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Disturbance history of an old-growth sub-alpine *Picea abies* stand in the Bohemian Forest, Czech Republic

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Abstract

Questions: What historical natural disturbances have shaped the structure and development of an old-growth, sub-alpine *Picea abies* forest? Are large-scale, high-severity disturbances (similar to the recent windthrow and bark beetle outbreaks in the region) within the historical range of variability for this forest ecosystem? Can past disturbances explain the previously described gradient in stand structure that had been attributed to an elevation gradient?

Location: Šumava National Park (the Bohemian Forest) of the southwest Czech Republic.

Methods: We reconstructed the site's disturbance history using dendroecological methods in a 20-ha study plot, established to span an elevation gradient. Growth patterns of 400 increment cores were screened for: (1) abrupt increases in radial growth indicating mortality of a former canopy tree and (2) rapid early growth rates indicating establishment in a former canopy gap.

Results: Spatial and temporal patterns of canopy accession varied markedly over the 20-ha study area, resulting in disturbance pulses that corresponded to an elevation gradient. On the lower slope of the plot, the majority of the trees reached the canopy during two pulses (1770–1800 and 1820–1840), while most trees on the upper slope accessed the canopy in one pulse (1840–1860). Historically documented windstorms roughly coincide with peaks in our disturbance reconstruction.

Conclusions: Our study provides strong evidence that these forests were historically shaped by infrequent, moderate- to high-severity natural disturbances. Our methods, however, could not definitively identify the agent(s) of these disturbances. Nevertheless, the recent mid-1990s windstorm and the ensuing spruce bark beetle outbreak may provide an analogue for past disturbance, as the duration and severity of these events could easily explain past patterns of growth response and recruitment in our results. Thus, it seems reasonable to assume the interaction of windstorms and bark beetles seen in the contemporary landscape has occurred historically. Finally, our results suggest that the previously documented elevation gradient in forest structure may not be related to elevation *per se* (lower temperatures and shorter growing season) but rather to changes in disturbance severity mediated by elevation.

Introduction

Natural disturbances are key drivers of forest ecosystem dynamics. Disturbances such as fire, windstorms and insect outbreaks strongly influence forest structure and composition (Pickett & White 1985; Foster et al. 1998). Natural disturbances play a major role in maintaining biological diversity, in part by creating or sustaining biological legacies, which provide critical substrates for a variety of organisms that may otherwise disappear from a site (Lindenmayer et al. 2006, 2010; Muller et al. 2008; Swanson et al. 2011). Variability in disturbance frequency, spatial pattern and severity, as well as the interaction between multiple disturbances, often create a

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mosaic of forest patches across large landscapes (Turner et al. 1998; Foster & Tilman 2000; Fraver et al. 2009; Turner 2010; Derose & Long 2011). Therefore, knowledge of the natural disturbance regime is essential for understanding forest dynamics at both the stand and landscape scale.

Throughout much of the 20th century, natural forest ecosystems in the temperate zone of Europe were described as existing in a dynamic equilibrium, characterized by a shifting fine-scale mosaic of different forest development stages (Leibundgut 1982; Remmert 1991; Korpel 1995). Within this conceptual framework, dynamics were thought to be maintained by endogenous gap-phase processes (e.g. senescence of old trees), while the influence of periodic larger-scale disturbances was largely ignored. Over the past decade, however, there has been increased emphasis on the dynamic character of forest ecosystems and the role of natural disturbances in driving ecosystem change in this region. For example, many recent studies have focused on the causes and consequences of natural disturbances, such as windthrow and bark beetle outbreaks, in European temperate forests (Splechtna et al. 2005; Nagel et al. 2006, 2010; Nagel & Svoboda 2008; Firm et al. 2009; Kucbel et al. 2010; Zielonka et al. 2010). These studies have made significant contributions to our understanding of natural forest ecosystems in this region.

Much of this recent work has been carried out in small, old-growth remnants in the Carpathian and Dinaric Mountains, particularly in mixed forest types dominated by *Fagus sylvatica* and *Abies alba*. Fewer studies have characterized the disturbance regime in sub-alpine forests dominated by *Picea abies*, yet these forests cover extensive mountainous areas of Central and Eastern Europe. Based on recent severe windstorms and spruce bark beetle (*Ips typographus*) outbreaks that caused widespread damage to *P. abies* forests in this region (Grodzki et al. 2003; Svoboda & Pouska 2008; Zielonka et al. 2010), there is reason to believe that the disturbance regime in these forests differs from that of mixed forest types, where disturbances primarily cause small- to intermediate-scale canopy damage (Nagel & Svoboda 2008; Kucbel et al. 2010).

The few studies that have examined disturbance histories in remaining sub-alpine, old-growth *P. abies* forests in Eastern Europe lend support to this view. In the Tatra Mountains of Slovakia, Zielonka et al. (2010) documented moderate to high-severity windthrow events during the past two centuries. Similarly, Svoboda et al. (2010) described stand development following a historical high-severity windthrow followed by a bark beetle outbreak in the Bohemian Forest of the Czech Republic. Finally, Holeksa et al. (2007) identified large patches of homogenously structured *P. abies* forests in the Western Carpathians that may have originated after large, stand-replacing disturbances.

The idea that large-scale, high-severity disturbances play an important role in natural *P. abies* forests in Central and Eastern Europe challenges the traditional view of forest dynamics for this system. This view holds that such events affect only forests made vulnerable through previous management practices, especially those that promoted even-aged monocultures. Determining whether large-scale windstorms and spruce bark beetle outbreaks are part of the historical range of variability (HRV) in sub-alpine *P. abies* forests in the region is important for two reasons. First, understanding the HRV has important implications for ecosystem-based resource management (Veblen 2003), particularly when resource managers are faced with decisions regarding salvaging vs non-intervention in post-disturbance situations (Grodzki et al. 2003; Jonasova & Prach 2004; Jonasova & Matejkova 2007; Svoboda et al. 2010). Second, retrospective studies of the HRV provide a context to evaluate the influence of future climate changes on disturbance processes and ecosystem dynamics. If climate change predictions prove true, the region is likely to experience an increase in the frequency and severity of both windstorms (Leckebusch & Ulbrich 2004; Leckebusch et al. 2008; Donat et al. 2010; Usbeck et al. 2010a,b and bark beetle outbreaks (Hlasny & Turcani 2009; Jonsson & Barring 2011; Jonsson et al. 2011). The interaction of these processes is especially important because spruce bark beetle outbreaks are often triggered by the simultaneous occurrence of large-scale windthrow (Wermelinger 2004; Okland & Bjornstad 2006) and high spring and summer temperatures (Aakala et al. 2011; Lausch et al. 2011). For example, the combination of these factors triggered an outbreak between 1990 and 2010 that killed about 10 000 ha of *P. abies* forests in the national parks in the Bohemian Forest on the border between Germany and the Czech Republic (Hais & Kucera 2008; Hais et al. 2009; Lausch et al. 2011).

The goal of this study was therefore to reconstruct the disturbance history of an old-growth, sub-alpine *P. abies* forest in the Bohemian Forest of the Czech Republic using dendroecological methods. The specific objectives were to: (1) determine whether large-scale, high-severity disturbances (similar to the recent windthrow and bark beetle outbreaks in the region) occurred historically; (2) identify the primary historical disturbance agents (e.g. wind, spruce bark beetle or their interaction); (3) estimate tree canopy mortality due to the recent bark beetle outbreak and the size and age structure of the post-outbreak tree cohort; and (4) determine whether past disturbances could explain the previously described gradient in stand structure that had been attributed to changes in elevation.

Methods

Study area and land-use history

This study was conducted in Šumava National Park (the Bohemian Forest) in the southwest Czech Republic. The study area is located in an old-growth forest remnant known as Trojmezná, which lies on a gentle north-facing slope at an elevation of about 1200–1350 m. Trojmezná is located on the ridge between Třístoličník and Plechý (48° 47′N, 13°49′E), which forms the border between the Czech Republic, Germany and Austria. Mean annual precipitation is about 1300 mm, and annual temperature averages about 4 °C. The soils consist of Leptosols and Dystric Cambisols derived from biotitic, coarse-grained granite. The study area is dominated by old-growth Norway spruce (*P. abies*) stands (Svoboda et al. 2006a,b; Svoboda & Pouska 2008) with abundant dead wood and rare wood-decomposing fungi (Pouska et al. 2010, 2011). In the past, the Bohemian Forest was partly affected by acid deposition but has been recovering during last decade (Santruckova et al. 2007).

The forest structure in the study area was described in Svoboda & Pouska (2008), who showed that the lower part of the area has a more heterogeneous structure, while the upper part near the ridge is more homogeneous. Based on historical forest maps, in 1874 the lower area was classified as an old-growth forest and the upper area as a two-storey stand with 30- and 70-year-old tree layers (Jelínek 2005) (Fig. 1). Historical management plans from 1870 to 1950 describe no regular logging activity in the area. During this time, the area was considered a protected forest. Since 1933, the entire study area has been part of a strictly protected nature reserve. Thus, it is very likely that the area was never significantly affected by forest management. High-mountain areas on the Czech side of the Bohemian Forest were still inaccessible in the first half of the 19th century, and the region was far from human settlement. Moreover, half of the stands in the southern Bohemian Forest region were still classified as old-growth according to the forest inventory from 1840. At this same time, the well-known Boubín old-growth forest was established, which is located about 20 km inland (closer to human settlement) from the study area, providing further evidence that the study area remained unharvested. It is also unlikely that harvesting based on the German or Austrian sides of the ridge affected this area, as this would require that timber be transported uphill, which is unlikely given the historical practice of winter harvests and log transport by sled. Nevertheless, we cannot entirely rule out the influence of past human activities in the study area; however, minor human impact should have little to no bearing on our results.

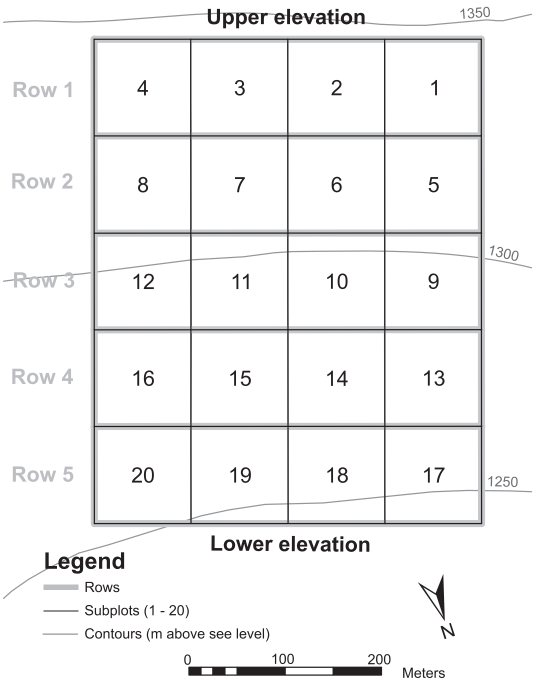

Fig. 1. Map of the study area showing the study plot (500 × 400 m) with 20 1-ha subplots (square cells). The grey rectangles show subplots merged to five rows (rows 1–5) according to their similarity in elevation, median age and disturbance history (see Fig. 2).

Although forests surrounding the study area were severely disturbed by windstorms in 1868 and 1870, which were followed in turn by widespread bark beetle outbreaks and salvage logging (Jelínek 2005; Svoboda et al. 2010), these events were not recorded for the study area. In 1991, Šumava National Park was established, and the study area became part of the park's core protected zone. A bark beetle outbreak began in the area in 1996, followed by the Kyrill windstorm in 2007 that struck the upper portion of the study area, which further intensified the bark beetle outbreak. By 2010 most canopy trees were dead on the Czech side of the ridge.

Field methods

In 2009 we placed a 20-ha rectangular plot (400 × 500 m) in the same area of the stand previously sampled by Svoboda & Pouska (2008). To capture the structural differences between the upper and lower parts of the stand, the plot was positioned using GIS overlays of aerial photographs and historic and recent management plans. The 20-ha plot was then divided into 100 × 100 m subplots for systematic sampling (Fig. 1). The shorter side of the plot was oriented parallel to the slope contour, so that subplots in each row had a similar elevation (rows 1–5; Fig. 1). We located the centre of each subplot using a GPS and established four sampling points 25 m from the centre in each of the cardinal directions. On each point, a fixed radius plot (10 m) was established, and five randomly selected, non-suppressed canopy trees (i.e. trees > 6 m tall and not overtopped by other trees) were cored, for a total of 400 cores. Suppressed trees were avoided because their growth patterns lack information important for disturbance history reconstruction. When the core was rotten, the closest tree with a similar diameter at breast height (1.3 m, DBH) was sampled. All cores were extracted at breast height.

To provide insight into the causes (i.e. wind or bark beetle) and consequences of past disturbance events, we compared the stand structural characteristics following the recent bark beetle outbreak with patterns of tree recruitment following historical disturbances. In 2010 we surveyed all canopy trees that survived the recent bark beetle outbreak, as well as the size and age structure of spruce saplings and small trees. These data were collected over the entire 20-ha plot. Saplings and trees were classified into four height classes (i.e. 1.3–1.9 m, 2.0–3.9 m, 4.0–5.9 m and > 6.0 m). We estimated the ages of saplings and small trees by counting the number of branch whorls above 1.3 m. In each of the five rows of the plot, this was done on a subsample of 20 randomly chosen stems in each height class, except for the 4.0–5.9 m height class, in which only ten samples were analysed. Trees over 6 m were excluded from age estimation because of the difficulty in counting whorls.

Dendroecological analysis

Increment cores were dried, mounted on wooden holders, shaved with a razor blade, and visually cross-dated using the marker year approach (Yamaguchi 1991). Annual ring widths were measured to the nearest 0.01 mm with a Timetable sliding-stage measuring device, and cross-dating was confirmed using COFECHA software (Holmes 1983). The series inter-correlation (0.600) and mean sensitivity (0.196) were relatively high for this region and given tree species. The pith was reached in 92% of the samples, while the remaining 8% were less than 1 cm from the pith. For cores that missed the pith, we estimated the number of missed rings based on the arcing and average growth of the innermost five rings (Duncan 1989). All ages in this study are expressed as recruitment ages at 1.3 m, the height at which trees were cored. Given that *P. abies* regeneration can persist for decades in shade and that it is difficult to assess the year of germination (Niklasson 2002), we felt it was reasonable to work with recruitment ages.

Growth patterns of each of the 400 increment cores were screened for evidence of past disturbance, namely: (1) abrupt increases in radial growth (releases) indicating mortality of a former canopy tree and (2) rapid early growth rates (gap-recruited trees) indicating establishment in a former canopy gap (Lorimer & Frelich 1989).

We used the boundary line criteria proposed by Black & Abrams (2003) to detect growth releases. This method has the advantage of scaling release criteria to account for varying pre-disturbance growth rates, thereby reducing the number of falsely identified releases typical of the standard percentage increase method (Black & Abrams 2003; Fraver & White 2005b). Potential releases were identified using the comparison of 10-year running means (Nowacki & Abrams 1997), where the maximum percentage growth change in each release pulse was used to date the disturbance. To minimize the influence of climate-related growth responses, we used only potential releases with a growth change above 50% (Splechtna et al. 2005; Firm et al. 2009). These potential releases were scaled relative to a species-specific boundary line for *P. abies,* using the previously published boundary line constructed for this species from this same region (Splechtna et al. 2005). Following the thresholds of Black & Abrams (2003), a moderate release was defined as any growth change value between 20% and 50% of the boundary line, and major releases were those greater than 50% of the boundary line. In our definition, a moderate release represents partial removal of a canopy tree or removal of neighbouring trees, while a major release represents loss of overtopping canopy trees.

Similarly, identifying gap-recruited trees requires a threshold that separates open-grown trees from those found under closed canopies, based on their juvenile growth rates (Fraver & White 2005a). Although this threshold is typically set at an arbitrary value, we developed a species- and site-specific threshold based on empirical data. We compared 5-year growth rates (measured at the point where the sapling was 4 cm DBH) of 44 suppressed saplings to those of 43 open-grown saplings of similar size. Open-grown saplings were collected on a large clear-cut in the proximity of the study site. Using logistic regression, we determined the optimal threshold – a mean growth rate of 1.93 mm year^{-1} (likelihood ratio $\chi^2 = 96.1$, $P < 0.0001$) – for separating suppressed and open-grown saplings. This threshold was determined by the intersection of specificity (an expression of the likelihood of false negatives) and sensitivity (likelihood of false positives) (Hosmer & Lemeshow 2000). Thus, trees with early growth rates greater than this threshold were assumed to have been recruited under open canopies. It is important to note that the 1.93 mm threshold for gap-recruited trees used in this study is rather conservative. Recent results from a *P. abies* forest in the Carpathian region, for example, indicate that this growth rate occurs in gap sizes above 1000 m^2 (M. Svoboda,

P. Janda, T.A. Nagel, S. Fraver, J. Rejzek, R. Bače unpubl. data), which is considerably larger than a gap created by one or two canopy trees.

For a small number of cores (15% from total number of cores), radial growth patterns failed to meet the criteria for release or gap-recruited trees. These cores were individually sorted based on a visual inspection of their overall radial growth patterns (Lorimer & Frelich 1989). The samples were placed into a gap-recruited group based on radial growth showing a declining, parabolic or flat growth pattern (Lorimer & Frelich 1989).

Construction of disturbance chronologies

Two disturbance chronologies were constructed from the dendrochronology data. The first was based on the total number of releases and gap-recruitment events. Because this analysis considers all gap-recruitment and release events (moderate and major), it may overestimate the amount of past canopy removal. The second disturbance chronology includes only gap-recruitment events and growth releases related to canopy accession (Lorimer & Frelich 1989); that is, only disturbance events that allowed trees to enter the canopy were included. Thus, releases in existing canopy trees caused by crown expansion into a gap, as well as moderate releases shown on trees that were later overtopped before reaching the canopy, were excluded from this chronology. We defined canopy accession as either gap recruitment or the first major release. In some cases, a moderate release was included when it was the first and only release evident on the core. It was not necessary to define a diameter threshold to identify releases related to canopy accession (Lorimer & Frelich 1989), because most trees were gap-recruited (74%), and the remaining trees that released did so during early growth stages.

To facilitate the interpretation of the disturbance history on the 20-ha plot, we performed a principal components analysis (PCA) using CANOCO for Windows (version 4.53; Biometrics, Plant Research International, Wageningen, The Netherlands). Although several variables in the data set did not meet the assumption of normality, we used this technique to describe patterns in the data to facilitate communication of our results; other ordination methods, such as non-metric multidimensional scaling, revealed similar patterns to those obtained with PCA. For the ordination, we constructed a matrix of the percentage of canopy-accessed trees for each subplot and decade. Secondary matrices containing the elevation and median age of the subplots were created to explore the relationship between these factors and disturbance patterns. Finally, we used the biplot diagram from the PCA with passively projected elevation and median age of the subplots. The first axis of the PCA ordination ultimately explained 60.7% of the original variation, and was strongly correlated with median age and elevation of the subplots (Fig. 2). Median age was similar among subplots of the same row and was inversely related to elevation (Figs. 1, 4). For these reasons, we merged subplots by row (see Fig. 1 for details) for further analyses of disturbance history. For each row in the study area, we constructed graphs that include both the age structure (recruitment at 1.3 m) and distribution of canopy accession events by decade. All disturbance chronologies were truncated when the number of living trees dropped below ten.

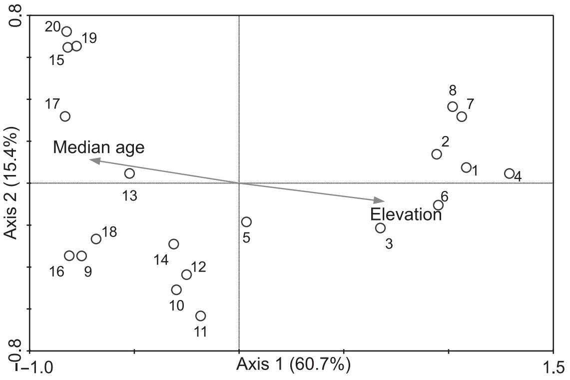

Fig. 2. Results of the principal components analysis (PCA), performed to facilitate interpretation of the disturbance history. The PCA was based on a matrix of the 20 subplots by percentage canopy accessions per decade. The first axis (explaining 60.7% variation) was strongly correlated with median age and elevation of the subplots.

Results

Disturbance history

Of the 400 trees included in the analyses, 74% fulfilled our gap-recruitment criteria. Most trees that recruited in gaps were identified from rapid early growth rates (80%), while identification of the remaining gap-recruited trees was based on the overall radial growth pattern (20%). In total, only 131 moderate and 86 major release events were detected on 172 (43%) trees. For most trees (80%), only one release was detected, and the majority of these release events (75%) occurred during early life stages (i.e. < 40 years old).

Disturbance histories varied among the five rows on the 20-ha study plot (Fig. 3). In general, there were two broad disturbance peaks. The first occurred during 1760–1790 on the lower slope (i.e. rows 4 and 5). In row 5, about 40% of the trees showed a release and 15% indicated gap recruitment during the 1760s. In the following two decades (1770–1790), about 40% of the trees in rows 4 and 5 indicated gap recruitment and about 35% of the trees in row 3 showed evidence of gap recruitment during last decade of

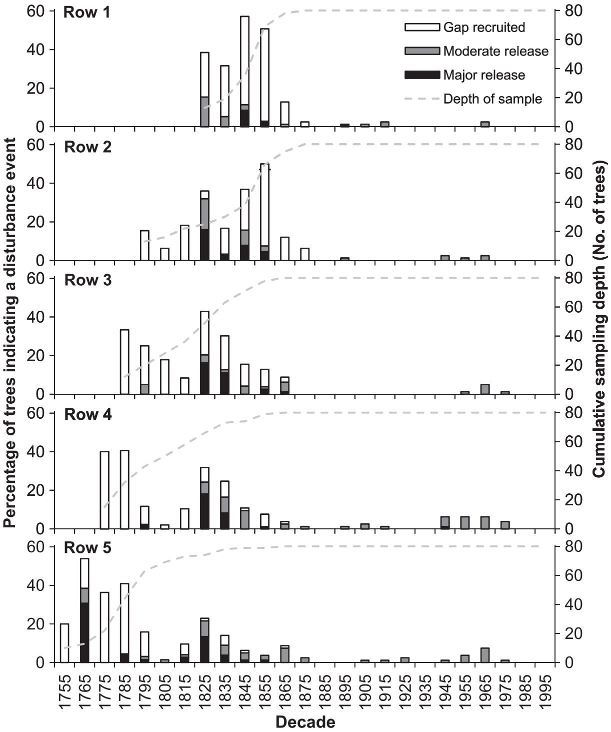

Fig. 3. Disturbance chronology based on releases and gap-recruitment events in each decade for each of the five rows. For each decade, mid-point is indicated. Chronologies were truncated when the number of living trees dropped below ten. The chronologies show two broad peaks in disturbance: one spanning 1760–1790 (primarily rows 4 and 5) and another spanning 1820–1860 (all five rows).

this period (1780–1790). In contrast, very few trees on the upper slope (i.e. rows 1 and 2) recorded a disturbance during this period. The second distinctive peak in the disturbance chronology occurred between 1820 and 1860 in all five rows, but there were clear differences among rows. On the lower slope (i.e. rows 4 and 5), 20–40% of the trees recorded a disturbance, mainly as releases, between 1820 and 1840. Trees on the upper slope (rows 1 and 2) showed a peak during 1840–1860, when 20–50% of trees indicated gap recruitment. The middle row revealed mixed patterns during this period, with a similar proportion of gap-recruited and released trees.

The age class distribution (i.e. recruitment at 1.3-m DBH) revealed generally continuous recruitment during 1710–1890, although most (93%) of the present canopy layer recruited during a period of about 100 years, from 1770 to 1870 (Fig. 4). Since about 1890, however, there was no recruitment of trees above 6 m in the plot. There were notable differences regarding the mode of canopy accession among the rows. On the lower slope, the percentage of trees that reached the canopy through release from suppression was about 36% and 40%, (rows 4 and 5, respectively), compared to only 11% and 18% on the

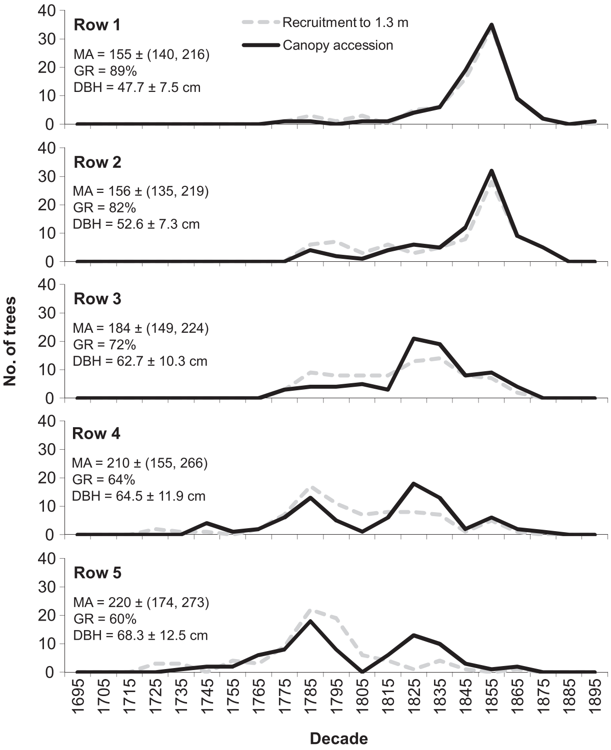

Fig. 4. Recruitment (at breast height) age structures and canopy accession events for each of the five rows. For each decade, mid-point is indicated. In this chronology, only canopy mortality events that allowed suppressed trees in the understorey or newly established trees to enter the canopy were included. Canopy accession was defined as either gap recruitment or the first major release (see Methods). Disparities between the two metrics highlight trees that have established but accessed the canopy through growth release in following decades. The plots show three pulses: 1770–1800, 1820–1840 (both evident in rows 4 and 5), and 1840–1860 (rows 1 and 2). Median age of trees (MA), percentage of gap-recruited trees (GR), and mean DBH (±SD) are listed on the left for each of the five rows. Values of MA are reported with 5th and 95th percentiles.

upper slope (i.e. rows 1 and 2, respectively) (Fig. 4). The distributions of both age and canopy accession showed three distinct pulses in different parts of the plot (Fig. 4). These pulses were generally characterized by fluctuations in recruitment and canopy accession lasting for several decades, with peaks during one or two decades. On the lower slope (i.e. rows 4 and 5), the first period of strong canopy recruitment occurred during 1770–1800, when 36% of the trees accessed the canopy through either release (4%) or gap recruitment (96%). A second pulse of increased canopy accession occurred in rows 4 and 5 during 1820–1840, when 34% of the trees accessed the canopy through either release (70%) or gap recruitment (30%). In this period (1820–1840), also row 3 in particular showed increased recruitment and canopy accession, when about 49% of the trees accessed the canopy through either release (46%) or gap recruitment (54%). On the upper slope (i.e. rows 1 and 2), there was one period of increased recruitment and canopy accession during 1840–1860. In this period, 61% of the trees accessed the canopy through mostly gap recruitment (87%). The distribution of trees that accessed the canopy in each decade generally tracked the recruitment age structure. The two distributions differed when trees accessed the canopy due to release from suppression, especially on the lower slope (i.e. rows 4 and 5).

Post-disturbance stand structure

The bark beetle outbreak that began in the 1990s, in addition to a windstorm in 2007 that downed scattered trees on the plot and further intensified the bark beetle outbreak, caused almost 100% mortality to mature trees throughout the 20-ha plot. Further, very few trees taller than 6 m were alive in 2010 anywhere on the plot. However, the density of surviving trees and saplings showed a striking gradient from low densities (upper slope) to relatively high densities (lower slope). For example, the mean density of trees over 4 and 6 m was below 12 ha^{-1} (Table 1), with the highest density on the lower slope (i.e. rows 4 and 5). The mean density of saplings in the height classes below 4 m was from 300 to 500 ha^{-1} on the lower slope (rows 4 and 5), whereas it was only 100 and 21 ha^{-1} on the upper slope (rows 1 and 2, respectively). On average, it took 15 and 30 years for small trees to grow from a recruitment height of 1.3–1.9 m to the 2.0–3.9 m and 4.0–5.9 m height class, respectively (Table 1).

Discussion

Our study revealed considerable spatial and temporal variation in canopy accession throughout the study area. On the lower slope, most trees reached the canopy during two pulses (1770–1800 and 1820–1840), while most trees on the upper slope accessed the canopy in one pulse (1840–1860). Since 1880, no trees accessed the canopy until the recent bark beetle outbreak that resulted in nearly complete loss of the canopy. We believe that these historical pulses in canopy accession are likely associated with windstorms or bark beetle outbreaks, or interactions of the two.

The mode of canopy accession during these three pulses provides further insight into the disturbance history of the study area. On the lower slope, most trees accessed the canopy in gaps during the first period (1770–1800), whereas release from suppression was the dominant mode of canopy accession during the second period (1820–1840). This pattern suggests the first pulse resulted from a disturbance that partially removed the canopy, providing many trees with access to the canopy. The second pulse likely resulted from a disturbance that removed the remaining canopy layer, releasing suppressed trees that established during the first event. On the upper slope, most trees accessed the canopy in gaps during 1840–1860, and there was no evidence of disturbance during the 1770–1800 period. Thus, these findings suggest that trees on the upper slope originated after a near stand-replacing disturbance or several successive high-severity disturbances.

Determining whether these canopy accession pulses resulted from single or multiple disturbance events presents a challenge. The fact that the pulses spanned three to six decades, with fluctuations around the peak, further confounds a clear interpretation. Based on the frequency of major releases in the disturbance chronology, it seems likely that the 1770–1800 pulse was initiated by a disturbance in the 1760s, although the high number of gap recruitment events during this pulse could also indicate a delayed response to an earlier disturbance. Synchronous releases throughout the plot indicate that the second and

Table 1. Mean density (ha^{-1}) of trees and saplings that survived the recent bark beetle outbreak for each of the five rows, showing much higher densities in the lower slope (i.e. rows 4 and 5). Lines below show mean age at 1.3 m (SD, *N* = number of samples). In general, it took about 4 years to reach height class 1.3–1.9 m, 13 years to reach class 2.0–3.9 m and 30 years to reach class 4.0–5.9 m.

Height class	1.3–1.9 m	2.0–3.9 m	4.0–5.9 m	> 6 m
	Density of saplings and trees (ha^{-1})			
	Mean age at 1.3 m (SD), *N* = number of samples			
Row 1	20	1	0	2
	5 years (3.7), *N* = 20	NA	NA	NA
Row 2	84	16	0	1
	5 years (3.6), *N* = 20	11 years (10.1), *N* = 20	NA	NA
Row 3	158	40	1	1
	4 years (3.5), *N* = 20	10 years (9.1), *N* = 20	NA	NA
Row 4	413	145	9	5
	5 years (4.7), *N* = 20	12 years (9.1), *N* = 20	29 years (14.4), *N* = 10	NA
Row 5	289	127	11	5
	4 years (3.5), *N* = 20	17 years (13.2), *N* = 20	32 years (21.4), *N* = 10	NA

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third canopy accession pulses may have been initiated by the same disturbance in the 1820s. However, major releases were also identified in several decades after the 1820s. These findings highlight the difficulty in dating historical disturbances, particularly when trees establish in open conditions during protracted periods following high-severity disturbance.

Several scenarios could explain the canopy accession pulses observed in this study. Multiple high-severity disturbances could have removed the canopy in several waves. This could include subsequent windstorm events, or a single windthrow that damaged a large proportion of the canopy, followed by a bark beetle outbreak spanning two or three decades. Such a pattern was observed during the recent bark beetle outbreak, which began around 1996 following several windstorms, and continued through 2009 until most of the canopy had died. The observed patterns could also be due to the slow recovery following a stand-replacing disturbance, particularly if the post-disturbance stand has a broad age structure resulting from a combination of small trees, advance regeneration and newly established seedlings. Because the early development of spruce seedlings and saplings is relatively slow (Niklasson 2002; Kupferschmid et al. 2006), it could take up to 30 years for recruitment to restock the stand. Moreover, damage to trees caused by heavy snow or ice in young, post-disturbance cohorts could further delay stand development, especially in a harsh mountain climate such as this.

The current post-disturbance structure of the small trees and advance regeneration lends support to the latter scenario. The upper slope, which had a dense and homogeneous canopy prior to the recent outbreak, had very little advance regeneration. Consequently, the post-disturbance stand will likely recover more slowly, resulting in a broad age structure similar to that of the former stand (Svoboda et al. 2010). In contrast, the lower slope, which was affected by several disturbances that created a more heterogeneous canopy structure, had more abundant advance regeneration. Saplings and small trees in this part of the plot will likely respond with an immediate growth release due to the loss of the canopy. Thus, projected differences in stand recovery between the upper and lower slopes are highly influenced by the pre-outbreak stand structures, which in turn are legacies of events that occurred over 150 years ago. Applying this reasoning to the historical disturbances documented here could explain the fairly rapid response following the 1820s disturbance in the lower slope, as well as the contrasting delayed response seen in the upper slope. Our study therefore supports the idea that forest structures left by past disturbances influence responses to and recovery from subsequent disturbances (Veblen et al. 1994; Everham & Brokaw 1996; Foster et al. 1998; Kulakowski & Veblen 2002).

The elevational gradient in disturbance reported here explains corresponding changes in forest structure that had previously been unexplained in this study area (Svoboda & Pouska 2008). Differences in tree density, vertical and horizontal tree layer structure, amount of dead wood and seedling and sapling density are consistent with the differences in the disturbance history between the upper and lower slope. Specifically, the upper part of the stand, because of its more recent and severe disturbance, is characterized by unimodal diameter and height distributions, a dense closed canopy, and sparse advance regeneration. In contrast, the lower part of the stand, because of its more distant and less severe disturbance, has a more heterogeneous structure and more abundant advance regeneration. That is, changes in forest structure may not be related to elevation *per se* – lower temperatures and shorter growing season (Dolezal & Srutek 2002) – but rather to changes in disturbance severity mediated by elevation. Because this structural gradient, described by Svoboda & Pouska (2008), extends beyond the current study area into a larger 600-ha area of old-growth, it is plausible that the disturbance history identified in this study explains the structure of the larger surrounding old-growth area. However, it is difficult to determine the extent of these historical events.

Dendrochronological methods alone cannot resolve whether wind or bark beetles were responsible for the

Table 2. Historical disturbances (windstorms and bark beetle outbreaks) in the Bohemian Forest for the period covered by this study. In many cases no information is available regarding exact location and extent of damage. These data were compiled from Zatloukal (1998) and Brázdil et al. (2004)

Date	Disturbance agent	Description
1710	Windstorm	Heavy damage by windstorm. Exact extent unknown
1718–1728	Windstorms and bark beetle outbreak	Damage by windstorm followed by bark beetle outbreak
1740	Windstorm	Heavy damage by windstorm. Exact extent unknown
1778	Windstorm	Unknown damage by windstorm
1801	Windstorm	Unknown damage by windstorm
1812–1813	Windstorms	Unknown damage by windstorm
1821–1822	Windstorms	Unknown damage by windstorm
1833–1840	Windstorms and bark beetle outbreak	Heavy damage by windstorm followed by bark beetle outbreak. Estimated volume of the disturbed wood is about 0.5 million m^3
1853	Windstorm	Unknown damage by windstorm
1859–1861	Windstorms	Unknown damage by windstorm
1868–1880	Windstorms and bark beetle outbreak	Heavy damage by windstorm followed by bark beetle outbreak. Estimated volume of the disturbed wood is about 3 million m^3

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disturbance pulses documented in this study; however, historical records may provide additional insight. Based on the work published by Zatloukal (1998) and Brázdil et al. (2004) (Table 2), several large-scale, high-severity windstorms damaged the Bohemian Forest during the last 500 years. Major windstorms occurred in decades that roughly coincide with peaks in our disturbance reconstruction (i.e. 1740, 1778, 1810s, 1820s and 1830s); however, the precise locations or extent of the disturbed area for these events is not known. The best-documented windstorms that severely disturbed large areas of the Bohemian Forest occurred in 1868 and 1870, which triggered a severe bark beetle outbreak (Svoboda et al. 2010). During a period of about 20 years, from the 30 000 ha for which we have historical data, about 10 000 ha of forest (3 million m^3 of wood) was severely disturbed on the Czech side of the Bohemian Forest (Svoboda and Wild 2007). Although this storm did not damage the study area, it provides evidence that high-severity windstorms are part of the natural disturbance regime for this region. Similarly, dendroecological studies from the Tatra Mountains (Zielonka et al. 2010) and the Carpathian Mountains (Panayotov et al. 2011) show that windstorms have played an important role in the natural dynamics of *P. abies* forests there as well.

Whether or not widespread bark beetle outbreaks are part of the natural disturbance regime for mountain spruce forests in Central Europe is rather controversial (Jonasova & Prach 2004). The bark beetle is considered a significant pest in intensively managed spruce stands in the region (Wermelinger 2004), yet its role in the dynamics of natural, mountain spruce forests is largely unknown. Historical documents report bark beetle outbreaks in the Šumava Mountains during the past several centuries; however, it is widely believed that historical outbreaks were the result of previous forest management practices that favoured even-aged spruce monocultures, especially on lower elevation sites outside the natural range of spruce. Bark beetle outbreaks can be triggered by severe windstorms, which create large amounts of dead wood, coupled with high spring and summer temperatures in the following season, which allow beetle populations to increase over a certain threshold, thereby triggering severe outbreaks (Okland & Bjornstad 2006; Aakala et al. 2011; Lausch et al. 2011). Documented windstorms (Table 2) during the period covered by this study suggest that some of the conditions needed for severe outbreaks occurred several times in recent centuries. As above, given the coincidence of these storms with the disturbance pulses detected in this study, we assume windstorms could be the initiating disturbance agent, although climatic factors may have also played a role. Further, given the close link between windthrow and bark beetle outbreaks witnessed in contemporary old-growth *P. abies* forests, it seems reasonable to assume this interaction has played a role historically in this region. In fact, the interaction of these two disturbances seen in the contemporary landscape (beginning in the mid-1990s and culminating with complete mortality by 2010) may provide an analogue for the protracted recruitment periods documented here. Finally, spruce bark beetle outbreaks triggered by natural processes are not unprecedented in old-growth forest landscapes. For example, large spruce beetle outbreaks are within the natural range of variability in conifer forests of North America (Baker & Veblen 1990; Veblen et al. 1994; Eisenhart & Veblen 2000; Berg et al. 2006; Derose & Long 2007, 2010; R.J. Derose & J.N. Long unpubl. data).

Our study yields important insights into the natural disturbance regime of mountain *P. abies* forests in Central Europe. Namely, we provide strong evidence that the forests in the study area were shaped by a history of infrequent, moderate- to high-severity disturbance events. These findings challenge the traditional view, which holds that small-scale endogenous tree mortality events (gap dynamics) drive the dynamics of these forests. Our results, however, should be viewed with sufficient caution when making generalizations about the disturbance regime of *P. abies* forests throughout Central Europe. In reality, it is likely that characteristics of the disturbance regime vary in space and time along a continuum from small-scale gap dynamics to infrequent, stand-replacing events. The few studies examining disturbance processes in old-growth *P. abies* forests in this region highlight such variability. In the northwest Carpathians, Szewczyk et al. (2011) revealed a history of small-scale gap disturbances. In the Rila Mountains of Bulgaria, Panayotov et al. (2011) documented considerable variation in disturbance history, from small-scale gaps to blowdown patches between 1 and 10 ha in size. Finally, Zielonka et al. (2010) described a history of large-scale (> 100 ha) stand-replacing wind disturbances in the Tatra Mountains. Additional studies in old-growth remnants across the region will facilitate a more thorough understanding of the historical range of variability in mountain *P. abies* forest dynamics.

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