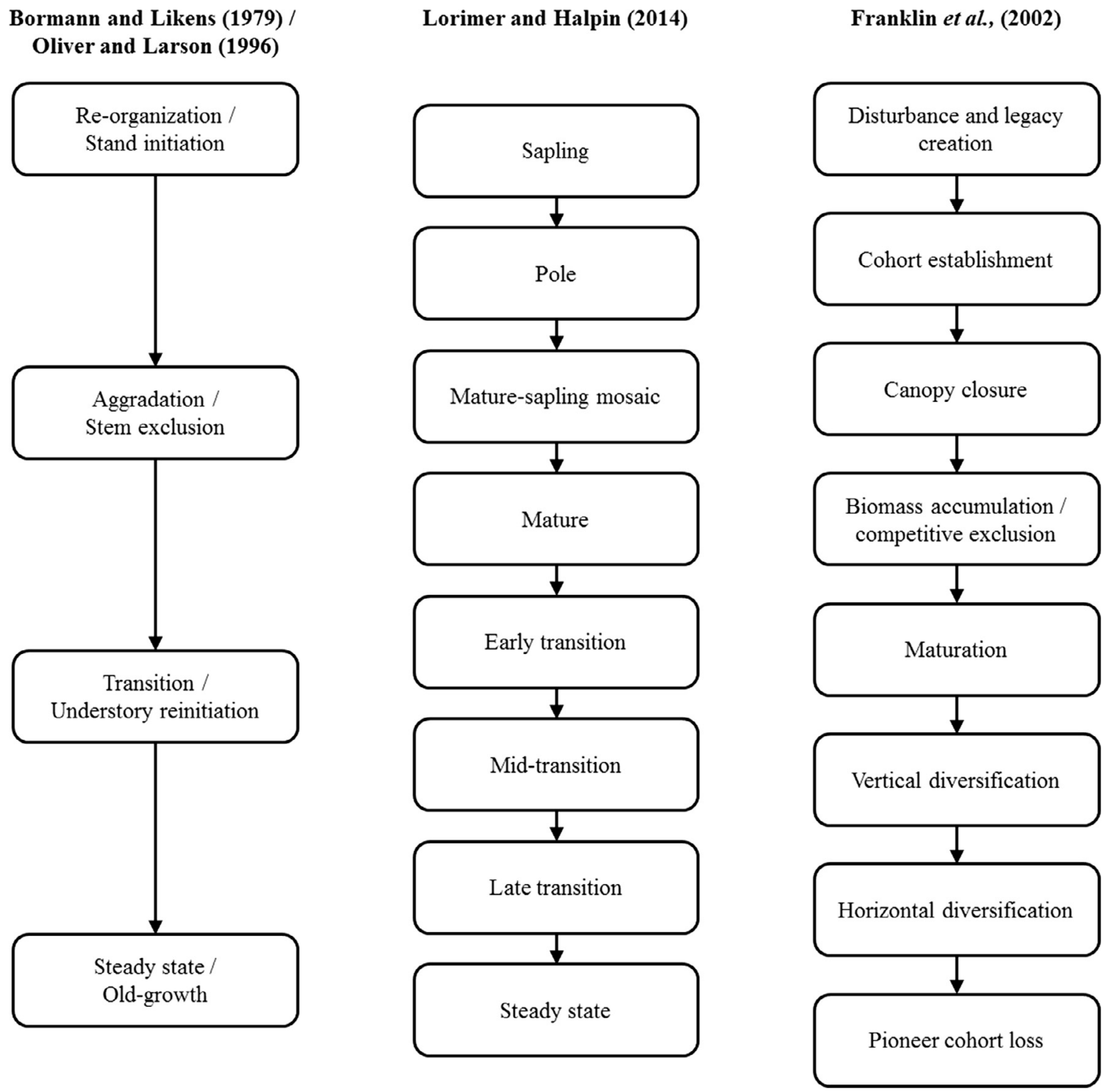

Fig. 1. Example conceptual frameworks characterizing forest structural stages. See References for detailed citations.

Appendix A). Local climatic conditions are influenced by topography and elevation, which ranges from 1,217 m to 1,713 m at study plots (Appendix A). Carpathian soil types and textures vary from site to site in association with local topography and mountain conditions within and among study sub-regions (Appendix A).

Despite a long history of human occupation, some of the largest tracts of remaining primary forests of Europe occur within the Carpathian Mountains (Veen et al., 2010). Although very rare in a regional context, these forests support an estimated 30% of all plant species in Europe (many of which are endemic and persist in a mosaic of forest and non-forest communities), large carnivore populations (including brown bear, wolf, and lynx), and many rare specialist species associated with old-growth forest structure (UNEP, 2007). Based on total basal area, Norway spruce was the dominant tree species (96.9%), with minor components of *Pinus cembra* L. (1.4%), and, in declining order of importance, *Abies alba* Mill., *Sorbus aucuparia* L., *Acer pseudoplatanus* L., *Fagus sylvatica* L., *Betula pubescens* Ehrh., *Populus* spp., *Salix caprea* L., *Pinus sylvestris* L., *Larix decidua* Mill., *and Ulmus* spp., which collectively accounted for 1.7% of total basal area. Although these forests are in remote locations with minimal anthropogenic disturbance for at least the past 150 years, they have been influenced by various natural disturbances. Windstorms, often followed by outbreaks of the native European spruce bark beetle (*Ips typographus*), are the most important natural disturbances in the region, causing tree mortality and regeneration responses at multiple spatial and temporal scales (Svoboda et al., 2014; Trotsiuk et al., 2014; Janda et al., 2017; Kulakowski et al., 2017).

2.2. Data collection

We sampled 453 plots in 31 areas of primary forests located across four sub-regions of the Carpathian Mountains: northern Romania (n = 93; Svoboda et al., 2014), southern Romania (n = 118), Slovakia (n = 145; Janda et al., 2017), and Ukraine (n = 98; Trotsiuk et al., 2014) (Fig. 2, Appendix A). Data from the southern Romania plots have not been published previously, and this is the first assessment combining all four sub-regions to assess the association between disturbance history and current forest structure across such an extensive area (> 1,000 km). Within each forest area, we established plots using a stratified-random design targeting the full distribution of primary forest conditions, including recently disturbed locations (Svoboda et al., 2014). Prior to sampling, we used GIS to overlay a grid over each area with cell sizes of either one or two hectares depending on stand area. We randomly assigned plots to the interior of cells (0.25 hectares or 0.49 hectares, respectively), basing the grid cell size on the total estimated size of each area. We established circular inventory plots,

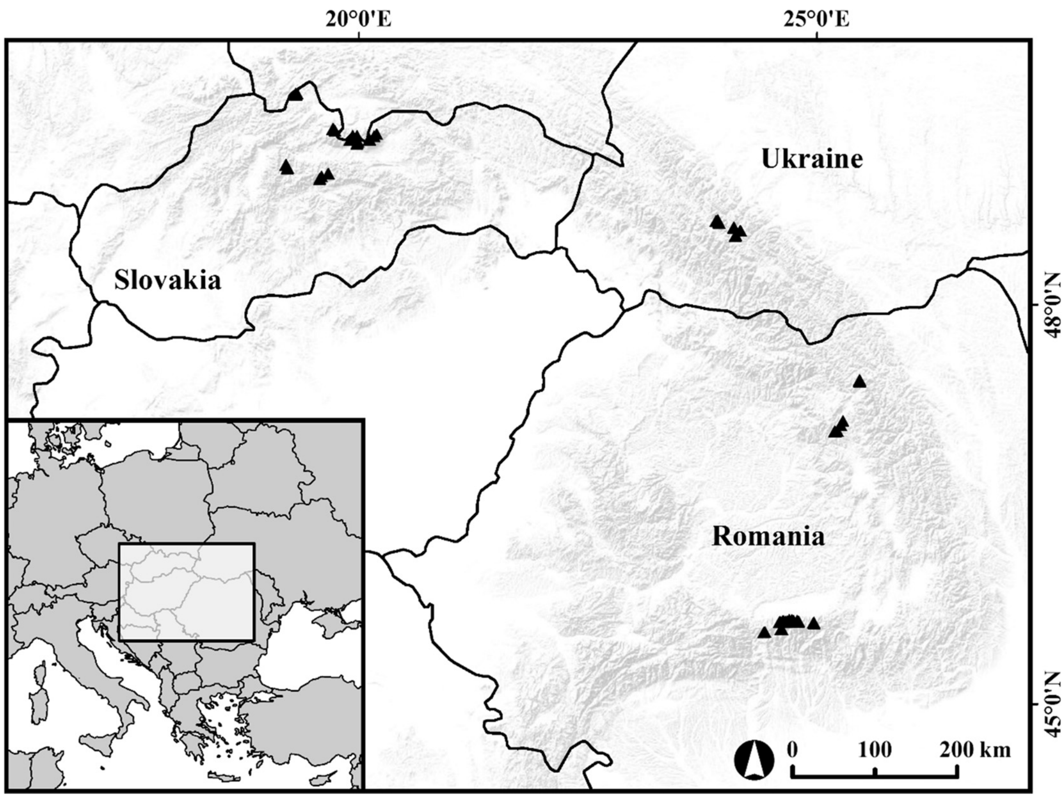

Fig. 2. Study region map showing sample plot locations (black triangles) across the Carpathian Mountain Range. We sampled forest plots (n = 453) in Slovakia, Ukraine, and Romania (see Methods and Appendix A for details). Inset map shows location within central and eastern Europe. Basemap service layers from ESRI, NOAA, and USGS.

recording location, elevation, aspect, slope, and slope position. Plot sample area was either 1,000 m^2 (0.1 ha; 17.84 m radius; n = 391) or 500 m^2 (12.62 m radius; n = 63) depending on live tree density (*i.e.,* smaller plots in higher density forests).

Our analyses and interpretations focus primarily on disturbance history and structure at the plot scale, recognizing that the inherent trade-off between plot size and number results in plots that are relatively small compared to tree heights and stand-scale disturbance dynamics. Because disturbance effects are heterogeneous, particularly in mixed-severity regimes, individual plots may exhibit either total canopy mortality or survival in a disturbance event that would be classified as moderate severity at a stand scale. Randomized locations and a large sample size ensure that our plots capture a wide range of conditions, and we emphasize relative differences among plots rather than absolute values of disturbance and structural attributes.

At each plot, we created stem maps for all trees with diameter at breast height (DBH) ≥10 cm, recording species, DBH, and live/dead status. We tallied all trees < 10 cm DBH within the plot in two height classes: seedlings were ≤1.3 m tall, and saplings were > 1.3 m tall and < 10 cm in DBH. Recognizing that seedling and sapling definitions vary among studies, our main focus was to contrast structural conditions among plots within this study rather than comparison with density estimates from other studies. We also measured crown projection in four cardinal directions of five randomly selected trees for disturbance history reconstruction (see Section 2.3). We surveyed downed deadwood using the line intersect method (Harmon and Sexton, 1996) based on five transects 20 m in length, tallying dead pieces ≥10 cm in diameter. Downed deadwood and tree regeneration seedlings were not recorded for some plots in northern Romania (n = 81).

2.3. Disturbance history reconstruction

We cored 25 or 15 randomly selected, non-suppressed trees within the 1,000 m^2 and 500 m^2 plots, respectively. For each tree, we extracted a single core at one meter above ground level to evaluate age, growth, and disturbance history. We mounted and sanded tree cores (n = 11,309) following standard procedures (Stokes and Smiley, 1996). Cores intersected the pith in 66% of trees, and an additional 32% were within 1 cm of the pith. For cores that did not intersect the pith, we estimated the number of missing rings after Duncan (1989). If a total age estimate was not possible, we excluded the sample from age-related analyses. We visually crossdated and verified tree cores using COFECHA (Holmes, 1983). We measured annual tree-ring widths to the nearest 0.01 mm using a stereomicroscope and a LintabTM sliding-stage measuring device in combination with TSAP-WinTM software (Rinntech, Heidelberg).

We reconstructed plot disturbance histories using canopy accession events, determined either as open canopy recruitment (based on rapid early growth rates) or as release events (indicated by abrupt, sustained increases in tree growth) (Frelich and Lorimer, 1991a; Svoboda et al., 2012). Specifically, open canopy recruited trees displayed an average annual growth rate of > 1.7 mm, 1.6 mm, 1.7 mm, and 1.3 mm for the initial 15 years of growth in northern Romania, southern Romania, Slovakia, and Ukraine, respectively (Svoboda et al., 2014; Trotsiuk et al., 2014; Janda et al., 2017). Further, we detected release events using the boundary line approach at the scale of each region (Black and Abrams, 2003). We adopted stricter criteria in comparison to Black and Abrams (2003) to exclude events not related to canopy mortality, such as short-term growth pulses or changes in growth rates of trees that were already part of the canopy (Lorimer and Frelich, 1989; Janda et al., 2017). Specifically, to be considered a valid release event (canopy disturbance), elevated growth rates had to exceed the pre-event 10-year running mean for at least seven years (Svoboda et al., 2014). Although multi-year dry or wet periods could result in elevated growth responses, high interannual variability in climate in the study region minimizes this potential false disturbance detection. In addition, release events had to occur in trees below a diameter threshold of 23 cm (a canopy tree threshold based on empirical analysis of this dataset; Janda et al., 2017). Multiple releases before trees reached this threshold were considered valid release events because Norway spruce may require more than one disturbance event to reach the canopy due to its intermediate shade tolerance (Lorimer and Frelich, 1989; Janda et al., 2017). Most canopy accession events were associated with open canopy recruitment (68.7%; n = 7,758), indicating that most disturbed areas were colonized either by very small (< 1 m) advanced regeneration or newly established seedlings. For a more comprehensive discussion of our canopy accession methods, see Svoboda et al. (2014), Trotsiuk et al. (2014), and Janda et al. (2017).

We then constructed disturbance chronologies based on the estimated timing of canopy accession events. Using current tree crown area (see Section 2.2), we calculated the percent of plot canopy area affected by an inferred disturbance event to avoid sampling depth bias towards recent events (Lorimer and Frelich, 1989). We estimated crown area based on a linear regression with DBH (crown area (m^2) = 0.4631 ∗ DBH + 0.8948; $R^2 = 0.61$; $P < 0.001$). We summarized disturbance chronologies as the percent of canopy area disturbed in a given decade. Based on this canopy disturbance percent, we then calculated the maximum severity disturbance event (MSDE) to characterize the disturbance history of each plot. We used a moving sum approach based on a 30-year window to evaluate the timing and severity (*i.e.,* percent plot canopy area killed) of the maximum severity disturbance event. We used this 30-year window rather than a 10-year window because decadal disturbance rates tend to underestimate disturbance rates due to the protracted post-disturbance response of Norway spruce in the region (Svoboda et al., 2014; Trotsiuk et al., 2014; Janda et al., 2017). We also estimated timing of disturbance using the middle of the 30-year window because the exact year of disturbance was largely undetectable due to extended periods of gap colonization (Svoboda et al., 2014; Trotsiuk et al., 2014; Janda et al., 2017).

2.4. Statistical analyses

We conducted separate classifications of all plots using two sets of variables: age-disturbance and structure. Age-disturbance variables were the mean age, standard deviation of age, and interquartile range (25–75%) of the age of all trees cored at each plot, the percent of cored trees that established prior to 1800, the MSDE (defined in Section 2.3), and the estimated year of MSDE. A higher mean plot age indicates that a greater percentage of the tree population was older, and higher standard deviation and interquartile range of ages indicate plots with multiple cohorts established during different disturbance events. Structural variables were the mean and standard deviation of DBH, basal area of live and dead trees > 10 cm DBH, diversity of live tree basal area within a plot as defined by the Gini coefficient (Zenner et al., 2015), total volume of downed deadwood, and densities of five tree size classes: seedlings, saplings, trees 10–30 cm DBH, trees 30–60 cm DBH, and trees > 60 cm DBH. We defined structural complexity as the combination of these multiple tree metrics rather than a single index or metric (McElhinny et al., 2005). Specifically, plots with abundant live trees, dead trees, and downed wood in multiple size classes exhibited the highest structural complexity (and *vice versa*).

To assess the multivariate relationships between disturbance history and current forest structure, we first classified plots using hierarchical agglomerative cluster analyses and then assessed the convergence among the two sets of clusters using transition matrices and an adaptation of Indicator Species Analysis. For the multivariate cluster analyses, we used Euclidean distance and Ward's linkage method (Ward, 1963), and we scaled all values to equalize variance among variables of different scales and units. We produced a dendrogram from each cluster analysis and determined the number of groups based on the distributions of input variables and logical interpretability of groups at different levels of the dendrogram.

Based on the clustering of the structural variables, we also evaluated differences in individual structure variables with one-way ANOVA and multiple comparisons using Tukey's HSD test after Tepley et al. (2013). We evaluated normality and homogeneity of variance assumptions using normal probability plots and Levene's test. If these assumptions were not satisfied, we used the Kruskal-Wallis test, followed by multiple comparisons using the Behrens-Fisher test (Munzel and Hothorn, 2001). We interpreted the significance of multiple comparisons at an α level of 0.05 and conducted these analyses in the R statistical environment (R Core Team, 2015).

We evaluated associations between disturbance history and current structure (conventional, divergent, convergent) by creating a matrix of the transitions from the disturbance cluster groups to the structure cluster groups, which we then graphed using the Gmisc package in R (Gordon, 2016). We quantified the statistical significance of these transitions by adapting Indicator Species Analysis (Dufrene and Legendre, 1997; hereafter referred to as indicator analysis), substituting disturbance history groups for species and using PC-ORD software version 6.22 (McCune and Mefford, 2011). For each disturbance history group, indicator analysis produces a value capturing the degree of association with each structural complexity group by comparing the observed maximum indicator value (one per disturbance history group) with that expected by chance (5,000 Monte Carlo permutations with random assignments of groups). Specifically, indicator analysis yields a P-value that is a non-parametric measure of the proportion of permutations in which the randomized maximum indicator value is greater than the observed value (McCune and Grace, 2002). Our analysis emphasizes the structure group with the strongest association for each disturbance history group, while accounting for different sample sizes among groups and different numbers of groups. Indicator values range from zero to 100 (0 = no association, 100 = complete association; Bakker, 2008; Donato et al., 2009). We only considered indicator values ≥12 with P-values < 0.01 to be strong associations (*sensu* Donato et al., 2009).

3. Results

3.1. Classification based on disturbance history

The cluster analysis based on disturbance history yielded six groups associated with two levels of timing (relatively old and recent) and three levels of maximum disturbance severity (relatively low, moderate, and high) (Fig. 3). The disturbance timing variables exhibited logical patterns of separation (mean age, disturbance year), and disturbance severity declined monotonically from high to low (Fig. 3B). Plots were relatively evenly distributed among the six disturbance history groups, with the exception of plots characterized by high-severity/recent (HR; 9%) and moderate-severity/old (MO; 29%) disturbances (Table 1).

As expected, the HR and high-severity/old (HO) disturbance history groups exhibited relatively similar levels of mean maximum disturbance severity (94% and 79% of canopy area disturbed, respectively) yet distinct mean ages (79 and 152 years, respectively) (Table 2). There were also very few trees that established prior to 1800, particularly in the HR group (Fig. 3B). In addition, the HR and HO groups showed clear periods of cohort establishment in the 20th and 19th Centuries, respectively (Appendix B), which also was reflected in the low standard deviation and interquartile range of age (Table 2, Fig. 3B).

For the moderate-severity/recent (MR) and MO disturbance history groups, mean disturbance severity was approximately 50% (Table 2). These groups also exhibited clear periods of cohort establishment in the 20th and 19th Centuries, respectively (Appendix B). However, their higher age standard deviation and interquartile range values indicated more dispersed tree establishment patterns than the high-severity groups (Fig. 3B).

The low-severity/recent (LR) and low-severity/old (LO) disturbance

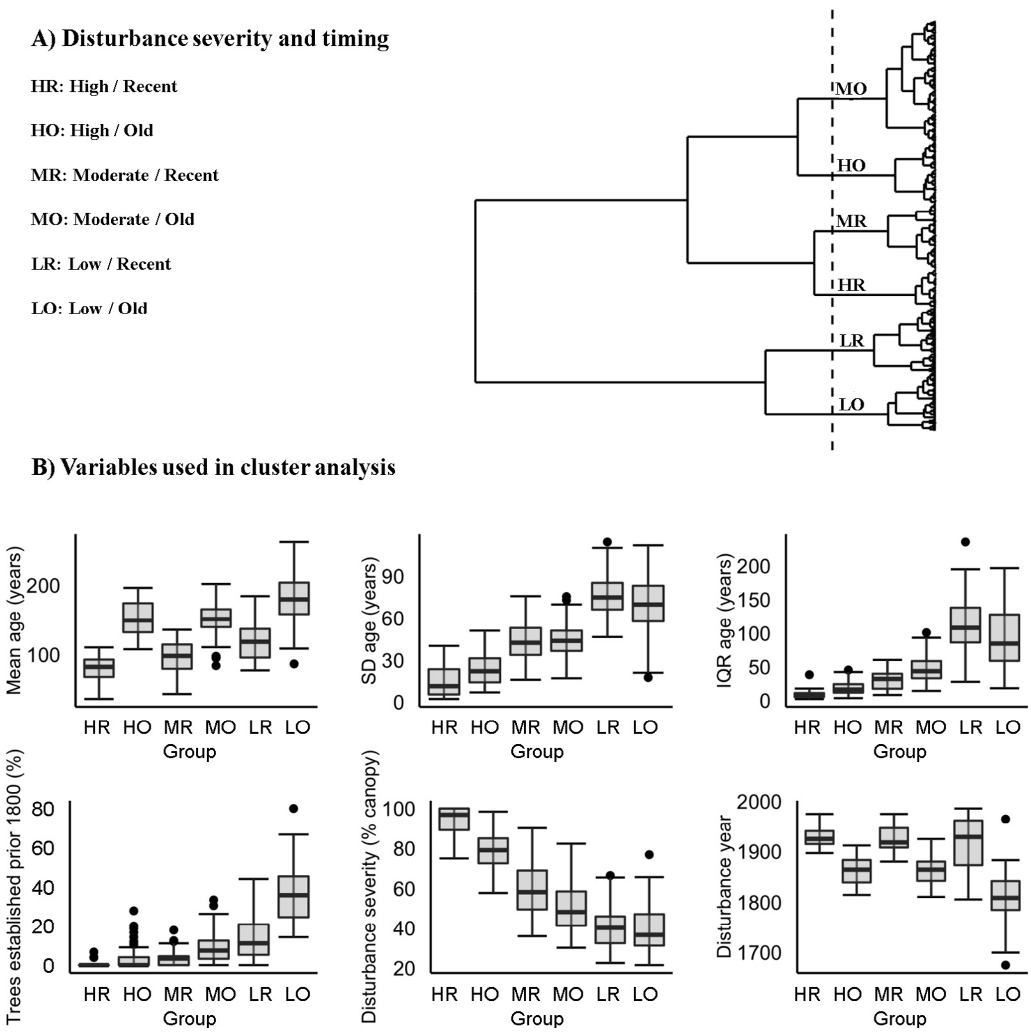

Fig. 3. A) Hierarchical clustering of 453 plots based on six age-disturbance variables: mean age, standard deviation of age, interquartile age range between 25th and 75th percentile (IQR age), percent of trees established prior to 1800, maximum disturbance event severity, and year of maximum disturbance event severity. The dashed line indicates level of the cluster dendrogram containing the six groups analyzed. B) Box-whisker plots of age-disturbance variables among the six cluster groups (solid line indicates median, box edges indicate 25th and 75th percentiles, whiskers indicate 2.5th and 97.5th percentiles, and points indicate outliers). Disturbance severity and year are based on the maximum severity disturbance event (MSDE; See Methods).

Table 1
Plot distributions among disturbance history groups derived from cluster analysis.

Group	Severity	Timing	Plot *n*	Plot%	Tree core *n*	Sum by severity (%)
HR	High	Recent	43	9%	1006	
HO	High	Old	68	15%	1695	24.5%
MR	Moderate	Recent	73	16%	1849	
MO	Moderate	Old	133	29%	3388	45.5%
LR	Low	Recent	65	14%	1611	
LO	Low	Old	71	16%	1760	30.0%

history groups exhibited relatively lower mean disturbance severity, although the values were approximately 40% (Table 2). These groups also showed multiple periods of cohort establishment in the 20th and 19th Centuries, respectively (Appendix B). For these groups, high values of age standard deviation and interquartile range indicated multiple scattered establishment events (Fig. 3B). The percentage of trees that established prior to 1800 in the LR and LO groups was relatively high, particularly the LO group, in which 37% of trees established prior to 1800 on average (Table 2).

Table 2
Comparison of age-disturbance variables of six groups derived from cluster analysis of 453 plots (See distributions in Fig. 3). The number of plots (*n*), mean, and SD of all variables are displayed for each disturbance history group.

Age-disturbance variable	HR (*n* = 43)		HO (*n* = 68)		MR (*n* = 73)		MO (*n* = 133)		LR (*n* = 65)		LO (*n* = 71)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Mean age of sampled trees (y)	79.12	(19.57)	151.51	(23.85)	96.61	(23.89)	153.19	(22.12)	120.63	(28.13)	178.38	(33.57)
Standard deviation of age of sampled trees (y)	14.45	(11.05)	23.54	(10.94)	43.01	(12.81)	43.92	(11.62)	76.50	(14.81)	69.49	(19.46)
Interquartile range (25–75%) of age of sampled trees (IQR age; y)	8.81	(6.09)	18.43	(9.49)	30.62	(13.55)	46.86	(18.65)	113.79	(38.38)	95.91	(46.83)
Percent of sampled trees established before 1800	0	(1)	3	(6)	3	(4)	9	(8)	13	(11)	37	(15)
Mean of maximum severity disturbance event (MSDE; % of plot area disturbed in a single decade)	93.55	(7.91)	78.85	(9.83)	60.07	(13.47)	49.80	(11.64)	40.86	(10.85)	38.91	(10.80)
Estimated year of MSDE (y)	1931	(21)	1861	(25)	1927	(27)	1863	(27)	1914	(51)	1810	(43)

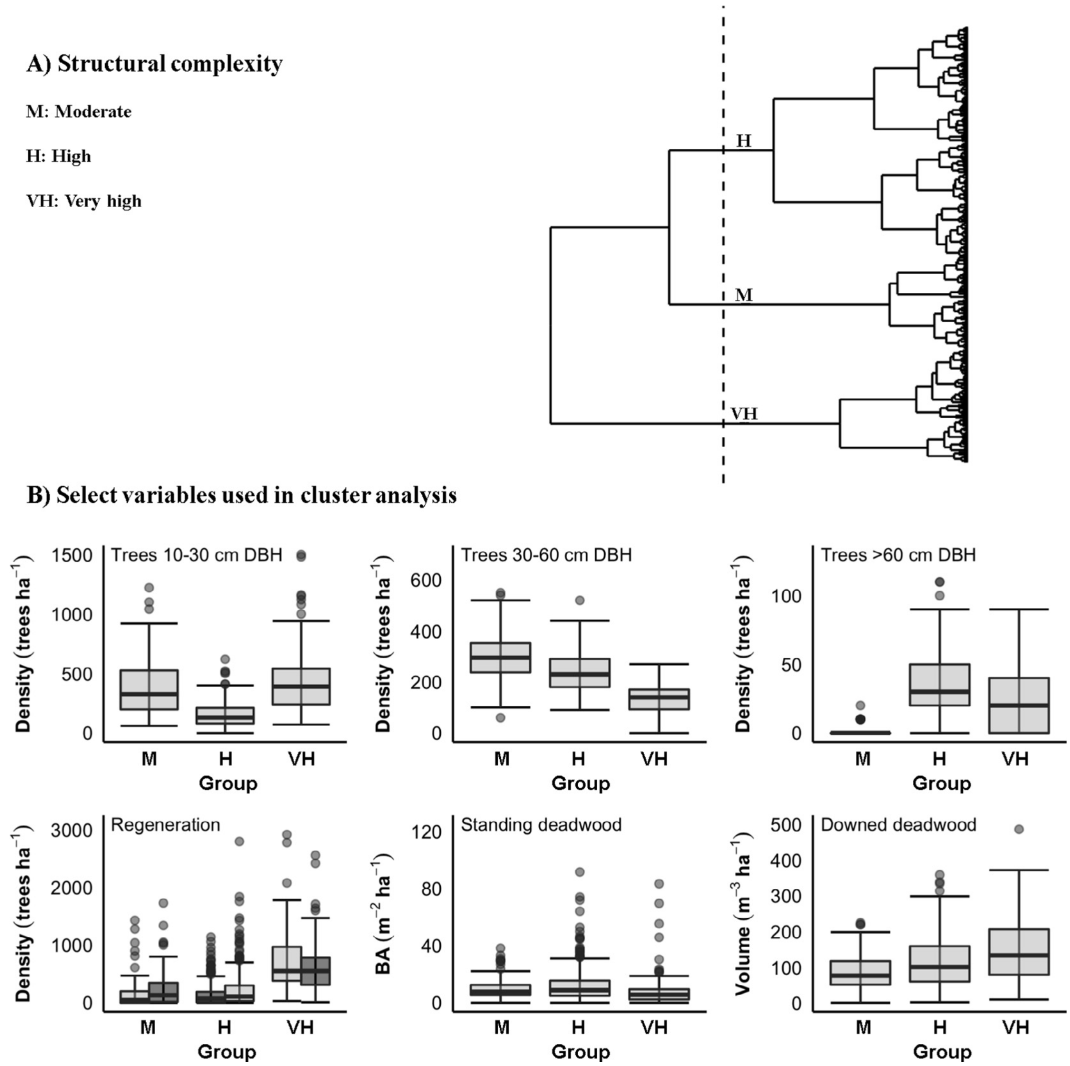

Fig. 4. A) Hierarchical clustering of 453 plots based on structural attributes produced three groups we classified as moderate (M), high (H), and very high (VH) structural complexity. The dashed line indicates level of the cluster dendrogram containing the three groups analyzed. B) Box-whisker plots of six selected structure variables among structural complexity groups (solid line indicates median, box edges indicate 25th and 75th percentiles, whiskers indicate 2.5th and 97.5th percentiles, and points indicate outliers). In the regeneration graph, light gray boxes represent seedlings (< 1.3 m height), and dark gray boxes represent saplings (were > 1.3 m height and < 10 cm DBH). See Table 4 for list of 11 variables used in cluster analysis.

Table 3
Plot distributions among structural complexity groups derived from cluster analysis.

Group	Structural complexity	Plot *n*	Plot %	Tree core *n*
M	Moderate	96	21	2427
H	High	239	53	5995
VH	Very high	118	26	2887

3.2. Classification based on forest structural complexity

The cluster analysis of plots by structural variables yielded three distinct groups along a gradient of increasing structural complexity (Fig. 4). Approximately 21% of all plots were classified in the moderate complexity group (M), 53% in the high structural complexity group (H), and 26% in the very high structural complexity group (VH) (Table 3). We characterize these three groups relative to each other as well as to more structurally simple forests such as even-aged plantations. Notably, all three complexity groups had average tree ages > 100 y and a time since maximum severity disturbance of > 50 years (Appendix C), indicating that young primary forests affected by recent disturbances are now relatively unusual across the sampled locations.

Plots in the M group exhibited significantly lower mean density of large trees, mean standard deviation of DBH, and a correspondingly low mean Gini coefficient compared to the H and VH groups (Table 4, Fig. 4B). Mean live basal area in the M group was significantly higher than in the VH group, and average downed deadwood volume was significantly lower than both the H and VH groups. Small tree density was relatively high in the M group and did not differ from the VH group, although the density of trees 30–60 cm DBH in the M group was significantly higher than the H and VH groups. Norway spruce seedling and sapling densities were significantly lower in the M and H groups compared to the VH group (Table 4).

Plots in the H group had the largest trees on average and highest mean density of trees > 60 cm DBH (Table 4, Fig. 4B). Despite a relatively high mean standard deviation of DBH and mean basal area that was significantly higher than the VH group, the H group had a significantly lower mean Gini coefficient (Table 4). The relatively high basal area of the H group was supported by the high density of medium and large trees. Density of spruce seedlings and saplings was relatively low, as in the M group, but downed deadwood was intermediate between the M and VH groups.

Plots in the VH group exhibited lower mean DBH and live BA

Table 4
Comparison of plot structure variables of three groups derived from cluster analysis of 453 plots (see distributions of first seven variables in Fig. 4). Superscript letters indicate significant differences according ANOVA or Kruskal-Wallis tests (multiple comparison via Tukey's HSD or Behrens-Fisher test, respectively; α = 0.05). The number of plots (*n*), mean, and SD of all variables are displayed for each structural complexity group.

Structure variable	Moderate (*n* = 96)		High (*n* = 239)		Very high (*n* = 118)	
	Mean	SD	Mean	SD	Mean	SD
Density of trees 10–30 cm DBH (stems ha^{-1})	395.8	$(258.7)^{a}$	153.2	$(106.2)^{b}$	442.3	$(278.5)^{a}$
Density of trees 30–60 cm DBH (stems ha^{-1})	297.7	$(99.5)^{a}$	237.4	$(76.5)^{b}$	132.8	$(54.7)^{c}$
Density of trees > 60 cm DBH (stems ha^{-1})	1.4	$(3.7)^{b}$	34.8	$(21.7)^{a}$	22.4	$(22.4)^{c}$
Density of Norway spruce seedlings (stems ha^{-1})	245.4	$(318.7)^{a}$	249.3	$(363.4)^{a}$	632.3	$(452.3)^{b}$
Density of Norway spruce saplings (stems ha^{-1})	152.1	$(261.7)^{a}$	146.4	$(204.0)^{a}$	722.6	$(517.7)^{b}$
BA of standing dead trees (m^2 ha^{-1})	10.0	$(7.7)^{a}$	12.8	$(13.1)^{a}$	8.8	$(12.2)^{b}$
Volume of downed dead wood (m^3 ha^{-1})	87.6	$(52.4)^{c}$	116.3	$(74.9)^{b}$	145.4	$(89.1)^{a}$
BA of live trees (m^2 ha^{-1})	50.6	$(12.0)^{a}$	53.4	$(11.6)^{a}$	38.2	$(10.2)^{b}$
Mean DBH of live trees (cm)	29.7	$(4.7)^{b}$	38.0	$(5.5)^{a}$	26.3	$(5.3)^{c}$
Standard deviation of DBH of live trees (cm)	9.9	$(2.0)^{b}$	14.9	$(2.8)^{a}$	14.5	$(4.3)^{a}$
Gini coefficient from live tree diameter distribution	0.35	$(0.06)^{c}$	0.39	$(0.08)^{b}$	0.52	$(0.07)^{a}$

compared to the M and H groups, reflecting the high density of trees 10–30 cm DBH and low density of trees 30–60 cm DBH (Table 4, Fig. 4B). The relatively high standard deviation of DBH and Gini coefficient indicated high diversity of tree sizes, which was influenced by the high density of large trees > 60 cm DBH. Significantly higher downed deadwood volume (125.7 m^3 ha^{-1}) and densities of seedlings and saplings in the VH group indicated dynamic forests with a diverse mix of live and dead structural components and multi-layered canopies.

3.3. Multiple structural development pathways: conventional, divergent, and convergent

Multiple structural development pathways were evident in the associations between disturbance history and current forest structure. In some cases, disturbance history groups (based on the timing and severity of disturbance) exhibited some affinity for structural complexity groups (Tables 5 and 6, Fig. 5), consistent with conventional structural development pathways. Specifically, the HR disturbance history group was a significant indicator of the M complexity group (indicator value 21; $P = 0.002$; Table 6), showing that the plots experiencing relatively severe and recent disturbance exhibited the lowest relative structural complexity. Similarly, the LR disturbance group was a significant indicator of the VH structure group (indicator value 28; $P = 0.002$; Table 6).

In other cases, plots from each disturbance history group were classified in multiple structural complexity groups, indicating divergent structural development (Table 5; Fig. 5). This divergent pathway was particularly evident for the MR and LO disturbance history groups, which were not significantly associated with any particular structural complexity group (indicator value < 12; $P > 0.01$; Table 6), despite the large number of plots in the H group (Fig. 5).

Additional lines of evidence demonstrated structural convergence, where multiple disturbance history groups were significantly associated with a single structural complexity group. Specifically, two different disturbance history groups (HO indicator value = 12; MO indicator value = 19; $P = 0.001$) were significantly associated with the H complexity group (Table 6, Fig. 5). Structural convergence also was evident in the considerable overlap of disturbance history variables among structural complexity groups, particularly for plot age and year of maximum disturbance (Appendix C) as well as the distribution of structural features within the disturbance history groups (Appendix D). For example, the density of trees 10–60 cm DBH, mean and SD DBH, and Gini coefficient exhibit similar patterns among disturbance history groups (Appendix D). In addition, the density of seedling and sapling regeneration and density of trees > 60 cm DBH varied widely and overlapped among the disturbance history and structural complexity groups (Appendix D).

Table 5
Plot distributions among disturbance history and structural complexity groups derived from two independent cluster analyses.

Disturbance history group	Structural complexity group			
	M	H	VH	Total
HR	27	9	7	43
HO	16	51	1	68
MR	13	32	28	73
MO	27	93	13	133
LR	3	19	43	65
LO	10	35	26	71
Total	96	239	118	453

Table 6
Indicator values from analysis assessing the degree of association between disturbance history groups and structural complexity groups derived from two separate cluster analyses.

Disturbance history group	Moderate complexity	High complexity	Very high complexity	*P*
HR	**21**	0	1	**0.002**
HO	7	**12**	0	**0.001**
MR	4	4	11	0.020
MO	10	**19**	2	**0.001**
LR	0	1	**28**	**0.002**
LO	2	5	10	0.033

Note: Indicator values can range from zero to 100. *P*-values are the result of 5,000 permutations with random reassignment of groups, yielding a non-parametric measure of the proportion of permutations in which the randomized maximum indicator value was greater than the observed value. Only indicator values ≥12 with *P*-values < 0.01 (bolded) were considered to be strong associations (*sensu* Donato et al., 2009).

4. Discussion

4.1. Forest structural development in a mixed-severity disturbance regime: more ways than one

This is the first large-scale European study based on intensive field inventories to demonstrate how mixed-severity disturbances can facilitate multiple pathways of forest structural development. The disturbance history groups described here represent distinct plot-level combinations of time since maximum disturbance and the amount of forest canopy removed (Fig. 3), and the three structure groups depict conditions that vary from moderate to very high structural complexity (Fig. 4). By linking two different but related aspects of forests (disturbance history and current structure), our analyses show that multiple, disturbance-mediated pathways can result in similar structural

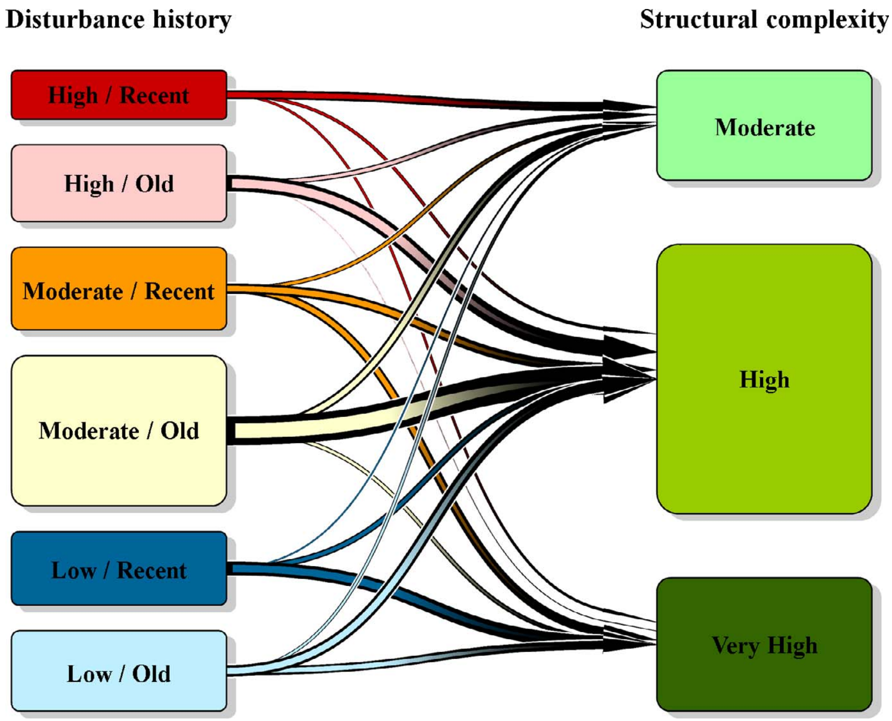

Fig. 5. Transition plot showing associations between disturbance history groups (red: high severity; orange: moderate severity; blue: low severity) and current forest structure groups (green). Box height corresponds to number of plots in each group. Line thickness corresponds to the relative number of plots associated with each pairwise combination (Table 5). We tested these transitions quantitatively with indicator analysis (Table 6). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

complexity over time and space. Importantly, these findings indicate 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 (*e.g.,* time since stand-replacing disturbance).

Prior studies suggest that long time periods are required to increase structural complexity in temperate forests following stand-replacement disturbance, especially for the accumulation of 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 (Spies et al., 1988). Our analyses provide evidence supporting both of our hypotheses that (1) some forests exhibit conventional pathways of structural development and (2) other forests exhibit either divergent or convergent pathways. In the cases where convergence is evident, multiple pathways associated with different combinations of disturbance timing and severity can result in similarly complex forest structure (Fig. 5). These results suggest that structurally complex forests can be associated with more than one disturbance history and that a lack of disturbance does not result in the most complex structure (Table 6). Indeed, natural disturbances may enhance structural complexity by causing tree mortality and tree regeneration, which increase the variability of dead and live structural elements, respectively (Tepley et al., 2013; Lorimer and Halpin, 2014). In turn, these biological legacies may set the stage for more heterogeneous impacts and responses of subsequent disturbances across a range of spatial and temporal scales (Johnstone et al., 2016). In this way, repeated disturbances can steer forests away from convergent pathways where structural components become homogenous at landscape scales (*i.e.,* tree density convergence following fire in Yellowstone National Park; Kashian et al., 2005).

This study builds on previous work illustrating complex mortality and regeneration processes operating in forests driven by mixed-severity disturbance regimes (*e.g.,* Woods, 2004; Lorimer and Halpin, 2014; Svoboda et al., 2014; Trotsiuk et al., 2014; Reilly and Spies, 2015; Janda et al., 2017). Focusing on primary, unmanaged forests with a single, dominant species (Norway spruce) enabled us to evaluate the influence of disturbance on structural complexity and development without the confounding influence of changing species composition or successional pathways (*i.e.,* where different species establish sequentially and exhibit differing environmental tolerance). In addition, because much of the literature on mixed-severity disturbance comes from ecosystems dominated by fire disturbance (*e.g.,* Hessburg et al., 2007; Halofsky et al., 2011; Perry et al., 2011; but see Nagel et al., 2014), this study in forests influenced primarily by wind and insects provides insights into the more general properties of mixed-severity disturbance regimes. Specifically, whereas fire tends to alter forest structure from below (disproportionately killing small trees), windstorms and bark beetles are important examples of disturbances that alter structure from above (*i.e.,* larger trees are more susceptible to both). As such, the survival of advanced regeneration provides a strong connection between prior forest structure and post-disturbance structural complexity and development (Macek et al., 2017). We note that although our study sites did not show evidence of fire, non-stand-replacing fire could be an important disturbance factor in parts of the Carpathian region during the Holocene (Feurdean et al., 2017).

4.2. Conceptual model of disturbance-driven structural development

Although forests have long been recognized as dynamic systems, conceptual frameworks typically depict stand development following stand-replacing disturbance events (*e.g.,* Bormann and Likens, 1979; Oliver and Larson, 1996; Franklin et al., 2002) (Fig. 1). In this conventional view, heterogeneity (including structural complexity) increases over time since disturbance as forests transition from relatively simple even-aged distributions to more diverse uneven-aged distributions regulated by diffuse, single-tree gap dynamics. Recent studies illustrate multiple pathways and the potential emergence of structural complexity (three-dimensional heterogeneity) in the immediate post-disturbance environment (*e.g.,* Donato et al., 2012; Lorimer and Halpin, 2014; Reilly and Spies, 2015; Dunn and Bailey, 2016; Halpin and Lorimer, 2016; Reilly et al., 2017), and our assessment complements such studies by explicitly characterizing the structural complexity associated with mixed-severity disturbance regimes [as quantified by Svoboda et al. (2014), Trotsiuk et al. (2014), and Janda et al. (2017)].

Here, we propose a conceptual model describing the full range of associations between forest disturbance history and structural

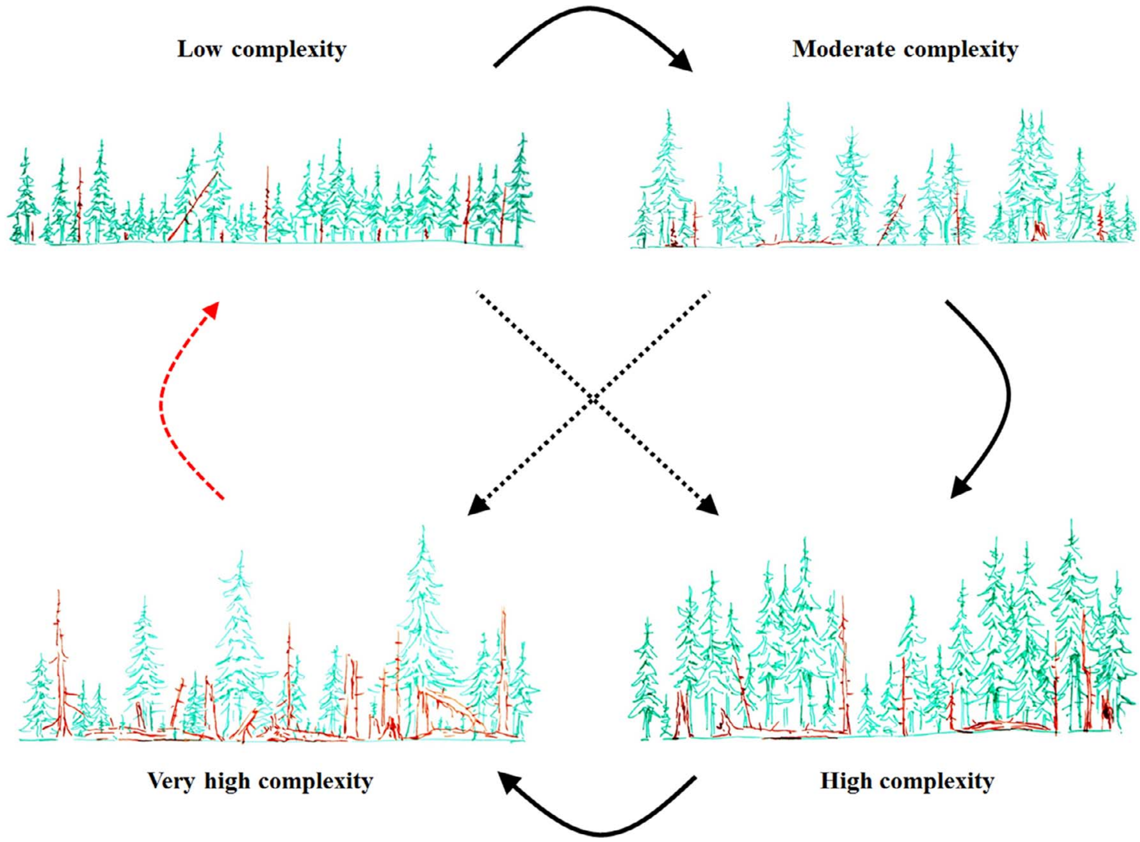

Fig. 6. Conceptual model of disturbance-mediated structural development in primary Norway spruce forests shaped by a mixed-severity disturbance regime. The forest images correspond to the structural complexity classes shown in Fig. 3, with the exception of low complexity (not assessed directly in this study but included for reference). Green indicates standing live trees, brown indicates standing and downed dead trees. Black solid arrows represent incremental transitions from lower to higher structural complexity associated with more recent and lower-severity disturbances (and concurrent tree growth). Black dotted arrows represent the effect of older, more severe disturbances. The red dashed arrow indicates the effect of even-aged silvicultural systems that reduce structural complexity. Note that these examples are shown on flat ground for simplicity, but steep terrain is an important factor in Carpathian Mountain forests. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

complexity in primary, unmanaged forests driven by mixed-severity disturbance regimes (Fig. 6). This framework recognizes the potential for structural convergence and divergence by integrating different combinations of disturbance severity and timing. As disturbances catalyze mortality and recovery processes at different scales, the associated live and dead structural attributes accumulate and propagate, resulting in different levels of structural complexity. Importantly, a given structural condition is not associated with only one disturbance history, and complexity can emerge at different points in time and space.

In addition, our conceptual framework illustrates how disturbance severity can have alternative effects on stand development that change over time. Disturbances can either reduce structural complexity (*i.e.,* a shift to an earlier stage of development) or accelerate development towards higher complexity (*i.e.,* a shift to a later stage of development), as demonstrated by Frelich and Lorimer (1991b), Hanson and Lorimer (2007), and Halpin and Lorimer (2016). An overarching concept evident from this analysis and framework is that disturbance is a ubiquitous process that imparts differential effects across space and time. Although the effect of a given disturbance event tends to decline over time, forests demonstrate strong ecological memory as trees regenerate and occupy available growing space (Johnstone et al., 2016). As such, disturbances can function as ecosystem editors (Jõgiste et al., 2017).

4.3. Uncertainties and future research

Future studies could explore additional temporal and spatial dimensions of disturbance-mediated structural development. Although our analyses focused on the most severe disturbances at the plot scale, most plots experienced at least one additional disturbance over the study period. In addition, our approach using 30-year windows of disturbance detection was not intended to identify cascading effects of the initial disturbance, such as expanding gaps or bark beetle outbreaks following windstorms. Future studies could evaluate a finer temporal resolution, which might resolve the timing and extent of individual windstorms and/or bark beetle outbreaks and the relative importance of advanced regeneration versus post-disturbance regeneration responses (Macek et al., 2017). Due in part to widespread disturbances across the study region in the 18th Century (Svoboda et al., 2014; Trotsiuk et al., 2014; Janda et al., 2017), our samples were limited to relatively mature forests (Fig. 3; Appendix C), so future studies could increase sampling in forests affected by more recent disturbance. In addition, the relatively small plot size in this study and emphasis on the plot scale has implications for the disturbance history classification herein. In some cases, an entire 0.1 ha plot randomly may fall within a high-severity disturbance patch that might be relatively small in a broader forest stand, resulting in a relatively high severity value and highlighting the scale dependence of disturbance analyses. The large sample size and randomized plot location partially address this issue, but we also focus the analysis and interpretation on the relative differences among disturbance history and structure groups. Because the inventory plots in this study occurred within sites and sub-regions (Fig. 2; Appendix A), opportunities exist for expanding this plot-scale analysis into larger spatial domains, as in Svoboda et al. (2014). However, the disturbance history and structural complexity cluster groups were generally intermixed within and among sub-regions (Appendix E), supporting our primary focus on the sub-hectare plot scale.

The monospecific nature of Carpathian spruce forests limits the number of potential forest successional pathways, but this simplicity enabled a more direct exploration of associations between disturbance and structure. Our analytical approach could be applied in forests with more diverse species mixtures, including conifers and hardwoods that exhibit different levels of shade tolerance (*e.g.,* Woods et al., 2004; Lorimer and Halpin, 2014; Nagel et al., 2014). Given the prevalence of mixed-severity disturbance throughout the world (Seidl et al., 2011; Thom and Seidl, 2015), we suggest that the divergent and convergent pathways demonstrated here might play a similar role in other temperate forests, although the distribution of disturbance severity and timing likely varies due to topography, climate, weather, and land-use pressures (Veblen et al., 1994).

Another important application of this work would be to quantify the influence of multiple structural development pathways on biodiversity and ecosystem services (Turner, 2010). Tree mortality and growth processes influence how local plant and animal communities coexist and change over time, and results from this study could be applied to identify the structural conditions that support particular umbrella species [*e.g.,* Capercaillie *(Tetrao urogallus)*; Mikoláš et al., 2017]. Moreover, because mixed-severity disturbances can create key elements of structural complexity – including vertical and horizontal heterogeneity as well as abundant deadwood – numerous other species are likely associated not only with disturbance-driven structure but also with the disturbance processes themselves. Structural complexity and disturbances also are key drivers of ecosystem services, such as carbon storage, recreation, and water resources (Turner, 2010; Thom and Seidl, 2015).

4.4. Summary and management implications

This intensive, field-based study of primary Norway spruce forests spanning numerous plots ($n = 453$) across the Carpathian Mountains indicates that mixed-severity disturbances generate complex forest structure in more ways than one. By linking distinct types of disturbance history and current forest structure at relatively local, subhectare scales, our analyses reveal multiple pathways of structural development. Although these forests exhibit some distinct and predictable associations between disturbance history and structural complexity, multiple lines of evidence indicate convergence of different disturbance histories into similar late-successional structural conditions.

By highlighting the variability of disturbance history and forest structure, this study also provides a historical baseline for comparison with recent and projected changes in climate and land use in mixed-severity systems (Seidl et al., 2011). Understanding the dynamics of natural forests – particularly how disturbances influence structural complexity – also may help managers quantify and anticipate changes in forest productivity, composition, habitat, and carbon storage, among other ecosystem services (Abrams and Scott, 1989; Franklin et al., 2007; North and Keeton, 2008; Bauhus et al., 2009; Fahey et al., 2010). In addition, identifying multiple, disturbance-mediated development pathways that result in late successional or old-growth structure will provide forest managers and policy makers with a broader, more flexible set of applicable silvicultural prescriptions and long-term planning scenarios. Such flexibility will be essential if disturbance regimes continue to change, forcing forest managers to grapple with higher levels of uncertainty and tree mortality. At the same time, high-severity disturbances can create diverse, early seral conditions that exhibit important elements of structural complexity (Donato et al., 2012).

At the landscape scale, forests shaped by mixed-severity disturbance regimes represent a shifting mosaic of structurally diverse patches at multiple temporal and spatial scales. Although efforts to manage for, conserve, and restore ecosystem services attempt to address dynamics across multiple scales (Perry et al., 2011), forest patches of less than a few hectares are often the most practical scale to implement multiple and often-competing management goals, with small patches acting as the building blocks. Increasing awareness of fine-scale natural disturbance processes operating in primary forests will improve adaptive management both within stands – a typical scale for management activities – and across the broader landscape.

A final key implication of this study is that contemporary forest structure is not consistently associated with a given disturbance history. Different disturbance histories can result in similar forest structures over time, and a single disturbance history can lead to different subsequent structural conditions (Johnston et al., 2016). Clearly, excessive tree mortality can hinder late-successional development, but some amount of recent disturbance can be conducive to the development of old-growth forest properties. Our findings highlight that the role of disturbance is not always intuitive and that time is not the only or even the most important determinant of structural complexity. Results from this study in primary forests can inform policies intended to emulate natural forest dynamics and foster resilience across mountain landscapes, 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).

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Appendix A. Brief description of sample plot locations

We established field plots ($n = 453$) in three countries across the Carpathian Mountain Range (Slovakia, Ukraine, Romania; Fig. 2). This appendix describes the four sub-regions, all of which contain Norway spruce forests with minimal prior anthropogenic disturbance. All plots were sampled between June and October from 2010 to 2014.

A.1. Northern Romania ($n = 93$)

In Northern Romania, plot elevation ranges from 1,267 to 1,666 m a.s.l. Mean annual temperature ranges among plots from 2.0 to 3.8 °C, and mean annual precipitation ranges from 827 to 925 mm y^{-1}, increasing with altitude. Bedrock is volcanic (andesites) in Calimani (Seghedi et al.,

2005) and crystalinic (phyllite, gneiss) in Giumalau (Balintoni 1996). Soils in this sub-region are diverse, including mainly podzols, while cambisols occur very rarely at lower altitudes, leptosols at stony and exposed sites, and stagnosols at wet sites (Valtera et al., 2013). See Svoboda et al. (2014) for further details.

A.2. Southern Romania (n = 118)

In Southern Romania, plots were located in remote valleys of the Făgăraș Mountains, where the largest remaining areas of primary montane Norway spruce forests (~7,000 ha) in Europe remain, due primarily to the inaccessibility of the terrain. Plot elevation ranges from 1,266 to 1,713 m a.s.l. The climate is temperate continental with a slight Mediterranean influence. Mean annual temperature ranges among plots from 2.8 to 5.0 °C, and mean annual precipitation ranges from 830 to 929 mm y^{-1}. Soils in this sub-region are variable, including mainly cambisols and some podzols in higher elevation, while leptosols occur at stony and exposed sites (Florea et al., 1994).

A.3. Slovakia (n = 145)

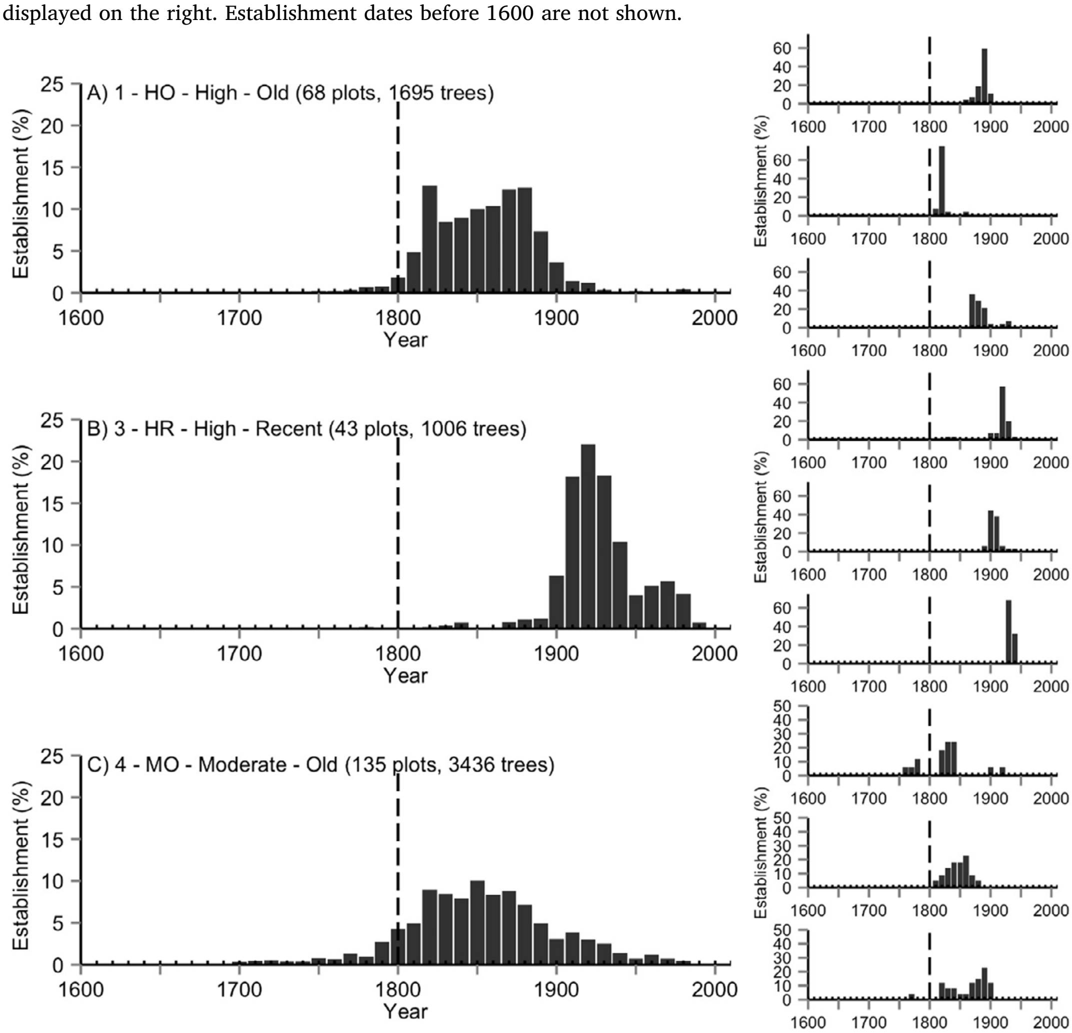
In Slovakia, plot elevation ranges from 1,223 to 1,536 m a.s.l. The overall the climate is cold and wet. Mean annual temperature ranges among plots from 1.6 to 3.4 °C, and mean annual precipitation ranges from 1,205 to 1,365 mm y^{-1}. The bedrock varies from acidic to basic minerals (Limestones, dolomites, Metapsammites, Andesites, Granitoids, Claystones, Sandstones). See Janda et al. (2017) for further details.

A.4. Ukraine (n = 97)

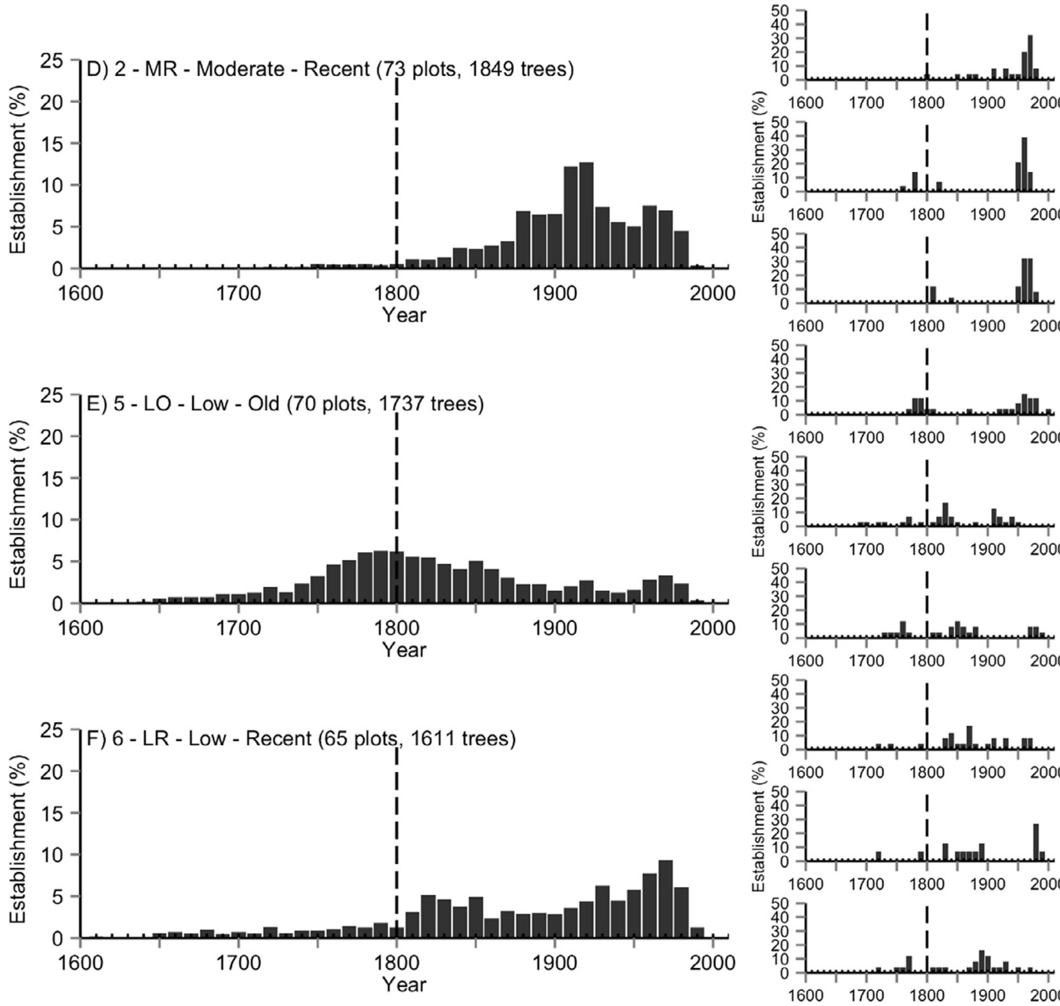
In the Ukraine, plot elevation ranges from 1,217 to 1,501 m a.s.l. These forests had been protected from selective logging or grazing by poor access and the rugged terratin (see Trotsiuk et al., 2014). Mean annual temperature ranges among plots from 1.8 to 3.9 °C, and mean annual precipitation ranges from 903 to 1,004 mm y^{-1}. Leptosols and albic podzols predominate on sandstone bedrock (Chernyavskyy and Shpylchak, 2011; Valtera et al., 2013). See Trotsiuk et al. (2016) for further details.

Appendix B. (Part 1 of 2). Age distributions of six cluster groups of plots based on age-disturbance variables

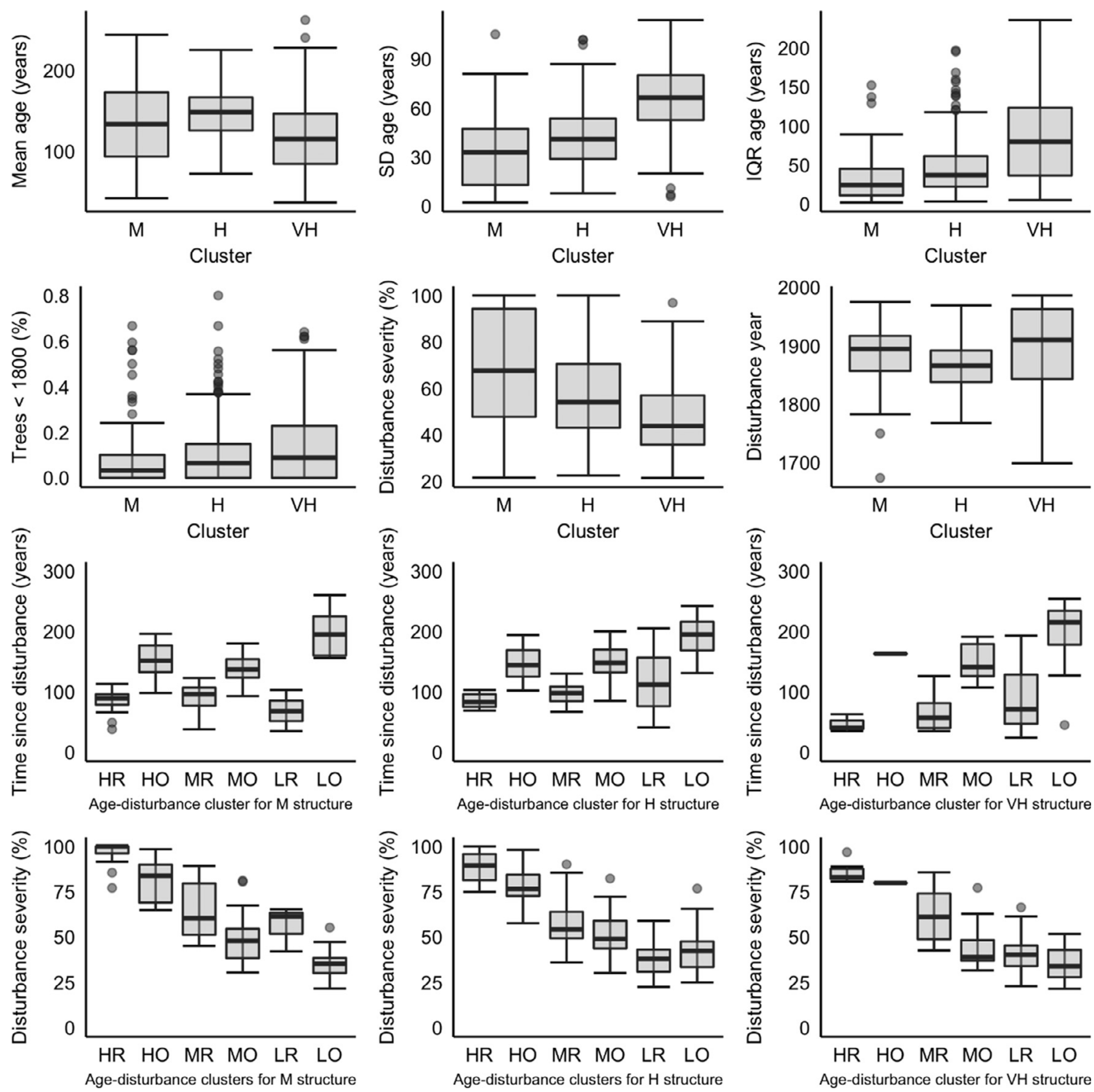
For each cluster, the combined establishment percentages by decade are displayed on the left, and three individual sample plot establishment percentages are displayed on the right. Establishment dates before 1600 are not shown.



Appendix B (Part 2 of 2)



Appendix C. Distribution of age-disturbance variables within structural complexity groups



Appendix D. Forest structure of age-disturbance clusters within structural complexity groups derived with cluster analysis

	HR		HO		MR		MO		LR		LO	
Structure variable	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Moderate complexity												
Density of trees 10–30 cm DBH (stems ha^{-1})	494	264	400	280	471	333	262	156	710	141	298	129
Density of trees 30–60 cm DBH (stems ha^{-1})	282	102	353	111	270	128	306	74	223	80	287	75
Density of trees > 60 cm DBH (stems ha^{-1})	0	0	3	4	1	3	2	5	0	0	3	5
Density of Norway spruce seedlings (stems ha^{-1})	140	170	149	151	142	281	400	455	237	257	403	223
Density of Norway spruce saplings (stems ha^{-1})	50	76	71	113	157	244	250	370	117	139	302	325
BA of standing dead trees ($m^2\,ha^{-1}$)	7.0	3.9	13.2	10.7	8.6	7.4	10.6	6.5	6.7	5.1	14.5	11.2
Volume of downed deadwood ($m^3\,ha^{-1}$)	51.2	62.8	66.9	48.8	59.0	48.6	84.2	50.0	75.0	83.7	114.4	71.3
BA of live trees ($m^2\,ha^{-1}$)	49.1	12.5	58.0	11.8	48.7	15.9	49.7	9.3	46.0	5.5	49.2	11.2
Mean DBH of live trees (cm)	27.7	4.6	30.5	4.4	28.0	5.1	32.2	3.8	23.5	1.7	30.8	3.2
Standard deviation of DBH of live trees (cm)	8.7	1.4	9.3	1.5	10.2	2.4	10.8	1.7	8.8	1.9	11.8	1.6
Gini coefficient of DBHs of live trees	0.33	0.06	0.32	0.06	0.37	0.04	0.35	0.06	0.38	0.05	0.39	0.04

High complexity												
Density of trees 10–30 cm DBH (stems ha^{-1})	224	111	93	78	236	122	141	85	234	123	131	93
Density of trees 30–60 cm DBH (stems ha^{-1})	316	72	276	84	228	65	236	71	179	42	206	64
Density of trees > 60 cm DBH (stems ha^{-1})	24	14	30	22	38	22	35	21	35	17	41	25
Density of Norway spruce seedlings (stems ha^{-1})	34	66	263	368	102	182	247	325	265	265	417	556
Density of Norway spruce saplings (stems ha^{-1})	77	114	109	151	88	110	147	230	187	152	248	266
BA of standing dead trees (m^2 ha^{-1})	6.2	5.3	12.8	9.9	6.8	5.0	13.8	15.5	17.1	14.4	15.1	14.3
Volume of downed deadwood (m^3 ha^{-1})	58.2	50.0	95.4	72.9	76.0	74.7	100.4	76.5	130.1	100.0	123.9	91.8
BA of live trees (m^2 ha^{-1})	61.5	13.1	55.3	12.8	55.4	13.2	53.0	10.6	46.7	9.0	51.5	9.7
Mean DBH of live trees (cm)	34.9	3.0	41.1	4.9	34.7	4.7	38.3	5.2	33.2	4.9	39.0	5.2
Standard deviation of DBH of live trees (cm)	13.8	2.6	12.6	2.4	15.5	2.3	15.0	2.5	17.0	2.1	16.6	2.6
Gini coefficient of DBHs of live trees	0.39	0.07	0.31	0.06	0.44	0.05	0.39	0.07	0.49	0.05	0.41	0.08
Very high complexity												
Density of trees 10–30 cm DBH (stems ha^{-1})	819	209	490	NA	581	356	259	118	368	202	403	224
Density of trees 30–60 cm DBH (stems ha^{-1})	77	44	230	NA	110	58	167	51	127	47	156	51
Density of trees > 60 cm DBH (stems ha^{-1})	3	8	10	NA	18	17	19	17	30	25	22	25
Density of Norway spruce seedlings (stems ha^{-1})	539	232	1240	NA	605	573	726	338	538	446	870	596
Density of Norway spruce saplings (stems ha^{-1})	939	409	550	NA	824	726	632	463	576	399	898	479
BA of standing dead trees (m^2 ha^{-1})	9.3	11.9	3.6	NA	9.5	10.0	12.0	17.5	9.9	14.7	4.4	3.8
Volume of downed deadwood (m^3 ha^{-1})	161.2	120.6	71.4	NA	162.4	112.6	101.6	51.6	120.2	98.4	100.0	77.6
BA of live trees (m^2 ha^{-1})	31.5	7.9	47.6	NA	35.8	10.8	37.7	6.3	39.1	11.2	41.1	8.9
Mean DBH of live trees (cm)	19.6	2.4	25.7	NA	23.4	5.1	30.4	3.9	27.4	4.8	27.4	4.5
Standard deviation of DBH of live trees (cm)	8.0	1.7	13.2	NA	12.7	3.7	14.9	4.1	16.2	3.6	15.1	4.4
Gini coefficient of DBHs of live trees	0.42	0.06	0.50	NA	0.52	0.07	0.46	0.06	0.55	0.06	0.51	0.07

Appendix E. Age-disturbance and structure classifications of plots by sub-region and site (see Tables 1 and 2 for cluster names and Appendix A for sub-region descriptions)

		Age – disturbance clusters (*n* plots)						Structural complexity clusters (*n* plots)		
Sub-region	Site ID	HR	HO	MR	MO	LR	LO	M	H	VH
Northern Romania	ROM_CAL	15	7	7	5	0	5	18	16	5
Northern Romania	ROM_GI1	0	1	4	4	11	6	0	10	16
Northern Romania	ROM_GI2	3	6	3	8	6	2	3	13	12
Southern Romania	ROM_FA0	2	1	2	3	2	2	2	10	0
Southern Romania	ROM_FA1	2	3	1	3	2	1	4	8	0
Southern Romania	ROM_FA2	1	5	2	3	0	1	4	7	1
Southern Romania	ROM_FA3	0	2	1	6	0	2	2	9	0
Southern Romania	ROM_FA4	2	4	1	3	0	1	3	7	1
Southern Romania	ROM_FA5	1	2	5	2	1	3	4	10	0
Southern Romania	ROM_FA6	0	3	1	7	1	0	1	10	1
Southern Romania	ROM_FA8	3	0	6	0	1	1	1	8	2
Southern Romania	ROM_FA9	4	1	6	1	0	0	2	10	0
Southern Romania	ROM_FA10	1	2	3	4	0	1	7	3	1
Slovakia	SLO_BEL	0	0	0	6	1	6	4	6	3
Slovakia	SLO_BYS	1	0	4	6	2	2	3	11	1
Slovakia	SLO_DUM	0	4	0	12	0	0	2	14	0
Slovakia	SLO_HLI	1	0	0	3	4	2	0	7	3
Slovakia	SLO_JAK	0	4	3	4	4	0	0	9	6
Slovakia	SLO_JAV	0	0	0	6	1	1	5	3	0
Slovakia	SLO_KOP	1	2	2	3	2	3	5	4	4
Slovakia	SLO_MED	0	2	1	4	0	0	1	6	0
Slovakia	SLO_OSO	0	3	1	6	2	2	2	12	0
Slovakia	SLO_PIL	0	2	0	5	2	2	1	9	1
Slovakia	SLO_SMR	0	5	1	2	0	1	0	9	0
Slovakia	SLO_TIC	3	0	4	2	4	1	1	7	6
Ukraine	UKR_GR1	3	2	3	5	3	2	7	6	5
Ukraine	UKR_GR2	0	0	1	3	4	7	3	4	8
Ukraine	UKR_GR3	0	4	2	4	1	4	6	3	6
Ukraine	UKR_SY1	0	1	0	6	7	6	2	2	16
Ukraine	UKR_SY2	0	1	5	5	2	2	2	5	8
Ukraine	UKR_SY3	0	1	4	3	2	4	1	1	12

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