



## Natural development and regeneration of a Central European montane spruce forest

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### ABSTRACT

Montane Norway spruce forests of Central Europe have a very long tradition of use for timber production; however, recently there has been increasing concern for their role in maintaining biological diversity. This concern, coupled with recent severe windstorms that led to wide-spread bark beetle outbreaks, has brought the management of montane spruce forests to the forefront of public policy discussions in Central Europe. In order to shed light on the natural development and current structure of mature montane spruce forests, we established four 0.25 ha research plots in a semi-natural montane spruce forest in the Šumava Mountains (The Bohemian Forest), Czech Republic. We mapped all trees, extracted increment cores for age and growth-pattern analyses, and inventoried all current tree regeneration, including the substrates on which it was found. Stands were characterized by uni-modal tree diameter distributions and high basal areas (56.6 m<sup>2</sup> ha<sup>-1</sup> on average), indicating a natural transition from the stem exclusion phase towards the understory reinitiation phase. The stands showed largely single-cohort recruitment age structures, however, with recruitment spanning seven decades. Our analyses suggest that this cohort existed as advance regeneration prior to major disturbances in the late 1800s, which included post-bark beetle salvage logging. Spatial pattern analyses of living and dead stems combined, showed an increase in uniformity of living trees, pointing to the role of natural density-dependent mortality. However, past growth patterns and historical documentation suggest that low intensity canopy disturbances (wind and snow) also caused mortality and diversified canopy structure. Because the stands developed naturally over the past 120+ years and thus escaped thinning operations, high volumes of coarse woody debris (94 m<sup>3</sup> ha<sup>-1</sup>) and snag densities (546 stems ha<sup>-1</sup>) have accrued. Advance spruce regeneration was quite abundant and existed primarily on deadwood substrates, even though these occupied only a small percent of stand area. Because of salvage logging in the late 1880s, these stands do not qualify, according to the traditional paradigm, as natural spruce forests. As a result, they are recently subject to active management practices including salvage logging that remove dead and dying trees. Given the importance of deadwood for forest regeneration and recovery from disturbance, as demonstrated in this study, we argue that dead wood removal may limit future natural regeneration in these stands. Thus, the purported benefits of removing dead and dying trees from semi-natural forests must be carefully weighed against the potential detrimental impacts on natural spruce forest regeneration and biodiversity.

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### 1. Introduction

Forests dominated by Norway spruce (*Picea abies*) cover a significant area of Central Europe's mountainous region. These forests have a very long history of human use, including timber

production and the protection of human populations and infrastructures from avalanches and flooding (Kräuchi et al., 2000; Brang, 2001; Spiecker, 2003). Recent concerns, however, have shifted forest management objectives to address biodiversity conservation (Kräuchi et al., 2000). As a result, two national parks have recently been created – one in the Czech Republic (Šumava National Park), the other in Germany (Bayerischer Wald National Park) – to protect montane spruce forests. Together, these two adjacent parks cover more than 100 000 ha of forested landscape. The formation of these parks has raised many scientific and practical questions regarding forest management and conservation practices in this region (Jonášová and Prach, 2004, 2008; Jonášová and Matějková, 2007; Müller et al., 2008; Hais et al., 2009).

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One prerequisite for the proper management of montane spruce forests is an understanding of their natural disturbance dynamics at both the stand and landscape level (Kuuluvainen, 2002; Lindenmayer et al., 2006). Such information provides the foundation on which sustainable forestry practices can be developed (Bergeron and Harvey, 1997; Seymour and Hunter, 1999). Management practices developed in the absence of such information may be unnecessarily controversial, inefficient, or counterproductive.

A number of studies from Central Europe have addressed natural dynamics of mixed mountain beech-fir forests (e.g., Nagel et al., 2006; Nagel and Svoboda, 2008; Šamonil et al., 2009). Yet few studies in this region have addressed natural dynamics of subalpine or montane Norway spruce forests (Motta et al., 1999; Holeksa et al., 2007; Zielonka et al., 2010). To date, most of the studies on the natural dynamics of Norway spruce forests have come from Fennoscandinavia (Hofgaard, 1993; Kuuluvainen et al., 1998; Wallenius et al., 2005; Fraver et al., 2008). Such studies are scarce in Central Europe because (1) large areas of unmanaged spruce forests in which to evaluate natural disturbances are quite rare, and (2) the long history of human land use makes it difficult to disentangle natural from anthropogenic influences (Motta et al., 2002). Given the differences in climate and primary disturbance agents, it is unlikely that inferences drawn from studies outside this region apply to forests of Central Europe. For example, the research focus on large wildfires in Fennoscandinavian spruce systems (e.g., Engelmark et al., 1994) has little relevance to Central Europe. Here, convective windstorms and spruce bark beetle (*Ips typographus*) outbreaks represent the potential large-scale disturbances (Dobrovlný and Brázdil, 2003; Wermelinger, 2004). Historically, these disturbances have received little research attention, in part because they were thought to play a minor role in forest dynamics and biodiversity (Korpel, 1995; Leibundgut, 1987), and in part because the amount of damage they caused was thought to be the result of previous forest management practices. However, a recent chain of events – severe windstorms in 1986, 1999, 2007, and 2008 that caused widespread forest damage leading to extensive bark beetle outbreaks – has called attention to such disturbances, suggesting their role may be greater than had been previously thought. These events have brought the management of montane spruce forests, particularly the practice of salvage logging, to the forefront of public policy discussions in Central Europe.

Thus, the general objective of this study was to reconstruct the disturbance history and development of a semi-natural montane Norway spruce forest in order to determine how these events have shaped its current structure and composition. The study site, located in the Šumava Mountains of the Czech Republic, represents the largest and best preserved natural (origin and development without human intervention) and semi-natural (minimal human intervention) spruce forests in the country. A previous study concluded that the forest structure differed throughout an old-growth portion of this site, probably as a result of the past disturbances and changing site conditions (Svoboda and Pouska, 2008). In this current study we examine an additional portion of this site that possesses a number of features characteristic of mature semi-natural forest, despite the known history of disturbance and salvage logging, which took place 130–140 years ago. In central Europe, where true old-growth forests (forests that have escaped harvest and reached an advanced stage of development) are quite rare, information on regeneration, stand development, and stand structure from such semi-natural forests is the best alternative for informing management decisions intended to emulate natural processes (Kulakowski and Bebi, 2004; Motta and Edouard, 2005). Our specific objectives were to (1) determine the stand origin and disturbance history of this site using historical documents and methods of dendrochronology, (2) assess the role of density-dependent mortality in shaping current forest structure using spatial pattern analyses,

and (3) evaluate seedling substrate preferences to further elucidate stand origin and development. Results from this study can inform management decisions in light of the recent establishment of national parks and subsequent major disturbances.

## 2. Methods

### 2.1. Study area and land-use history

This study was conducted in Šumava National Park (the Bohemian Forest), southern Czech Republic. The study area is immediately adjacent to a 600-ha tract of what is considered the best example of an old-growth spruce forest in the Czech Republic. The area lies on a gentle north-facing slope (elevation about 1100–1200 m) below the old-growth site on the ridge between Třístoličník and Trojmezna (48°47'N, 13°49'E). The mean annual precipitation at this altitude is about 1200–1400 mm, and the mean annual temperature is about 4 °C (Svoboda et al., 2006b). The soil substrate in this area consists of Lithic Leptosols, Hyperskeletal Leptosols (Humic and Dystric), and Dystric Cambisols. These soils are derived from biotitic coarse grained granite. The forest is dominated by Norway spruce (*P. abies*), with rowan (*Sorbus aucuparia*) forming a minor component (Svoboda et al., 2006a; Svoboda, 2007; Svoboda and Zenáhlíková, 2009). The Bohemian Forest was in the past affected by acid deposition and has been recovering during last decade (Šantrůčková et al., 2007).

We selected the study area in part by using historical forestry management plans that contained age structures, species composition, logging intensity, and areas disturbed by wind, bark beetle and salvage logging, with data extending back to 1856 (Jelínek, 2005). These plans were digitized and linked with aerial photos (historical and recent), and recent forestry plans in a GIS. Based on these GIS overlays, we selected an area of about 300 ha that had been classified as old-growth forest before 1868. Documented windstorms in 1868 and 1870 led to wide-spread outbreaks of the spruce bark beetle in this area, which began around 1869 and persisted at least through 1880–1890 (Jelínek, 2005). The salvage logging that followed transformed the area into a young post-disturbance stand. Maps from 1902 show the area to be in the 0–20 year age class (Jelínek, 2005). There were no records of tree planting in management plans.

The forest developed naturally (i.e., without human intervention) in subsequent decades. Canopy disturbances from snow and wind damage between 1922 and 1933 (Jelínek, 2005) caused patchy tree mortality, which no doubt affected competitive interactions and growth rates in surviving trees. As of 1948 the study area formed part of the large no-entry military zone, and no major management measures were undertaken until 1989 when the military zone was abolished. In 1991, Šumava National Park was established, and the study area became part of the park's core protected zone. However, patchy wind damage and bark beetle outbreaks in the early 1990s created controversy regarding management, and the area was ultimately withdrawn from the core zone in 1995, at which time about half of the area was salvage logged.

### 2.2. Data collection

Four 0.25 ha (50 m × 50 m) permanent sampling plots (plots A–D) were established in the study area in 2006 and 2007. Plot locations were selected according to the following constraints: (1) plots must be centered within the larger remnants of closed-canopy forest to avoid edge effects; (2) plots must be dispersed as regularly as possible across the study area; (3) plots could not include anomalous site conditions such as stream corridors, rock outcrops, or evidence of recent salvage logging.

Electronic and laser measuring devices linked to a GIS (Field-Map®, Monitoring and Mapping Solutions, Ltd.; [www.fieldmap.cz](http://www.fieldmap.cz)) were used to establish the plots, map all trees and down woody debris (DWD), map and measure tree crown projection areas, and establish a grid for regeneration surveys. The areas of individual tree crowns were summed in a GIS to calculate the percent canopy openness for each plot. For each tree  $\geq 5$  cm diameter at breast height (1.3 m, DBH), we recorded DBH and height; for each stump ( $\leq 1.3$  m height,  $\geq 10$  cm basal diameter), we recorded top diameter; and for each piece of DWD  $\geq 10$  cm diameter and  $\geq 2$  m length, we recorded large and small end diameters, length, and decay class (using a five-class system as per Maser et al., 1979). The volume of each DWD piece was calculated using the conic-paraboloid formula, which has greater accuracy than traditional formulae (Fraver et al., 2007). Volumes of pieces in decay classes IV and V were multiplied by cross-sectional height–width ratios (0.86 and 0.50, respectively) to adjust for collapse during decay (ratios determined from decayed Norway spruce in Sweden, unpublished data).

To analyze tree age structure and radial growth patterns, we divided the plot into twenty five 10-by-10 m cells and extracted one increment core at breast height from the canopy tree nearest the cell center. We then conducted a complete inventory of tree regeneration by dividing each plot into hundred 5-by-5 m cells. Within each cell, we recorded the number and heights (in 10-cm classes) of spruce and rowan saplings  $>20$  cm height, but less than 5 cm DBH. We also recorded the substrates occupied by each, using the following four categories: down logs, tree stumps, leaf litter and vegetation. Spruce and rowan seedlings  $<20$  cm were surveyed in this same way, but only in the central 16 cells in each plot.

### 2.3. Data analysis

#### 2.3.1. Stand origin and disturbance history

Increment cores were attached to wooden mounts and shaved with a scalpel before analyses. The cores were visually cross-dated by identifying narrow marker years (Yamaguchi, 1991). Ring widths were measured to the nearest 0.01 mm using a stereomicroscope and a Time-Table sliding-stage measuring device in conjunction with PAST32 software. Following measurement, cross-dating was verified with COFECHA software (Holmes, 1983). For cores that missed the pith, we used Duncan's (1989) method to estimate the number of years missed, based on the mean growth rate of the innermost five complete rings. Because Norway spruce seedlings can become established and persist for decades under shade, we consider an individual to be recruited into the stand only when it surpasses breast height. Thus no attempt was made to estimate tree ages since germination; we simply refer to the number of annual rings at breast height as the recruitment age (we return to this topic in Section 4).

We evaluated each tree-ring series (i.e., growth pattern derived from each core) for evidence of rapid early growth, as such evidence indicates the tree experienced open, free-to-grow conditions at the time it reached breast height (Lorimer and Frelich, 1989). Trees were considered to be open-recruited if the mean ring width for the first 5 years in the series exceeded 1.93 mm (determined by binary logistic regression of sapling growth in open and closed-canopy positions, Janda et al., in press), and the subsequent growth pattern was declining, parabolic, or flat (Frelich, 2002).

To further shed light on stand development, we produced standardized growth chronologies, using all properly dated cores, to evaluate stand-level growth patterns through development. We separated the data into two groups: trees forming members of a large cohort established in the 1890s, and those that existed, presumably as advance regeneration, prior to that large cohort. The

chronologies were developed using the ARSTAN program (Cook and Krusic, 2005) by first fitting a horizontal line through the mean ring width for each tree-ring series, then dividing ring widths by the fitted values, resulting in a unit-less index for each year in the series (Fritts, 1978). Individual indexed series were then averaged to produce the two standardized chronologies. Using the horizontal line, as opposed to a curve-fitting technique, does not detrend the series, and thus maintains low- to medium-frequency growth trends, assumed to be largely the result of disturbance (Veblen et al., 1991).

#### 2.3.2. The role of density-dependent mortality

We used spatial pattern analyses of living and dead trees to shed light on the role of density-dependent mortality in past stand development. First, we tested for a shift from aggregation toward uniformity through stand development, which would suggest density-dependent thinning from competition (Kenkel, 1988). Second, we tested if the pattern of living trees was more uniform than that of the living and dead trees combined, also implicating competition as a driving factor (Duncan, 1991; Shackleton, 2002).

A pair-correlation function (Wiegand and Moloney, 2004) was used for analysis of the spatial patterning. This function is analogous of the widely used Ripley's  $K(r)$  function (Ripley, 1981; Diggle, 1983), but is considered to be more powerful at detecting spatial patterns across scales (Wiegand and Moloney, 2004). Approximate 95% confidence envelopes were determined using the 5th lowest and 5th highest value of 99 Monte Carlo simulations under the complete spatial randomness null model. Note that this is not a goodness-of-fit test with exact confidence intervals (Loosmore and Ford, 2006; Getzin and Wiegand, 2007). All analyses were performed using the Programita software (Wiegand and Moloney, 2004).

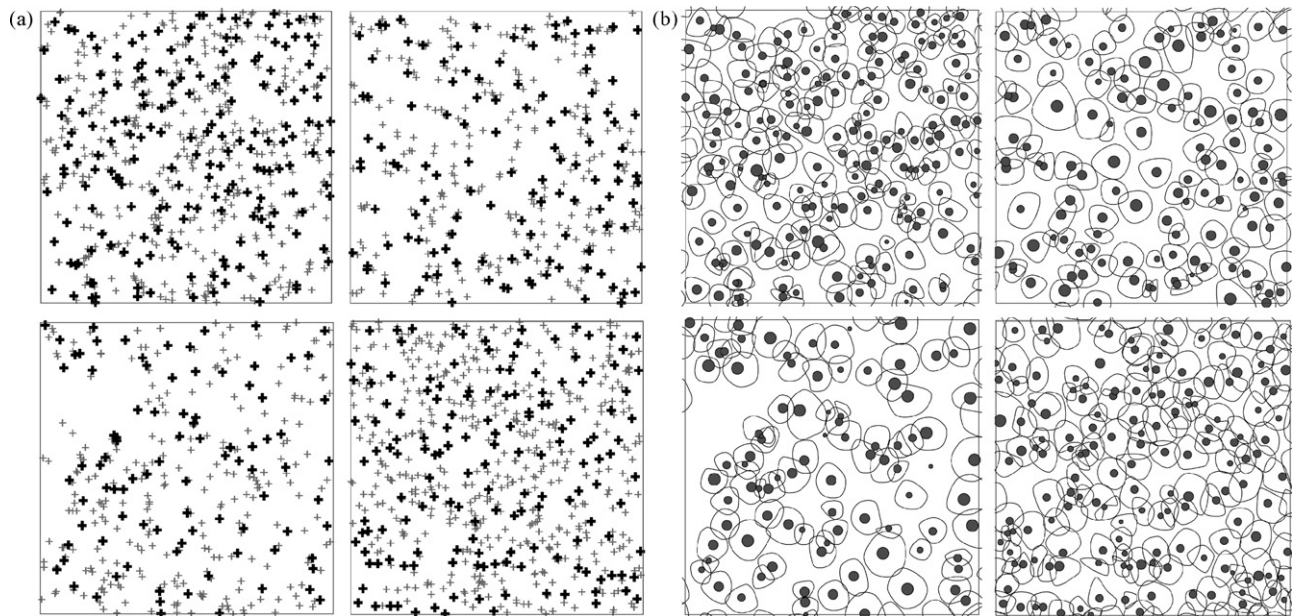
To address the first question, we assessed the spatial pattern of live and dead trees (pre-mortality pattern), testing against a heterogeneous Poisson process. A heterogeneous Poisson process was chosen because our plots were influenced by first-order heterogeneity (Fig. 1). Using methods proposed by Wiegand and Moloney (2004), a circular moving window with a fixed radius  $R$  was used to estimate intensity (i.e., mean number of events per unit area). Therefore, our results may be interpreted only up to a radius of  $R = 10$  m.

To address the second question, we compared the spatial pattern of live trees (post-mortality pattern) to that of live and dead trees combined. We reasoned that a shift from a random distribution of live and dead trees (reflecting the pattern of early tree establishment) to a uniform distribution of live (i.e., surviving) trees would suggest density-dependent mortality from competition. We then determined if the live trees formed a uniform spatial distribution using univariate random labeling as the null model (Wiegand and Moloney, 2004). Specifically, this test assesses whether the surviving trees are a random subset of the joined (live and dead spatial) pattern. This was accomplished by computing the function  $g(r)$  from the observed data, then randomly re-sampling sets of dead trees from the joined pattern and generating the appropriate confidence limits. A similar approach was used by Getzin et al. (2006).

#### 2.3.3. Tree regeneration and substrate preferences

We used the  $\chi^2$  statistic to test the null hypothesis that tree regeneration density was independent of substrate type. The area occupied by litter and vegetation substrates (i.e., microsites) was visually estimated in each 5-by-5 m cell. For down-log and tree-stump substrates, the area was calculated as a trapezoid (logs) or a circle (stumps) projected onto the ground. Data were pooled from all cells and plots for analysis.





**Fig. 1.** (a) Stem maps of living (bold dark cross) and dead (grey cross) trees, showing a general trend toward spatial uniformity in living trees when compared the combined pattern of living and dead trees, suggesting density-dependent mortality. (b) Maps of living trees and crown projection areas (dot size proportional to tree diameter), showing considerable canopy patchiness, even though these sites have not reached the old-growth stage. In both panels, Plots A and B are in the upper left and right, and Plots C and D are in the lower left and right.

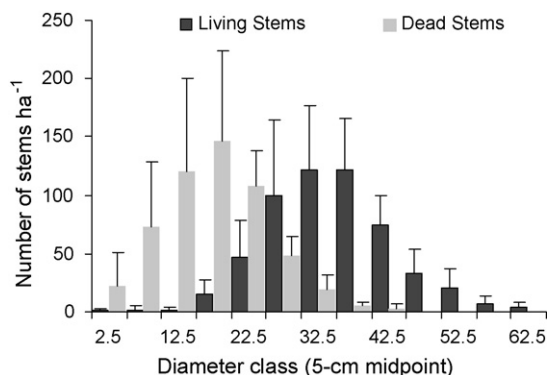
**Table 1**  
Structural characteristics of the study plots. BA = basal area ( $\text{m}^2 \text{ha}^{-1}$ ); DWD = down woody debris; seedlings are tree stems <20 cm height; saplings are  $\geq 20$  cm height.

	Live trees		Snags		Saplings Stems $\text{ha}^{-1}$	Seedlings Stems $\text{ha}^{-1}$	DWD vol. $\text{m}^3 \text{ha}^{-1}$	% Canopy Openness
	BA $\text{ha}^{-1}$	Stems $\text{ha}^{-1}$	BA $\text{ha}^{-1}$	Stems $\text{ha}^{-1}$				
Plot A	63.8	732	19.2	868	3600	52,225	51.3	30.7
Plot B	60.2	480	20.7	548	5664	35,325	61.8	36.6
Plot C	49.3	364	10.5	276	13,404	20,650	123.6	41.6
Plot D	52.6	628	11.8	492	24,560	62,925	141.0	19.0
Mean	56.5	551	15.6	546	11,807	42,781	94.4	32.0

### 3. Results

#### 3.1. Stand structure

Norway spruce accounted for nearly 100% of basal area, with rowan the remainder. Data pooled across plots revealed a mean live-tree basal area of  $56.5 \text{ m}^2 \text{ha}^{-1}$  and density of  $551 \text{ trees ha}^{-1}$ , with snag basal area at  $15.6 \text{ m}^2 \text{ha}^{-1}$  and density of  $546 \text{ snags ha}^{-1}$ .



**Fig. 2.** Diameter distribution of the living and dead trees (plots pooled) showing the living trees to be larger than the dead trees, suggesting competition as the mortality agent as stands developed through the stem exclusion stage. Errors bars represent standard deviations.

The mean seedling density was  $42781 \text{ ha}^{-1}$ , of which 100% were Norway spruce. The mean sapling density was  $11807 \text{ ha}^{-1}$  of which 91% were Norway spruce, the remainder being rowan. The mean DWD volume was  $94.4 \text{ m}^3 \text{ha}^{-1}$ , after adjusting for collapse of advanced decayed pieces (see Section 2.2). Though the current vertical canopy structure is rather homogenous within a site (i.e., canopies occurring in one strata), the horizontal canopy structure is quite patchy, as shown in Fig. 1. In addition to this within-site patchiness, canopy openness varied quite a bit from plot to plot, with a mean of 32% openness ( $\text{SD} = 9.7$ ). Coarse woody debris existed across the range of decay classes; however, it had highest abundance and volume in classes III and IV (sites pooled). Table 1 provides additional plot-level structural data. Both living and dead spruce trees showed unimodal bell-shaped diameter distributions (Fig. 2, sites pooled), with the peak in dead-stem diameters about 15–25 cm, and the peak for the live stems about 30–40 cm.

#### 3.2. Stand origin and disturbance history

Age structures clearly show a major cohort being recruited in the 1890s and the two decades that followed (Fig. 3). However, numerous trees had become recruited in the decades prior to 1890, resulting in a prolonged recruitment period spanning seven decades (Fig. 3). Analyses of growth patterns suggest open conditions during four of these early decades, as sizeable percentages of trees recruited in the 1870s, and 1890s through 1910s met the radial-growth criteria for open-grown conditions (Fig. 3). Further,



sphere (Hofgaard, 1993; Kuuluvainen, 1994; Fraver and White, 2005). The combination of these successive events – establishment of advance regeneration, windstorm, bark beetle outbreak, and salvage logging, all occurring during early stand development – explains the prolonged recruitment period, which spans seven decades.

Several lines of evidence reveal that this forest has undergone natural developmental processes following its initiation in the late 1800s. The relatively high density and basal area of living trees (56.5 m<sup>2</sup> and 551 trees ha<sup>-1</sup>), the high density of dead trees (546 snags ha<sup>-1</sup>), coupled with the unimodal diameter distributions depict a mature stand in transition from stem exclusion to understory re-initiation development stages (Oliver and Larson, 1996). The declining stand-level growth pattern, following an initial period of rapid growth, is also indicative of this stage of stand development (Veblen et al., 1991), as is the relatively uniform, single-strata canopy structure. This uniformity existed despite the prolonged recruitment period (spanning seven decades), which is consistent with Korpel's (1995) finding that Central European spruce forests in favorable site conditions develop more or less homogenous closed canopies, even if within-stand age diversity reaches 100 years or more.

Competitive interactions, in part mediated by low-severity canopy disturbances, have also played an important role in the natural development of this forest. The post-mortality spatial pattern of living spruce stems, compared to the pre-mortality pattern of living and dead trees, was more uniform in three of the four plots, which suggests density-dependent mortality as a result of competition for resources (He and Duncan, 2000; Shackleton, 2002; Castagneri et al., 2010). Perhaps not coincidentally, the plot on which this general pattern was not seen (Plot C) had the highest percent canopy openness and correspondingly lowest density of living trees, suggesting that canopy disturbances have played a larger role, thereby disrupting the spatial pattern that would have developed primarily from competition. The sheer number of snags seen on all plots (exceeding that of trees) further attests to the strong influence of past competition in this forest. Canopy disturbances, however, alter these competitive interactions by selectively removing trees, thereby increasing resource availability to surviving neighbors. Documented canopy disturbances from snow and wind in the 1920s (Jelínek, 2005) can explain the stand-level variability in growth during that time (Fig. 1), and such disturbances likely explain further variability in the 1940s and 1960s. Additional evidence for such disturbances were seen as abrupt and sustained increases in growth (i.e., growth releases) on a number of individual trees during these decades (data not shown). Finally, the high growth variability seen in the 1990s is attributed to documented wind storms at that time (Fig. 3). The patchiness in canopy structure caused by these disturbances can be seen in maps of canopy projections for each plot (Fig. 1). Thus both competition and low-severity disturbance by wind and snow influence growth rates and mortality, and they contribute to horizontal structural diversity at the stand level.

However, competition and low-severity disturbances alter stand structure in quite different ways. In this case of competition, smaller stems are more likely to die because of poor resource acquisition (Kozłowski et al., 1991; Oliver and Larson, 1996). This result was borne out in the diameter distributions of living and dead trees: although both had uni-modal distributions, the peak in the dead-tree distribution was about 40 cm lower than that of the living trees. In the case of disturbances, larger trees with exposed crowns are more likely to be killed by wind or snow loads (Brokaw et al., 2004; Canham et al., 2001). Indeed, in these stands we observed numerous large trees with damaged crowns and broken tops.

By affecting larger and smaller trees differently, competition and wind disturbance, in combination, create an abundance and

diversity of deadwood sizes. The volumes of coarse woody debris reported here fall within the natural range of variability for true old-growth spruce forests from throughout the northern hemisphere (e.g., Kuuluvainen et al., 1998; Jonsson, 2000; Siitonen et al., 2000; Fraver and White, 2005). The snag volumes reported here are unusually high, even for old-growth, owing to the transition from stem exclusion to understory re-initiation.

#### 4.2. Tree regeneration and substrate preferences

The current abundance of spruce seedlings and saplings was strongly and positively linked to the presence of coarse woody debris. Even though coarse woody debris substrates occupied only several percent of the total plot area, the proportion of spruce saplings growing on such sites ranged from 50 to 80%. The importance of these fallen logs and decayed stumps as 'nurse logs' for spruce regeneration has been well recognized in Central Europe (Hunziker and Brang, 2005; Motta et al., 2006; Zielonka, 2006; Baier et al., 2007; Bače et al., 2009). Because of this strong link between spruce regeneration and coarse woody debris, the pattern of regeneration was not spatially random and varied according to substrate. In particular, regeneration often formed strikingly linear patterns (not shown), reflecting the presence of fallen logs. This linearity can also be seen in the current tree strata, at times in conjunction with stilt roots, both reflecting the existence of former suitable nurse logs, which would have been present during stand establishment in the late 1800s.

The extremely high density of advance regeneration (Table 1) is attributable to a combination of abundant suitably decayed nurse logs and the presence of small canopy openings, which have led to current canopy openness ranging from about 19–42% among plots, as well as considerable patchiness in canopy cover (Fig. 1). Contrary to our results, relatively lower densities of advance spruce regeneration have been reported in montane forests in this same geographical region (Jonášová and Prach, 2004; Kupferschmid et al., 2006; Rammig et al., 2007; Heurich, 2009). However, in contrast to our study, most sites included in these studies had been repeatedly thinned to control bark beetle outbreaks as well as other pests, which removed the source of dead and dying trees that ultimately become suitable nurse logs. Thus, our results highlight the importance of coarse woody debris, as well as partial canopy openings, for the regeneration of spruce in these forests.

### 5. Conclusions and implications for forest management

Results from this mature, semi-natural montane spruce forest show that, in the absence of human intervention, natural processes such as density-dependent mortality and low-severity canopy disturbances have created ample deadwood, both as snags and down woody debris, even though this forest has currently not reached the old-growth stage where such structures might be expected. These processes have also created considerable horizontal patchiness, further adding to the overall structural heterogeneity of the site. The high coarse woody debris volumes, which lie within the natural range of variability of true old-growth spruce forests (above), as well as the occurrence of coarse woody debris in various sizes and states of decay, also highlight the conservation value of these stands for maintaining deadwood-dependent organisms (Martikainen et al., 1999; Siitonen, 2001; Kuuluvainen et al., 2002; Penttilä et al., 2004; Pouska et al., 2010). Our results also show that these abundant downed logs serve as the primary substrates for successful spruce seedling establishment. The ability of this forest to accrue advance regeneration, even at the end of the stem exclusion stage, is critical for forest recovery following future disturbances, such as windthrow or bark beetle outbreak.



In Central Europe, removing dead, dying or damaged trees during thinning or salvage operations is a common practice in montane spruce stands. The practice is justified on the grounds that it will reduce their susceptibility to attack by various pests or their vulnerability to damage once attacked (Wermelinger, 2004). Repeated entries of these types have led to dramatic reductions in coarse woody debris abundance in central Europe (Bütler et al., 2004; Lachat and Bütler, 2009). As a result, the quality and quantity of nurse logs suitable for spruce regeneration is correspondingly low, which dramatically reduces the density of advance regeneration. Recent concerns over the failure of natural spruce recruitment following stand-replacing disturbances in Central Europe (Kupferschmid et al., 2006; Rammig et al., 2007) might be most easily attributed to the absence of nurse logs owing to these past management practices. Because dead wood requires several decades to decay to the point of providing suitable seedbeds (Zielonka, 2006), these practices compromise spruce regeneration for decades beyond their initial occurrence. Without dead wood to support spruce regeneration, we must rely on artificial regeneration (i.e., planting), which is especially expensive and laborious in mountain regions, and may not be feasible over large areas. Thus, the purported benefits of removing dead and dying trees from semi-natural forests must be carefully weighed against the potential detrimental impacts on natural spruce forest regeneration and biodiversity.

Because of salvage logging in the late 1800s the fairly homogeneous vertical canopy structure, these stands do not qualify – according to the traditional paradigm – as natural spruce forests (Korpel, 1995). By not qualifying, they are thought to have limited conservation value, and are thus subject to active management practices, including salvage logging. However, recent studies suggest that this paradigm should be at least partly reconsidered (Kulakowski and Bebi, 2004; Holeksa et al., 2007; Svoboda and Pouska, 2008; Zielonka et al., 2010), because semi-natural stands may also contain significant structural elements that support biodiversity. Infrequent moderate- to high-severity disturbances such as windstorms and bark beetle outbreaks in semi-natural forests may diversify these stands, thereby enhancing these structures (Müller et al., 2008). The stands and stand structures evaluated in the current study are ideal examples of semi-natural forests that developed following this type of high-severity disturbance. In fact, Svoboda and Wild (2007) showed that in the Bohemian Forest region several thousand hectares of forests similar to the one evaluated here may exist.

The conservation value of semi-natural, maturing spruce forests has been documented elsewhere in northern Europe. For example, both Storaunet et al. (2000) and Jönsson et al. (2009) found that spruce forests 100–150 years post-disturbance (i.e., comparable in age to stands in the current study) contained many, but not all, the important structures of true old growth. This fact forms the basis of the *woodland key habitat* programs of Nordic and Baltic countries, in which areas are voluntarily set aside, regardless of their management histories, because they support structures and species important for biodiversity protection. Adopting such a view in Central Europe may be timely given the demonstrated structural attributes of semi-natural stands, as well as the scarcity of true old-growth forests in this region.

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