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Past disturbances and intraspecific competition as drivers of spatial pattern in primary spruce forests

T. Després,† L. Vítková, R. Bače, V. Čada, P. Janda, M. Mikoláš, J. S. Schurman,
V. Trotsiuk, and M. Svoboda

Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, Praha 6 –Suchdol,
Prague 16521 Czech Republic

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Abstract. The role of density dependence in shaping spatial patterns in tree distributions presumably changes throughout stand development. However, empirical investigations into developmental processes are often limited by a lack of long-term data on disturbance history, which further limits the ability to assess the role of spatial variation in site conditions (e.g., slope, aspect, mean annual temperature). This study included data from 289 plots within 26 primary forest stands of the Carpathian Mountains; stands were dominated by Norway spruce (*Picea abies*) and driven by mixed-severity disturbance regimes. We assessed spatial patterns in living tree positions, tree diameters, and the relative position of living trees to dead trees. Random forest classification was used to discriminate between disturbance history, tree density, and site conditions and their effects on the observed spatial patterns. At the stand scale, distances between trees of equal diameter were more uniform that expected (tree diameter was showing repulsion), while tree positions and dead trees were mostly distributed randomly. The processes that best explained the spatial patterns were identified as self-thinning mortality and past disturbances (100–150 yr). This study demonstrated that the plot and stand-scale spatial patterns resulted from the combination of past disturbances and density-dependent legacies derived from earlier forest development stages.

Key words: density-dependent mortality; disturbance history; intraspecific competition; *Picea abies;* spatial pattern.

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† **E-mail:** tiphaine.despres@uqat.ca

INTRODUCTION

Competition and disturbance are primary constraints on forest population structure (Coomes and Allen 2007, Coomes et al. 2012). Our understanding of how the contribution of these processes changes through time is limited by the time-span of observational datasets documenting how tree populations change following a disturbance. However, competition and disturbance have differing effects on the spatial distribution of mortality and surviving trees (Coomes and Allen 2007, Aakala et al. 2012, Lutz et al. 2014, Gendreau-Berthiaume et al. 2016). Pairing analyses of spatial patterns in tree distributions with disturbance history reconstruction is considered an effective alternative to long-term monitoring of developmental changes in stem dynamics (Coomes and Allen 2007, Lutz et al. 2014).

Neighboring trees compete to intercept available light and the intensity of this competition increases with tree density, contributing substantially to mortality in high-density early-successional stands (Coomes and Allen 2007, Murrell 2009, Larson et al. 2015). Density-dependent mortality induces thinning in patches of high tree density, thus promoting spatial uniformity in the surviving trees (i.e., repulsion; Peet and Christensen 1987, Larson et al. 2015); density effects thus decline in importance as stand develops. As surviving trees approach their maximum longevity and external sources of variation accumulate (e.g., disturbances), density-independent mortality is expected to introduce increased randomness of tree spacing, thus resulting in higher spatial heterogeneity (Aakala et al. 2012, Després et al. 2014, Gendreau-Berthiaume et al. 2016).

Density effects impose limits on development patterns, such as relationships between productivity and density, but the character of this trajectory could be influenced by environmental factors (Weller 1987). Maximum growth rates are likely to intensify competitive effects (Schwinning and Weiner 1998), and longevity is also likely influenced by site conditions, which may influence density-independent factors (He and Duncan 2000, Piao et al. 2013). When considering forest spatial patterns, dismissing site heterogeneity could lead to incorrect interpretations about past density-dependent effects (He and Duncan 2000, Piao et al. 2013).

Disturbances drive forest dynamics by influencing the spatial arrangement of trees; stand-replacing disturbances (e.g., windstorm or insect outbreaks) revert the forest structure to an earlier successional stage (Frelich and Reich 1995). In contrast, periodic low- to moderate-severity disturbances (e.g., windthrow or partial insect outbreaks) create multi-layered canopies that contribute to more structurally complex forests (i.e., old-growth forest structure; Halpin and Lorimer 2016). Mixed-severity disturbance regimes—defined by high spatiotemporal variability in both severity and frequency—also influence forest structural features, such as biomass and age structure, as observed by, for example, Trotsiuk et al. (2016) and Janda et al. (2017) in forests dominated by Norway spruce (*Picea abies* (L.) Karst.) in the Carpathian Mountains. We know of no existing literature that explores forest spatial patterns and accounts the local disturbance history.

Our objective was to assess the role of mixed-severity disturbance histories in tree spatial patterns in primary forests (i.e., forest relatively uninfluenced by human activity, sensu Svoboda et al. 2014) at the plot and stand levels; we also considered site conditions, density dependence, and mortality. More specifically, the following questions were addressed: (1) In the absence of interspecific competition, do recent disturbances induce the aggregation of trees and mortality (Aakala et al. 2012, Larson et al. 2015)? In addition, in the case of low disturbance rates, does intraspecific competition (i.e., self-thinning of young Norway spruce trees) result in repulsion patterns (Kenkel 1988)? Is mortality randomly distributed in older plots and stands as in other temperate primary forests (Aakala et al. 2012, Larson et al. 2015)? (2) Do site conditions influence density-dependent mortality and the tree spatial organization at the plot or stand levels (He and Duncan 2000, Piao et al. 2013)?

Materials and Methods

Study area

This study was conducted in the primary forests of the Carpathian Mountains (Romania, Ukraine, and Slovakia), a mountain range with forests dominated by Norway spruce and European beech (*Fagus sylvatica* L.). We define "primary forest" according to Svoboda et al. (2014): a forest showing little to no evidence of human activity that persists under a natural mixed-severity disturbances regime, but not necessarily in late-successional stages of development. The study area of the primary Norway spruce forest is estimated to be approximately 4000 ha. All sampled stands were located in mature to old-growth developmental stages. The mixed-severity disturbance regime of the area is characterized by windstorms and bark beetle (*Ips typographus* L.) outbreaks (Svoboda et al. 2014, Janda et al. 2017). Regeneration after disturbances is mainly composed of Norway spruce and rowan (*Sorbus aucuparia* L.) species (Bače et al. 2017). The elevation of the study sites is between 1235 and 1713 m above sea level (mean = 1435 m a.s.l.). The mean annual temperate ranges between 1.4° and 5.0°C. We used a base period of 1950–2000 to evaluate temperature, which was estimated using the change factor method to downscale Climatic Research Unit (CRU) data and Worldclim provided the high-resolution dataset; the downscaling was done by the Landscape Dynamics, WSL laboratory. The mean annual precipitation in the region ranges between 500 and 2000 mm (Antolović et al. 2013). In frequency, Norway spruce accounted for 95.1% of the total living sampled tree species; *S. aucuparia*

L. and *Abies alba* Mill. comprised 2.4% and 1.0%, respectively; and the remaining 1.5% consisted of *Pinus cembra* L., *Acer pseudoplatanus* L., *Betula pendula* Roth., *Fagus sylvatica* L., *Larix decidua* Mill., and *Salix* spp.

Data collection and processes

We established 548 circular plots (each 1000 m^2 in area) in 32 stands between 2010 and 2014 using a stratified random design (Svoboda et al. 2014). Plots spanned from 45.55° N to 49.52° N and from 19.20° E to 25.47° E (see Appendix S1: Table S1 for details). Diameter at breast height (1.37 m height; dbh), species, and location were recorded for all living and dead trees ≥10 cm dbh and crown area projections for five living trees ≥10 cm dbh per plots. Twenty-five randomly selected canopy trees within each plot were cored to analyze radial growth and determine tree age. Only sampled plots that contained at least 30 living trees were selected for the spatial analyses (Park et al. 2005, Aakala et al. 2012). Plots with at least 30 living and 10 dead trees were used for the living vs. dead trees marked point pattern analyses (He and Duncan 2000). Filtering was also conducted at the stand level; all stands containing less than four plots were discarded from the analyses. Using the above criteria, 289 plots from 26 stands were used for the spatial analysis of living trees and 133 plots from 19 stands were utilized for the bivariate analysis of living vs. dead trees (Appendix S1: Table S1).

At the stand level, the mean annual temperature, slope, aspect, and country name represented the site conditions (at the plot level, the stand name was added). The mean annual temperature was estimated using CRU and Worldclim as described above (see *Study area* section). Slope and aspect were recorded on all plots. Slope was measured from the center of the plot on a 20-m transect (10 m uphill and 10 m downhill from the plot center) using a Vertex. Aspect was measured by compass in the direction of the largest slope from plot center. Slope and aspect can affect the size and frequency of the gap regime, and, per se, the spatial pattern (e.g., high northerly slopes should be more prone to large gap regime patterns and result in greater spatial aggregation with small trees inside gaps and large trees along the edge; Hunter and Parker 1993). At the stand scale, we used the mean of plot slope and aspect measurements. The site location, represented by the stand and country names, was used as a proxy for the distance between the plots and stands, respectively, to highlight any regional similarities (e.g., soil characteristics).

Plot age was estimated using the mean age of the five oldest trees at each plot; this is considered to be a suitable method for estimating plot age in multi-cohort stands subjected to mixed-severity disturbance regimes (Di Filippo et al. 2016, Trotsiuk et al. 2016, Janda et al. 2017). To estimate the stand age, the mean of all plot ages was calculated.

Increment cores were processed following standard dendrochronology methods (Stokes and Smiley 1968). Two radial growth patterns were considered as follows: (1) abrupt, sustained increase in growth rates (releases), and (2) rapid early growth rates (gap recruitment) that indicate recruitment in a former canopy gap (Svoboda et al. 2014). We used the boundary line criterion method to assess the growth releases from individual increment cores (Black and Abrams 2003). Because growth releases could last for several years, we used the maximum percentage growth change of each release to date disturbances. All increment cores were used to reconstruct individual plot-level disturbance histories. The number of growth releases and gap recruitment events was converted to a total canopy area disturbed for each decade, following the approach of Lorimer and Frelich (1989). This method is based on the current crown area of each tree assuming that crown area of trees that responded to the original gap formation approximates the size of the original gap. Current crown areas were predicted from dbh based on a linear regression fitted to the 1445 measured trees (five per plot). Individual tree canopy areas were then linked to the year of release, and tree-level disturbance events were summed annually and expressed as the proportion of total canopy area, resulting in a plot-level disturbance chronology. Total canopy area recruited was calculated for all trees currently present in the stand. Averages over plot-level disturbance severities were produced to estimate stand-level disturbance histories. Disturbances were summarized based on the number of disturbance events and the cumulative amount of disturbed canopy area at the plot and stand scales. Short, medium, and long time periods representing the 50, 100, and 150 yr prior to 2014, respectively, were used to assess both disturbance indicators.

Data analyses

*Spatial analyses.—*At the stand scale, plots were considered to be homogeneous (i.e., stationary) and isotropic due to the similar climatic and topographic conditions. Primary Norway spruce forests tend to be driven by mixed-severity disturbances, which are, by definition, stochastic processes leading to spatial randomness, but they can also promote aggregation in recently disturbed areas and, by extension, younger developmental stages (Svoboda et al. 2014). We used the univariate cumulative $L(r)$ function (i.e., square-root-transformation of the cumulative Ripley's $K(r)$) to quantify the discrete (tree positions: TreePos) and continuous (dbh) variables (Illian et al. 2008). Bivariate $L_{12}(r)$ function was computed to define the pattern of living vs. dead trees (Dead) (Illian et al. 2008). Random labeling hypothesis of living and dead trees was tested for the bivariate function because the mortality processes were expected to be stochastic at the study sites (Goreaud and Pélissier 2003, Hou et al. 2004, Velázquez et al. 2016). Replicate patterns were computed to combine each plot within one stand and capture the full statistical power of the plot-level results (Illian et al. 2008, Raventós et al. 2010, Baddeley et al. 2015). Replicate patterns were calculated using means of observed and simulated test values from the plot level.

All univariate and bivariate patterns at plot and stand scales (i.e., replicated patterns) were tested for complete spatial randomness and random labeling hypotheses (for the bivariate pattern) using the rank envelope tests (Myllymäki et al. 2017). This method allows rejection of the null hypothesis using the prescribed significant P value (Wiegand et al. 2016, Myllymäki et al. 2017). We computed 2499 simulations for each rank envelope test (Myllymäki et al. 2017). Univariate patterns with a statistically significant P value and an observed value below (above) the envelope denoted repulsion (aggregation). For the bivariate pattern, a significant P value and an observed value below (above) the envelope represented negative correlation, segregation (positive correlation, attraction) between dead and living trees.

*Random forest.—*Random forest models (Breiman 2001) were used to rank the variables from disturbance history, site conditions, and tree density relative to different observed spatial patterns. Random forest models are non-parametric models (based on multiple regression) used to rank explanatory variables by their level of importance. Random forest models yielded 14 and 13 variables for the plot and stand levels, respectively. The following variables were used for the plot and stand levels: tree age, basal area, and tree density representing the forest structure, number of disturbances events (nb events), and cumulative sum of disturbed canopy area (cumSum CA) at 50, 100, and 150 yr prior to 2014, which was used as a proxy to the disturbance history. The mean annual temperature, slope, aspect, country name, and stand name represented the site conditions at the plot level.

The variable selection using random forest (VSURF) method was used to rank and select important variables from the random forest models (Genuer et al. 2015). The VSURF method is based on two prediction performances of the random forest: the out-of-bag error (OOB) and the variable importance. To compute the estimated OOB error, the model used a subsample of the regression trees to compute predictions and compare them with the remaining regression trees (named out-of-bag trees). Thus, the estimated OOB error rate measured the model misclassification rate for classification and the mean square error (MSE) for regression (Genuer et al. 2010, 2015). If the OOB error is 0%, an over-fitting model is denoted (i.e., a perfect model). If the OOB error is below 40%, the model is considered to be suitable (Breiman 2001).

The variable importance used in VSURF is based on the permutation importance indices. It consists of randomly permuted values of one variable and computed disturbed OOB error that will be compared with the undisturbed OOB error. The greater the difference between the disturbed OOB and the undisturbed OOB errors, the higher the variable importance will be, and vice versa (Genuer et al. 2010, 2015).

To rank and select the variables from VSURF models according to their importance, we chose to stop the variable selection at the interpretation level, which is a conservative approach, sensu Genuer et al. (2010, 2015). Important variables that were highly related to the spatial pattern were selected, and only the poorly related variables were removed from the model. A total of 3000 trees were simulated to build the random forest models.

All importance variables found using VSURF were individually tested against spatial pattern groups (i.e., random, repulsion/segregation, and aggregation/attraction) using the Kruskal–Wallis test. When the Kruskal–Wallis test was significant ($P < 0.05$), a post hoc pairwise comparison Nemenyi test was performed to discriminate the effect of each spatial pattern group on the importance variable.

All statistical tests and spatial analyses were conducted in R (R Core Team, 2016). The spatial statistics were computed using the package "spatstat" (Baddeley and Turner 2005), and the rank envelope tests were done using the package "GET" (available at https://github.com/myllym/GET; Myllymäki et al. 2017). The "VSURF" package was employed for the random forest VSURF model (Genuer et al. 2015), and "PMCMR" package was used for the post hoc pairwise comparison Nemenyi test (Pohlert 2014).

Results

Stand scale

Stand ages ranged between 141 and 280 yr (mean = 218.6 ± 30.5 significant difference [SD]; see Appendix S1: Table S1 and Fig. S1 for plot age distributions). The mean basal area (±SD) and living tree density were 55.06 m^2/ha (±7.88) and 546.81 stems/ha (±114.91), respectively (Appendix S1: Table S1). At the stand scale, the random pattern was the most common for the tree positions (TreePos; 50.0%) and the random labeling between living vs. dead trees (Dead; 63.2%); nonetheless, repulsive spatial distribution was observed for dbh in all 26 stands (Table 1). Positive correlation (i.e., attraction) between dead and living trees accounted for 31.6% of the stand-level spatial patterns, and the aggregation patterns for the TreePos represented 11.5% (Table 1). The mean OOB error results from the VSURF models were between 16.7% and 50.3% (mean = 28.7% ± 13.5 SD; Table 2).

At the stand scale, no random forest models were computed for the dbh mark because all stands displayed repulsion. For the TreePos, the mean temperature and the cumulative sum of the disturbed canopy area within the last 100 yr best explained the spatial pattern (Table 2), although the mean OOB error was high (50.3%). Stand age and tree density were the best variables that explained the spatial pattern for Dead at the stand scale (Table 2).

Table 1. Spatial patterns at plot and stand levels, classified as aggregation, random, or repulsion according to the rank envelope test (see *Materials and methods* for more details).

			Patterns‡		
Scale	Mark†	*n*	Aggregation	Random	Repulsion
Plot	TreePos	289	23	237	29
	dbh	289	1	192	96
	Dead	133	18	112	3
Stand	TreePos	26	3	13	10
	dbh	26	0	0	26
	Dead	19	6	12	1

† TreePos—tree position only; dbh—tree diameter at 1.37 m; Dead—living vs. dead trees.

‡ Aggregation for "Dead" mark denotes mutual attraction (i.e., positive correlation) between dead and living trees, while repulsion denotes mutual repulsion (i.e., negative correlation) between dead and living trees.

Table 2. Random forest results for each scale and marks; 3000 decisions trees were analyzed.

Scale	Mark†	Mean OOB‡	Interpretation selected variables
Plot	TreePos	0.1852	Stand name, basal area, density, mean temperature, nb events 100
	dbh	0.3169	Density, mean temperature, country name
	Dead	0.1666	Age, mean temperature, cumSum CA 150
Stand	TreePos	0.5031	Mean temperature, cumSum CA 100
	dbh	NA§	NA
	Dead	0.2632	Age, density

Notes: The selected variables from VSURF were ordered by decreasing level of importance (the first variable is the most important) based on the 14 and 13 variables at the plot and stand scale, respectively. The tested variables were as follows: country name, age (yr), number of disturbance events in the last 50, 100, and 150 yr (nb events), cumulative sum of disturbed canopy area in the last 50, 100, and 150 yr (cumSum CA), mean annual temperature (°C), slope (%), aspect (%), basal area (m^2/ha), tree density (stems/ha), and stand name (for the plot-level analyses only). OOB, out-of-bag error; VSURF, variable selection using random forest.

† TreePos—tree position only; dbh—tree diameter at 1.37 m; Dead—living vs. dead trees.

‡ Mean OOB—mean OOB rate from 0 to 1.

§ Replicated dbh patterns all showed repulsion; random forest analysis could not be performed.

Plot scale

At the plot scale, random spatial pattern was most common for the TreePos, dbh, and Dead variables, accounting for 82.0%, 66.4%, and 84.2%, respectively (Table 1). The positive correlation (i.e., attraction) varied from 0.3% for the dbh to 8.0% for the TreePos and 13.5% for the Dead pattern (Table 1).

For tree position at the plot scale, the stand name ranked first in importance following by the basal area, tree density, mean temperature, and disturbance indicators (number of events in the last 100 yr; Table 2). For the dbh marks at the plot scale, the tree density, mean temperature, and country name variables best explained the spatial pattern (Table 2). The spatial patterns describing the living vs. dead trees at the plot scale were mainly explained by the plot age and mean temperature, but also the cumulative sum of the canopy area disturbed in the last 150 yr.

Spatial pattern variables interpretation

The interpretation of variables selected using VSURF models, such as tree density, annual mean temperature, or the cumulative sum of disturbed canopy area in the last 100 or 150 yr, was tested individually (Appendix S1: Fig. S2). The majority of them did not show any SD between the spatial patterns (Appendix S1: Fig. S2). At the stand scale, the selected parameters were not significant when the parameters were tested individually. However, in the case of the random labeling between living and dead trees at the stand scale, positive correlation between living and dead trees was mainly observed for stands under 205 yr of age and where the tree densities were above 540 trees/ha (Fig. 1).

DISCUSSION

Tree spatial pattern is driven by multiple processes in the Carpathian Mountains primary Norway spruce forests (Table 2; Fig. 1), including density-dependent mortality, disturbance legacies, and site conditions (i.e., site location and mean annual temperature; Table 2). Although the study stands were in mature or old-growth developmental stages, the developmental differences between younger and older stands (i.e., younger stands were defined as stands under 205 yr old with a tree density above 540 trees/ha) explain variations in tree patterns. Stands younger than 205 yr had a high proportion of positive correlation (i.e., attraction) between dead and living trees, with 71% of stands displaying a positive correlation (Table 2; Fig. 1). Density dependence is recognized as an important driver of early-successional forest dynamics (Coomes and Allen 2007, Larson et al. 2015), but its effects taper off as tree densities decline throughout maturation toward old-growth stages (He and Duncan 2000). Therefore, the density-dependent mortality observed in this study could be considered a relic from previous developmental stages, eventually leading to random mortality that is commonly observed in older, late-successional stands (Aakala et al. 2012, Larson et al. 2015).

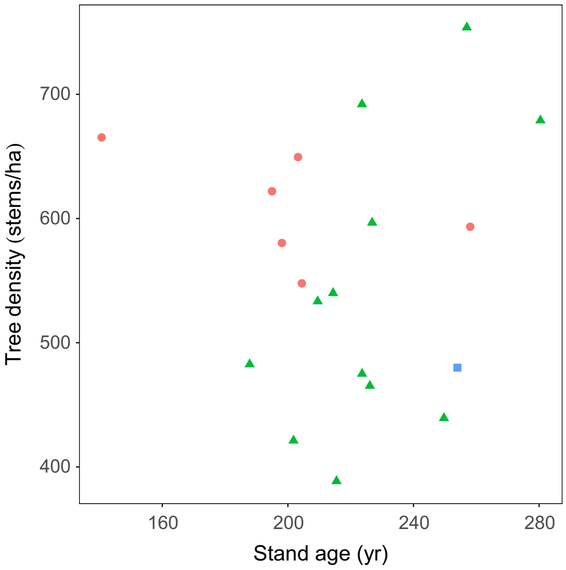

Fig. 1. Spatial pattern of living vs. dead trees in relation to the stand age (yr) and tree density (stem/ha) at the stand scale. Green triangles represent a random pattern, red circles denote a positive correlation (i.e., attraction) between dead and living trees, and blue squares indicate a negative correlation (i.e., segregation).

The uniformity of spacing between similarly sized trees (i.e., dbh spatial pattern displayed repulsion at the stand scale; Table 1) is considered to be the result of the density-dependent mortality that promotes spatial uniformity among surviving trees (Kenkel 1988, Yu et al. 2009). In the absence of interspecific competition (95.1% of the sampled trees were Norway spruce) and recent stand-replacing disturbances, the self-thinning process seems to be at least a partial driver of the spatial pattern. This suggests that the density-dependent mortality and the intraspecific competition during the earlier development stages had an impact on forest structure in later development stages (Kenkel 1988, Zhang et al. 2009, Gendreau-Berthiaume et al. 2016).

Density-dependent and independent processes also interact with site conditions, such as temperate and soil characteristics (Getzin et al. 2006, Piao et al. 2013). Of all the tested variables that described site conditions (i.e., mean annual temperature, slope, aspect, or site location to highlight any regional similarities, such as soil characteristics), only mean annual temperature appeared to play a role in spatial patterns (Table 2). The mean annual temperature can limit the tree growth and maximum size, leading to smaller-statured forests at higher altitudes (Holeksa et al. 2007). In addition, the mean annual temperature has indirect effects on mortality by promoting insect outbreaks (e.g., bark beetle outbreaks) during warmer periods. Warmer temperatures could also reduce available soil moisture for trees, which can lead to drought events (Williams et al. 2013). However, the mean annual temperature was significant only for one pattern: the dbh at the plot scale (random patterns were significantly linked to cooler sites compared to repulsion patterns; Appendix S1: Fig. S2b). Perhaps, slower growth in higher altitudes would allow random patterns to persist in post-disturbance sites; indeed, disturbances probably introduce randomness in stand structure. Thus, the mean annual temperature is not likely the main driver explaining spatial patterns of trees.

Slope, which might affect disturbance rates by increasing the number or size of gaps due to the higher tree vulnerability on steep slopes (Hunter and Parker 1993), aspect, which might influence tree growth rates by temperature and exposure to sunlight, and site location did not play a role in tree spatial patterns. Only the country location was selected from the random forest analysis for dbh at the plot scale (Table 2). Perhaps, steep slopes and northerly aspects in the Carpathian Mountains did not influence the disturbance rates through an increased number or size of gaps, as was expected (Hunter and Parker 1993).

Disturbances that occurred during earlier developmental stages (i.e., 100–150 yr prior to sampling) influenced current spatial patterns (Table 2). The cumulative sum of disturbed area from the last 100 and 150 yr selected by the random forest model (Table 2) corresponded with large disturbances in the western Carpathians some time during the mid-19th century (Janda et al. 2017). Related to these high-intensity disturbances, density-dependent mortality was ongoing 100–150 yr ago, which promoted self-thinning and repulsion among trees as they grew. In contrast, recent disturbances (i.e., 50 yr prior to sampling) did not have a significant impact on current tree spatial patterns. The disturbance intensity and frequency were lower in the past 50 yr (e.g., no recent stand-replacing disturbances in the study area; Svoboda et al. 2014, Janda et al. 2017, Bače et al. 2017), and the density-dependent mortality was minimized because there was less regeneration colonizing recent gaps; thus, self-thinning and tree repulsion were relatively minor processes among more mature cohorts. Other studies have demonstrated that stochastic, frequent, and small-scale disturbances can drive temperate forest structure by accelerating processes that promote greater complexity and random tree spatial patterns (Woods 2004, Fraver and White 2005, Halpin and Lorimer 2016, Meigs et al. 2017). Thus, in addition to self-thinning process and site condition effects, disturbances occurring during younger developmental stages leave a legacy evident in later developmental stages.

Our main finding was that tree spatial patterns of Norway spruce forests in the Carpathian Mountains developed from disturbances and the resultant density-dependent legacies that occurred about 100–150 yr ago, when the post-disturbance forest was composed of more areas in early development stages. We anticipated that density-dependent competition early in stand development would induce uniformity in tree distributions (Lutz et al. 2014); however, this study revealed some processes underlying tree distribution patterns in primary Norway spruce forests. Self-thinning processes during the density-dependent developmental stages induced tree diameter repulsion and then, in later developmental stages, density-independent mortality. Our study confirmed that site differences, as indicated by location, and mean annual temperature, which may influence stem packing, need to be considered in demographic treatments of forest processes (He and Duncan 2000, Piao et al. 2013). This dataset provides rare insight into the demographic processes involved in stand dynamics of monospecific forests, a critical component underlying mechanism-based predictions of numerous forest processes (Coomes et al. 2012). Applying similar efforts into studies of commingling, monospecific and mixed stands (especially forest types dominated by *Fagus sylvatica* L.) will provide deeper insight into the relationships between life-history differences and ecosystem functions, and it can help improve forecasts of shifting species distributions and forest functions.

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SUPPORTING INFORMATION

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