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The legacy of primeval forests – a dendroecological reconstruction of selected forest stands across the Šumava National Park

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Abstract

Despite prehistoric colonization, forests with limited evidence of human activities have been preserved throughout the centuries in the Bohemian Forest, thus they are promising from the point of view of well-preserved primeval legacy. Hence, we present a dendrochronological analysis of 5 spruce and mixed forest stands with the highest protection status within the Šumava National Park (Czech Republic), supplemented by archival records to uncover their historical development and naturalness. Based on 210 increment cores from 6 research plots of 0.2 ha, an age structure analysis and chronology of historical disturbance events were performed for each stand. Most trees regenerated after windstorms in the 1870s, but a significant proportion of the forest structure in many stands was established much earlier. About 13% and 2% of trees reached more than 200 and 300 years, respectively. Site-specific disturbance histories showed substantial spatial and temporal variability among the stands, probably as a result of anthropogenic disturbances, identified using archival materials. Although all examined stands were affected by humans in the past through grazing, logging or air pollution, the forest continuity was not entirely interrupted, preserving in the form of ancient trees and as well as high deadwood volume.

Key words: Bohemian Forest, dendrochronology, disturbance history, primeval forests, tree rings

Introduction

The Bohemian Forest, one of the largest transboundary protected areas in Central Europe, hosts two national parks: The Bavarian Forest National Park (Germany) and the Šumava National Park (Czech Republic). These parks represent a mountainous region that has been protected from extensive human deforestation activities for centuries, in contrast to most other forested areas in Central Europe. Despite the increasing evidence of prehistoric settlements in the Šumava foothills (Dreslerová et al. 2020, Kozáková et al. 2020), intensive colonization of the Bohemian Forest was relatively delayed, dating to the high medieval period during the 12th century (Beneš 1996). Nevertheless, higher elevations remained untouched until the 18th century, when colonization supported by the glass-work industry culminated (Beneš 1996). Although many settlements were established in the mid-18th century in the central part of the Šumava Mountains, lumberjacks cut down timber primarily in nearby forests, and thus the mountain summits were still covered by primeval forests until the 19th century, utilized for no more than grazing or hunting purposes (BRŮNA et al. 2016). More extensive harvesting activities including up mountain ridges occurred in the mid-19th century. Nevertheless, 26% of woodland vegetation was older than 120 years even in the 1860s, thus representing old-growth forests (BRŮNA et al. 2013). During the same period, a detailed portrait of the life and people in the Šumava Mts. was described in novels by the Czech author KLOSTERMANN (1894), suggesting intact, hardly accessible forests covering a substantial area of the mountains. Besides these direct anthropogenic influences, atmospheric pollution, which peaked in the 1970s and 1980s throughout Central Europe (ELLING et al. 2009, OULEHLE et al. 2010), negatively affected the tree physiology of spruce forests in the Bohemian Forest (ŠANTRŮČKOVÁ et al. 2007), with the undisputed impact on present forest extent. Despite past human activities, 6.4% area of the Šumava National Park and Protected Landscape Area has been classified as relicts of old-growth forest in 2012 (including original, natural and near-natural stands in sensu VRŠKA et al. 2017), corresponding to an area of more than 10 000 ha (NATURAL FORESTS DATABANK, www.naturalforests.cz). Although the extent of such stands in the ridge zone on the Czech side of the border (JANDA et al. 2014, ČADA et al. 2016) and the surroundings of the Boubínský Primeval Forest, hereinafter Boubin (KAŠPAR et al. 2020), has been well documented, area of forests with a well-preserved primeval legacy has not been fully explored at lower elevations. It is possible that there are still forests with primeval continuity throughout the Šumava Mountains. While intact forests with no direct human impact are less likely to be found, first generation forests after the primeval phase are a more promising target.

Since time immemorial, Central European spruce mountain landscapes and the Bohemian Forest in particular have been shaped by high-severity, stand-replacing disturbances, occurring approximately every century (ČADA et al. 2013). From the perspective of the extent as well as volume of disturbed timber, the most important wind events in the Czech Lands were documented in 1740, 1801, 1833, 1868 and 1870 (BRÁZDIL et al. 2017a, 2017b, 2018a, 2018b), and more recently in 2007 (the Kyrill storm) and 2017 (the Herwart storm). It is widely accepted that such strong events are accompanied by bark-beetle outbreaks (*Ips typographus* (L.)), an integral component of the natural dynamics of mountain spruce-dominated forests (MÜLLER et al. 2008, THOM et al. 2013, KULAKOWSKI et al. 2017). In the Šumava Mountains, one of most exceptional wind events were a series of disturbances during 1868–1870, that together with a subsequent bark beetle outbreak disturbed at least partially 40% of the area, with the highest severity at elevations from 1000–1150 m a.s.l. (BRŮNA et al. 2013). Apart from large-scale windstorms affecting greater areas of the Czech Republic, many local wind events have also been recorded over the centuries (BRÁZDIL et al. 2004). Although they have been very well documented based on chronicles, newspapers, forestry and meteorological records, knowledge on the intensity of these processes as well as past disturbance regimes of natural forest stands are difficult to extrapolate from these data. Therefore, tree-ring analysis is a very useful tool for detecting rapid growth changes following canopy disturbances during a tree's lifespan. As opposed to tree-size structure analyses, which are sometimes misleading and inadequate for evaluating stand naturalness, tree-ring analysis together with information on tree-age structures offer comprehensive insights into the origin and development of forest stands. Nevertheless, drawbacks of this dendrochronological method should be taken into consideration: the relatively time-demanding tree sampling and processing, and the difficulty of differentiating natural and anthropogenic disturbances. However, combining tree-ring analysis with historical maps can provide credible documentation of the range and severity of past landscape changes related to both human impacts (BRŮNA et al. 2010) as well as natural disturbances at the landscape level (JELÍNEK et al. 2005, BRŮNA et al. 2013). The aim of this study was thus to link archive materials with tree-ring data to reconstruct the origin and development of selected forest stands with the highest protection status throughout the Šumava National Park, enabling an evaluation of their naturalness and primeval forest continuity. To accomplish this, we furthermore evaluated the characteristics of the stand structures with an emphasis on dead wood volume. We hypothesize that examined forests might demonstrate first generation after primeval forest. Such secondary stands, originating outright from the primeval forests, were affected to a limited extent by forest pasturing or harvest activities during the last centuries, retaining tree-species composition and stand-structure heterogeneity of the original forests. The presence of both trees originating in primeval forests as well as their offspring in a form of natural regeneration preceding harvest activities can maintain the legacy of the original forests.

MATERIAL AND METHODS

Study sites

Our study was conducted in 5 forest stands throughout the Šumava National Park in the Bohemian Forest, situated in the western part of the Czech Republic (Central Europe). In particular, they involve the districts of Svojše (Dračí skály), Modrava (Vyderský svah), Horská Kvilda (Tetřevská slať), Borová Lada (Vlasatá), and Přední Zvonková (Smrčina). Ranging from 673 to 1170 m a.s.l., the stands are dominated by Norway spruce (*Picea abies* (L.) Karsten), with an admixture of European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) at some localities. Positions of particular localities including basic descriptive characteristics are shown in Figure 1 and Table 1. The stands are predominantly characterized by the strictest protection statuses within the national park (natural zones in sensu Czech Nature and Landscape Protection Act).

Sampling design

In 2020, one circular research plot of 0.2 hectares in size was established at each locality, with the exception of Smrčina, where two research plots were placed due to the considerable habitat variability as well as species composition. As we aimed to select plots with the highest potential of primeval forest continuity, we considered the following criteria: a rich tree-species and size structure, the presence of windthrow topographical features (e.g. pits and mounds), deadwood and giant trees, and no indicators of recent felling as far as possible. Subsequently, a detailed tree census was performed within each stand by using Field-Map technology (www.field-map.com), including the position, dimension, height, tree species, health and social status of all living and dead trees of diameter at breast height (DBH) ≥10 cm. These measured attributes served as a basis for ongoing dendrochronological research as well as for calculations of wood biomass volume within each plot.

Table 1. Characteristics of the stands.

Locality/ Attribute	Dračí skály	Tetřevská slať	Vyderský svah	Vlasatá	Smrčina 1	Smrčina 2
Nature conservation zone	natural	natural	natural	near-natural	natural	natural
District	Svojše	Horská Kvilda	Modrava	Borová Lada	Přední Zvonková	Přední Zvonková
Altitude (m a.s.l.)	673	1138	957	964	1170	975
Latitude (°)	49.1174289 N	49.0293542 N	49.0359883 N	48.9767783 N	48.7485833 N	48.7556979 N
Longitude (°)	13.4974367 E	13.5364700 E	13.5022733 E	13.6494692 E	13.9204000 E	13.9336401 E
Forest type	Fir-spruce ravine	Bog spruce	Spruce ravine	Beech-spruce	Beech-spruce	Fir-spruce -beech
Tree-species composition (%)*	PCAB 68/40	PCAB 100/100	PCAB 100/100	PCAB 81/61	PCAB 57/79	PCAB 30/41
	FASY 3			FASY 17/25	FASY 41/21	FASY 63/46
	ABAL 27.5/60			ABAL 1/10	ABAL 2	ABAL 7/13
	ACPS 1.5			ACPS 0.5/3		
				POTR 0.5/1		

* Tree-species composition in % from total number of living trees (ahead of slash) and from total standing timber volume (behind slash); Tree codes: PCAB – *Picea abies* (L.) Karsten, FASY – *Fagus sylvatica* L., ABAL – *Abies alba* Mill., ACPS – *Acer pseudoplatanus* L., POTR – *Populus tremula* L.

In order to study the age structure as well as reconstruct past disturbance histories, tree-ring width analysis (i.e. dendrochronology) was applied. With regard to tree-species variability, we randomly sampled 30 canopy trees with crowns exposed to direct sunlight (i.e. exposed trees) and 5 subcanopy supressed individuals in each plot. Only trees without mechanical damage or rot were sampled, thus in cases of an insufficient sample size within the plot we cored neighbouring individuals outside the circle. Using an increment borer we sampled one core per tree at a height of 1.3 m above ground in the contour line direction to eliminate any effects of reaction wood. Only samples with ≤3 cm deviation to the pith were accepted, and if we missed the pith sampling was repeated up to a defined tolerance. The sampling cavity was then plugged with grafting wax. In total, 210 increment cores were obtained and analysed (180 exposed trees, 30 suppressed).

Processing of dendrochronological data

In the laboratory, dried increment cores were treated following standard dendrochronological procedures (SCHWEINGRUBER et al. 1990), including mounting into a wooden lath, grinding and smoothing using 400 grit sandpaper to improve the quality of the wood structure for measurements. Core series were scanned using an Epson LA2400 scanner at 1600 DPI resolution, and tree-ring widths were then measured in WinDENDRO software (RÉGENT INSTRUMENTS 2014) with 0.01 mm accuracy. Following measurement, core series were cross-dated using the marker year method (YAMAGUCHI 1991) in PAST 4 software (SCIEM 2007). During this process, tree-ring series from individual trees were compared mutually with each other and with a standard chronology constructed for Boubin (KAŠPAR et al. 2020), allowing for the elimination of errors due to measurement as well as the occurrence of false or missing rings. The quality of cross-dating was statistically evaluated by COFECHA software (HOLMES 1983).

For age structure analysis we first calculated the number of rings to the centre for cores that missed the pith using a pith locator (APPLEQUIST 1958) to obtain the recruitment age. It is necessary to note that the number of years based on this approximation might be overestimated, usually in cases of very small tree rings during juvenile growth. On the other hand, the absolute ages of trees are likely even higher due to the sampling height of 1.3 m, since the average time that trees need to reach the height 1–1.3 m spans from 8 to 14 years depending on the tree species (ŠAMONIL et al. 2009, TROTSIUK et al. 2012, ŠAMONIL et al. 2013).

Summary disturbance histories for each locality were elaborated based on the evidence of two types of disturbance recorded in tree-ring series: (i) initial juvenile growth in a gap,

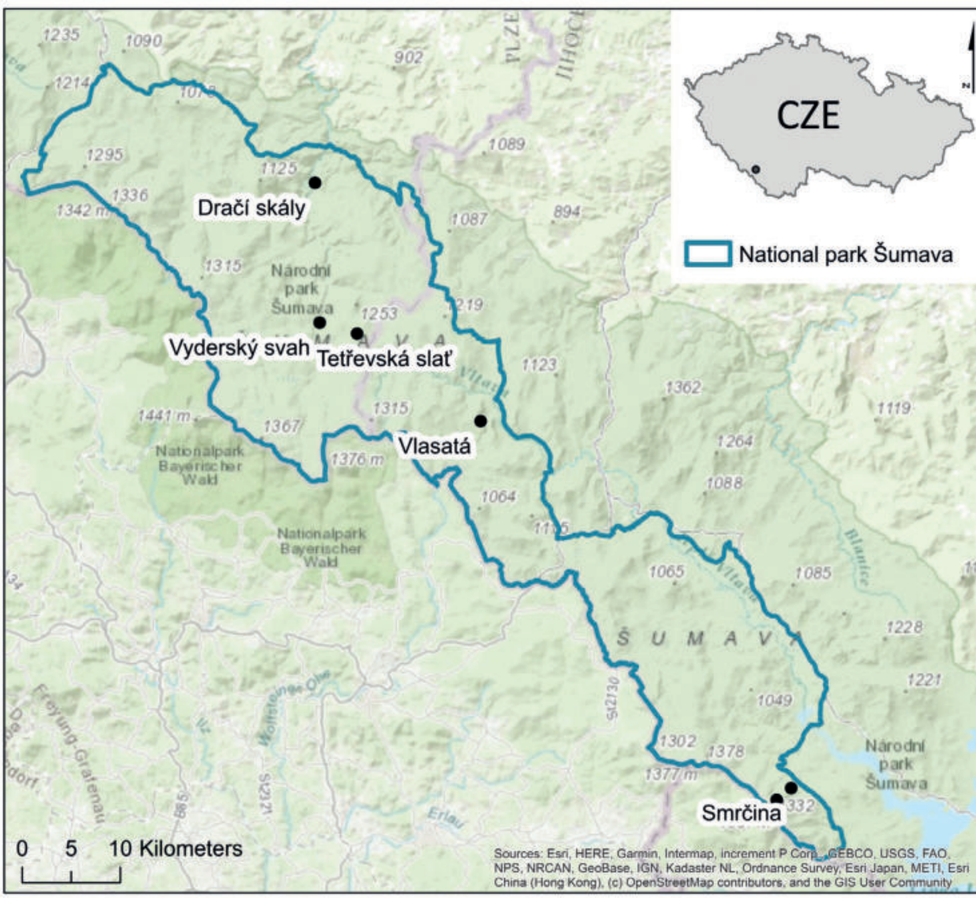

Fig. 1. Positions of the stands in the Šumava National Park and within the Czech Republic.

i.e. gap origin (Lorimer et al. 1988); and (ii) reaction of a tree to the death of adjacent tree during subsequent growth in the form of abrupt growth changes, i.e. release (e.g. Frelich 2002). Only exposed trees were included into the analysis of disturbance history (N = 30 cores/plot). The threshold for gap origin was calculated according to the standard approach by Lorimer et al. (1988). We estimated average juvenile growth for five consecutive tree rings in the time for a tree to reach 6 cm DBH, and assumed that a tree germinated in a canopy gap if exceeding a predefined threshold. We used identical thresholds as in KAŠPAR et al. (2020) for Boubin: 1.60 mm for conifers, and 1.53 mm for broadleaves.

Before studying growth pulses during subsequent growth, i.e. releases, we eliminated false lateral responses of exposed canopy trees by restricting the calculation purely on tree-ring segments that had not reached the canopy (see Lorimer & Frelich 1989). The threshold of the diameter beyond which the probability was less than 5% that a tree could have been overtopped before the growth release was derived from Kašpar et al. (2020), who estimated this parameter for Boubin. Thus, all the sequences exceeding 56 cm (conifers) and 55 cm (broadleaves) were excluded from further analyses. For the detection of growth releases, the boundary line technique (BL; Black & Abrams 2003) was applied. This method is based on a comparison of the percent growth change (GC) between two 10 year intervals (Nowacki & Abrams 1997) with the average prior radial growth over the past 10 years (PG). First, we constructed a boundary line expressing maximum growth plasticity separately for every tree species. Our robust data set supplemented with dendrochronological data from other parts of the Šumava Mts. (Kašpar et al. 2020) allowed for the production of a new regional boundary line that represents the diverse gradient of forest ecosystems throughout the Šumava region. In total, we used 269 439 and 128 077 tree rings for *Picea abies* and *Fagus sylvatica*, which according to Black et al. (2009) is sufficient for this calculation. As for *Abies alba*, we did not reach the recommended minimum data set of 50 000 tree rings (N = 30 201), and thus a higher uncertainty in release detection must be take into account (but see Nagel et al. 2007, who used a similar data set of silver fir for BL construction). To model BL, GC and PG were computed for every tree ring. Subsequently, all PG values were divided into 0.5 mm intervals, with the exception of the first centimetre segment that was classified into 0.25 mm intervals (Splechtna et al. 2005). Unlike Black & Abrams (2003), who calculated BL based on the average of the top 10 GC values in each category of PG, we defined a less strict criterion of 1% GC as being more appropriate for robust data sets with the occurrence of extreme values. Therefore, the 1% highest values of GC in each PG interval were averaged and fitted by a negative exponential function using the nonlinear least squares method in R software (R Development Core Team 2019). The best fit was estimated on the basis of the coefficient of determination (R^2). In the second step, local 10-year GC maxima were scaled to BL values for the appropriate year. The resulting percentage of BL was used as a measure of the growth response magnitude, and considered as a weak, moderate or major release from suppression if exceeding 25%, 50% and 100%, respectively. For these calculations we used the package TRADER (Altman et al. 2014) in R software.

As a measure of the release severity, the proportion of canopy area disturbed (CAD, %) in a particular decade was chosen. For that purpose, the relation between diameter at breast height and current exposed crown area for every tree species was derived from KAŠPAR et al. (2020). Based on the knowledge of the canopy area of the disturbed trees and maximal sum of exposed canopy area of all trees, the proportion of disturbed canopy area was calculated in each decade separately for different release intensities. Finally, a graph of the summary disturbance history was created linking the proportion of canopy area disturbed (upper part) and proportion of gap originating trees (bottom part) for each decade. These discrete features thus provide a complex picture on past disturbance dynamics, allowing both the origin of the stands as well as the occurrence of important disturbance events to be unravelled. To maximize the credibility of the results, the chronology was truncated if the sample size dropped below five samples.

Archive records

Analyses of disturbance histories provide a complex picture of the past disturbance dynamics of studied forest stands, but without detailed knowledge of their primary drivers. Thus, if possible such analyses should be supplemented by additional historical material. In our case, we studied historical written as well as map records. The incidence of extreme wind events for Czech Lands has been well documented by BRÁZDIL et al. (2004), serving us as a basis for the validation of natural disturbances. To study the historical development as well as human impacts we used several historical map sources, namely maps of the State District Archive in Český Krumlov, maps of the Archive of the State Administration of Land Surveying and Cadastre (https://ags.cuzk.cz/archiv), maps of the Geoinformatics Laboratory of the University of J. E. Purkyně in Ústí nad Labem (http://oldmaps.geolab.cz), and historical forestry maps of the National Museum of Agriculture (https://www.starelesnimapy.cz). We focused on the First (1764–1768) and the Second (1836–1852) Military Surveys, both at a scale of 1 : 28 800, and the Third Military Survey (1877–1880) at a scale of 1 : 25 000. Moreover, we studied maps of the Stable Cadastre (1826, 1 : 2 880) and historical forestry maps of different time frames and scales. In order to study more recent material, we also used historical aerial photographs from the Archive of the State Administration of Land Surveying and Cadastre (https://ags.cuzk.cz/archiv), available from the 1930s for the whole territory of the Czech Republic.

RESULTS AND DISCUSSION

Characteristics of timber volume

The volume of standing trees was rather variable among the research plots, ranging from 500–1200 m^3/ha (Table 2). There were two localities with outstanding growing stocks, i.e. Dračí skály and Smrčina 2. By the volume of standing biomass, the studied localities are fully comparable with remnants of primeval forests in the Šumava Mts., where the volume of standing dendromass ranges from 400 to 1100 m^3/ha (KAŠPAR et al. 2020). As for lying stems, the volume reached 60–150 m^3/ha. With an average amount of 99.5 m^3/ha, the volume of dead biomass is significantly higher in our localities than in remnants of primeval forests in the Šumava Mts., where it comprises 53.5 m^3/ha (KAŠPAR et al. 2020). On the other hand, lying stems in Boubin have even much greater volume based on this study (264.5 m^3/ha), probably as a result of the presence of older trees as well as the absence of past forest management associated with deadwood removal. Our results are also comparable with those in a semi-natural montane spruce forest in the Šumava National Park (SVOBODA et al. 2010), where mean down woody debris was found to be 94.4 m^3/ha.

Table 2. Standing and lying timber volume for particular stands, separated by tree species and type of mortality.

Locality	Tree species*	Standing timber volume (S)					Lying timber volume (L)				S+L (m^3/0.2 ha)	S+L (m^3/ha)
		Dead standing	Snag	Standing living	Breakage living	TOTAL	Snag	Uprooting	Snapped	TOTAL		
Dračí skály	PCAB	2.19	0.81	94.33		97.33	1.85	15.37	12.10	29.32	126.65	633.25
	FASY			0.17		0.17				0.00	0.17	0.85
	ABAL	0.99	2.89	143.85		147.73				0.00	147.73	738.65
	ACPS			1.01		1.01				0.00	1.01	5.05
	TOTAL	**3.18**	**3.70**	**239.36**	**0.00**	**246.24**	**1.85**	**15.37**	**12.10**	**29.32**	**275.56**	**1377.80**
Vyderský svah	PCAB	0.49	3.11	122.93	0.14	126.67	6.33	0.63	4.97	11.93	138.60	693.00
	TOTAL	**0.49**	**3.11**	**122.93**	**0.14**	**126.67**	**6.33**	**0.63**	**4.97**	**11.93**	**138.60**	**693.00**
Tetřevská slať	PCAB	5.30	1.90	95.18		102.38	2.80	3.16	6.78	12.74	115.12	575.60
	TOTAL	**5.30**	**1.90**	**95.18**	**0.00**	**102.38**	**2.80**	**3.16**	**6.78**	**12.74**	**115.12**	**575.60**
Vlasatá	PCAB	3.95	1.09	88.29		93.33	3.04	4.96	7.87	15.87	109.20	546.00
	FASY		0.41	36.94		37.35	0.28	0.81	1.14	2.23	39.58	197.90
	ABAL			15.55		15.55				0.00	15.55	77.75
	ACPS			4.50		4.50				0.00	4.50	22.50
	POTR			1.40		1.40				0.00	1.40	7.00
	TOTAL	**3.95**	**1.50**	**146.68**	**0.00**	**152.13**	**3.32**	**5.77**	**9.01**	**18.10**	**170.23**	**851.15**
Smrčina 1	PCAB	25.44	0.84	66.97		93.25	1.63	3.87	5.24	10.74	103.99	519.95
	FASY		4.48	20.54		25.02	5.36	5.27	1.99	12.62	37.64	188.20
	ABAL		0.17			0.17				0.00	0.17	0.85
	TOTAL	**25.44**	**5.49**	**87.51**	**0.00**	**118.44**	**6.99**	**9.14**	**7.23**	**23.36**	**141.80**	**709.00**
Smrčina 2	PCAB		2.30	82.67		84.97	9.09	0.38	14.48	23.95	108.92	544.60
	FASY	1.00		93.86	0.10	94.96			0.02	0.02	94.98	474.90
	ABAL			25.51		25.51				0.00	25.51	127.55
	TOTAL	**1.00**	**2.30**	**202.04**	**0.10**	**205.44**	**9.09**	**0.38**	**14.50**	**23.97**	**229.41**	**1147.10**

* PCAB – *Picea abies* (L.) Karsten, FASY – *Fagus sylvatica* L., ABAL – *Abies alba* Mill., ACPS – *Acer pseudoplatanus* L., POTR – *Populus tremula* L.

The size structure of living trees roughly emulates the growing stock (Fig. 2), with substantial species-specific effect. The observed left-skewed distribution with a predominance of individuals in the lowest diameter class up to 19 cm generally resembles the decreasing trends in diameter structure detected for montane mixed primeval forests (e.g. VRŠKA et al. 2009, ŠEBKOVÁ et al. 2011). However, at some stands (Dračí skály, Smrčina), the size distribution showed rather bimodal shape with two peaks in the thinnest and in the middle diameter classes as described for some European deciduous or mixed montane forests (NAGEL & DIACI 2006, HOLEKSA et al. 2009, TROTSIUK et al. 2012). The dimensions significantly differ among the tree species (ANOVA, $p<0.05$), with the highest DBH reaching silver fir (median = 70.2 cm), followed by European beech (median = 31.7 cm) and Norway spruce (median = 24.0 cm). Most likely, past human impacts in the form of grazing may play an important role in this relationship, generally favouring the growth of silver fir (VRŠKA et al. 2009). Additionally, the absence of *Abies alba* in lower dimension classes is also a consequence of its higher preference by game, thus explaining the high share of silver fir trees in larger size classes.

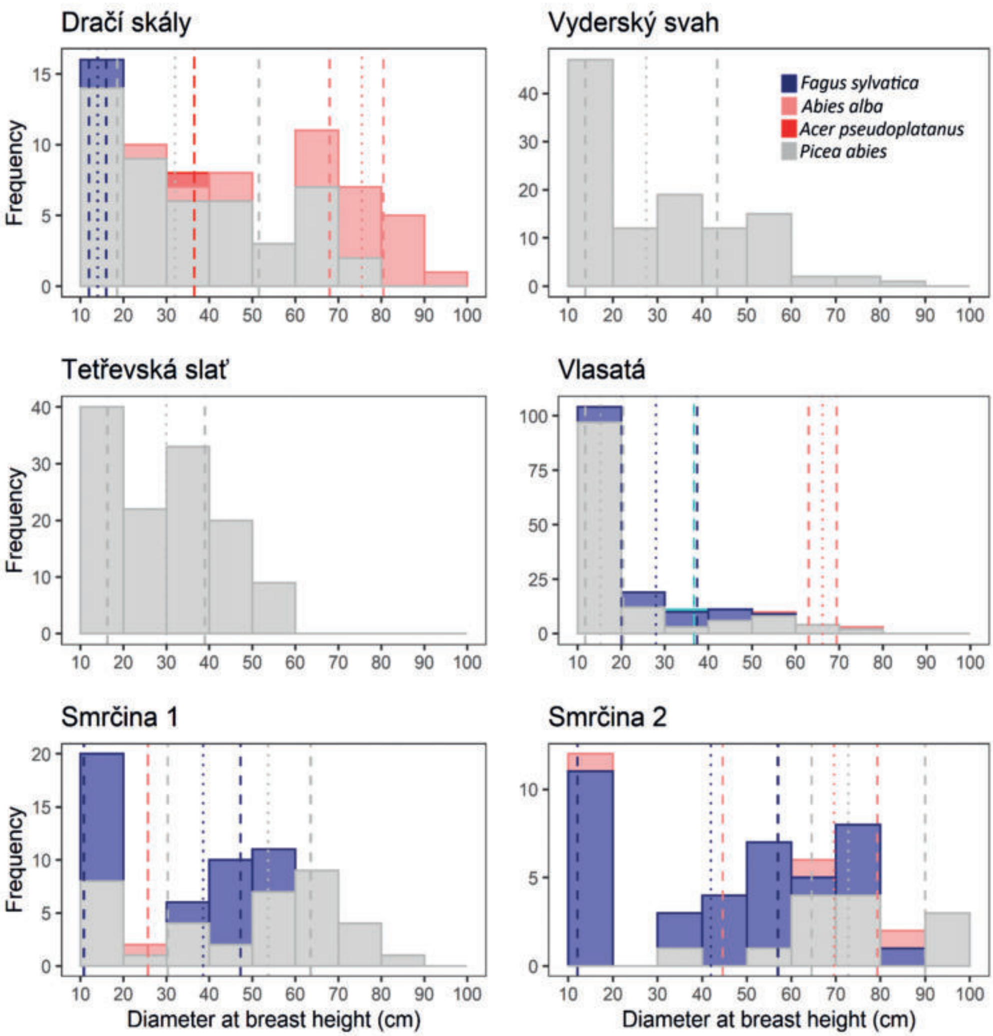

Fig. 2. Tree-size structure for particular stands and tree species. The dotted line shows the median, while dashed lines define 25% and 75% quartiles.

Table 3. Ages of the five oldest trees for each stand based on estimations of absolute ages and number of tree rings at 1.3 m.

Dračí skály			Vydерský svah			Tetřevská slať		
Absolute age	No. tree rings	Species	Absolute age	No. tree rings	Species*	Absolute age	No. tree rings	Species*
~ 240	231	ABAL	~ 220	209	PCAB	~ 460	326	PCAB
~ 190	165	ABAL	~ 210	216	PCAB	~ 360	359	PCAB
~ 160	161	PCAB	~ 210	212	PCAB	~ 340	338	PCAB
~ 160	147	ABAL	~ 210	211	PCAB	~ 250	247	PCAB
~ 150	148	ABAL	~ 210	159	PCAB	~ 250	253	PCAB

Vlasatá			Smrčina 1			Smrčina 2		
Absolute age	No. tree rings	Species	Absolute age	No. tree rings	Species*	Absolute age	No. tree rings	Species*
~ 260	197	FASY	~ 500	208	FASY	~ 280	190	FASY
~ 200	96	FASY	~ 310	301	PCAB	~ 260	261	FASY
~ 160	158	ABAL	~ 310	294	FASY	~ 230	238	FASY
~ 150	126	FASY	~ 290	266	PCAB	~ 230	197	FASY
~ 150	147	PCAB	~ 240	238	PCAB	~ 230	232	FASY

Age structure

From the perspective of mean stand age, the oldest forest stands were at Smrčina (Smrčina 1 median <190 yrs, Smrčina 2 median = 161 yrs) and at Tetřevská slať (median = 166 yrs), followed by Dračí skály (median = 142 yrs), Vlasatá (median = 135 yrs), and the youngest at Vyderský svah (median = 111 yrs) (Fig. 3). The majority of studied stands regenerated during the decades 1870–1900 after the series of severe windstorms in the 1870s and subsequent bark beetle outbreaks (Dračí skály, Vlasatá) or later (Vyderský svah). While the origin of some localities can be dated to the end of the 18th century (Smrčina, Tetřevská slať), the presence of older trees within stands indicates that the main bodies of stand structure were established much earlier, allowing us to consider these individuals as relicts of primeval forests. Generally, there is a relatively high share of old trees in the analysed data set (Table 3), with 20% of individuals reaching more than 200 years and nearly 3% older than 300 years. Considering the fact that the oldest trees had been classified as exposed, recounting to the overall forest structure based on the actual proportions of exposed and supressed trees within the forest structure is inevitable. Thus, it makes 13% and 2% of trees older than 200 and 300 years, respectively. Therefore, on the basis of mean stand age, Smrčina and Tetřevská slať are analogous to remnants of primeval forests in the vicinity of Boubin (Kašpar et al. 2020), where the mean ages of beech and spruce individuals gained 160 and 162 years, respectively. Considering the mean peaks of tree establishment, these two stands are also comparable with other montane spruce forests within the Šumava Mts. (Jezerní Mt., Můstek Mt.), established during the 1860s and 1870s (Čada & Svoboda 2011). Despite slight differences in mean age among tree species in some localities, we can generally conclude that species composition did not play a significant role in absolute tree age in 1.3 m (ANOVA, p = 0.935).

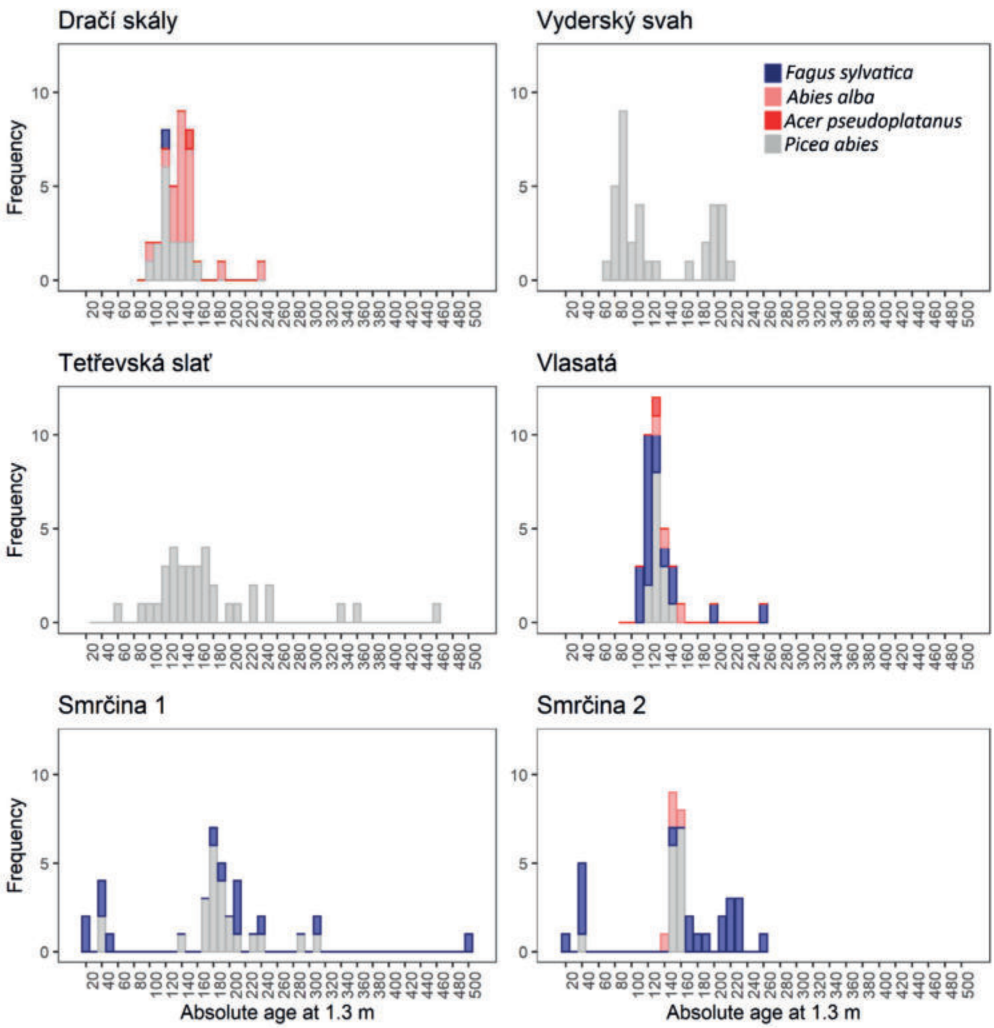

Fig. 3. Age structure for particular stands and tree species based on estimations of absolute age at breast height (1.3 m).

Disturbance history

Site-specific disturbance histories showed substantial spatial and temporal variability, and were rather simplified in comparison with other primary spruce or mixed forest stands in the Bohemian Forest (ČADA et al. 2016, JANDA et al. 2014, KAŠPAR et al. 2020). As mentioned above, some localities originated after severe disturbances in the 1870s (Dračí skály, Vlasatá), resulting in successive gap-recruitment waves during subsequent decades exceeding up to 60% of all rejuvenating trees (Fig. 4A and 4D, bottom part). On the other hand, the forest at Tetřevská slať recruited gradually over several decades under the canopy, with the absence of any strong events (Fig. 4C, bottom part). Specific regeneration modes were observed at Smrčina and Vyderský svah. While partially germinating under the canopy during the preceding period, trees experienced a considerable regeneration peak in gaps in the 19th (Smrčina, Fig. 4E-F, bottom part) and 20th (Vyderský svah, Fig. 4B, bottom part) centuries. It is important to note that there were differences in the timing of strong regeneration episodes between research plots 1 and 2 at Smrčina, challenging the investigation of the primary disturbance agent during these periods.

The mean decadal disturbance rate (as demonstrated by the canopy area disturbed) was variable among the examined stands, ranging from 5.9% (Smrčina 1) to 12.7% (Vyderský svah). The average at the regional scale for all localities was 9.3% CAD. This number is fully comparable with the Žofínský Primeval Forest (ŠAMONIL et al. 2013), where 11% mean canopy loss per decade was measured. On the other hand, SCHURMAN et al. (2018) found a much lesser mean disturbance rate (3.9% canopy removal) in primary montane spruce forests across Central Europe from the Bohemian Forest to the southern Carpathians. However, they used different metrics and criteria for disturbance calculations.

Our analysis of summary disturbance history revealed several periods with substantial canopy area disturbed during various periods, indicating rather local-scale disturbances. The strong wind episode during the 1870s was present in our data only to a minor extent at some localities (Dračí skály, Tetřevská slať, Vlasatá), but it was not a dominant event of release chronology as expected. One reason might be the fact that most of the trees recruited after the windstorm (Fig. 3, Fig. 4). Against expectations, we did not detect a noticeable canopy accession event to the Kyrill storm (2007) at any of the studied forest stands. At the same time, we did not notice any significant evidences of recent wind mortality in the form of windthrow or breakage, assuming the Kyrill storm was not such a strong event as expected. In summary, the only disturbance, synchronous across the majority of the stands (excluding Tetřevská slať and Smrčina 1), was atmospheric pollution during the 1970s and 1980s, detected in the tree-ring data in the form of rapid growth pulses due to the dieback of neighbouring trees, primarily *Abies alba*. Nevertheless, releases connected with a post-pollution recovery and increased nitrogen deposition favouring the growth of silver fir (PINTO et al. 2007, ELLING et al. 2009) might be the contributing factor of intensive canopy disturbances in the 1980s. Besides the above-mentioned episodes, some local events leading to extensively disturbed canopies were also seen in the data: the 1820s and 1850s at Smrčina (46% and 45% CAD, respectively), the 1910s at Vyderský svah (44% CAD), 1940s at Tetřevská slať (36% CAD), and 1960s at Vlasatá (24% CAD). As unknown factor of these disturbances, in next step, we focused on studying historical documents to uncover the character of these disturbances (i.e. natural vs. anthropogenic).

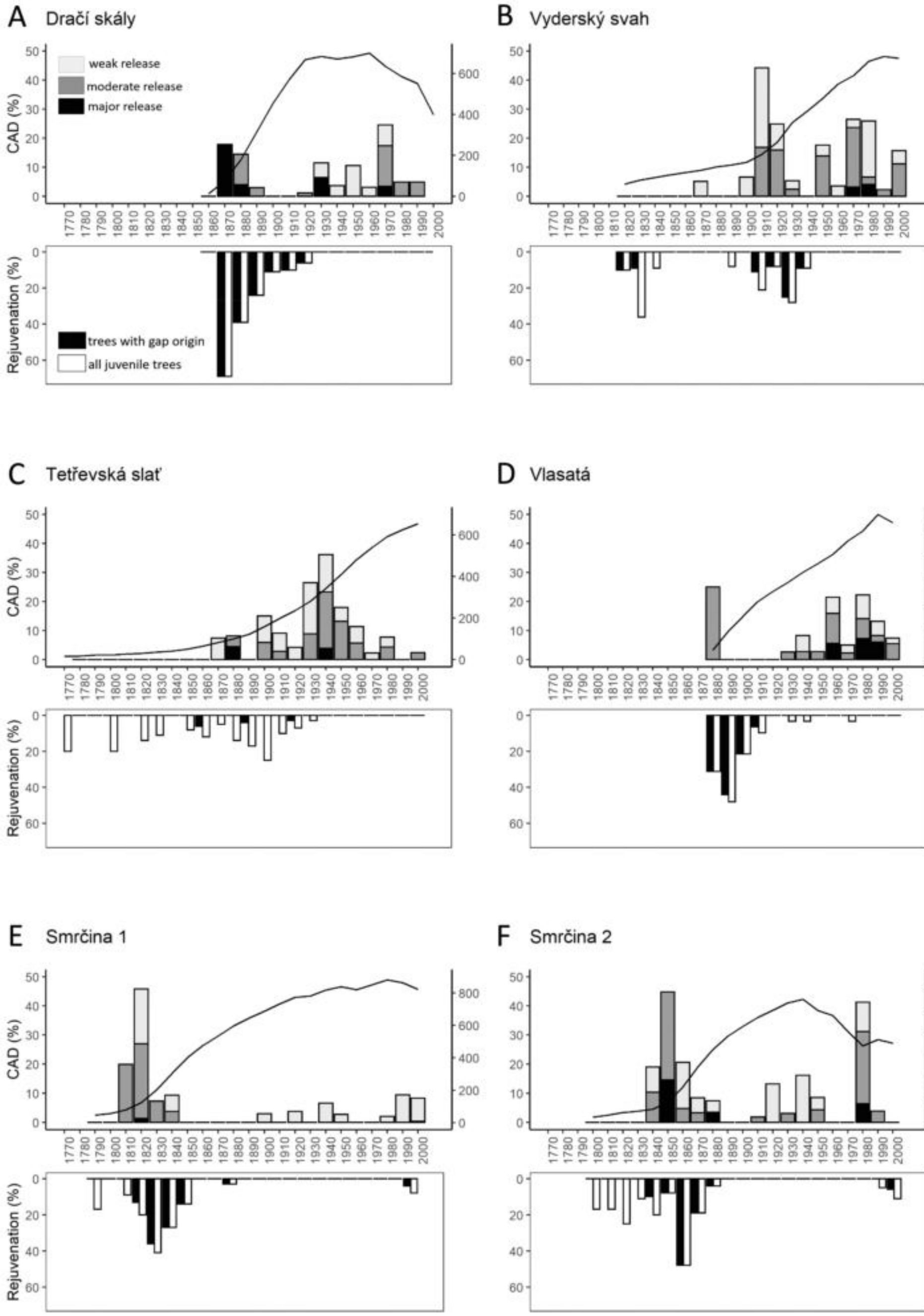

Fig. 4. Summary disturbance histories developed separately for each stand. Upper charts show canopy disturbed area (CAD, %) from the total sum of canopy area (sample depth, m^2) in particular decades. Bottom charts represent the proportion of trees with gap origin.

Differentiating natural vs. anthropogenic disturbances using archival records

Based on our study of historical records, evidence of past human impacts were clear in the majority of the examined forest stands except for Dračí skály, where adequate historical map material is missing. Nevertheless, we can say that all the localities were continuously covered by forest at least up to the beginning of the 19th century. Since that time, anthropogenic activities in a form of grazing, logging or drainage has been detected, forming forest landscapes with different consequences.

Cattle grazing using alpine farming system or forest pasture, culminating in the 19th century in the Šumava Mts. (DRESLEROVÁ 2015), is one of the example of such activity, resulting in the reduction of the highest Šumava summit forests in past. Historical maps confirmed the existence of pasture at the top of the Smrčina Mountain from 1826 (Fig. 5A) until the second half of the 19th century. While the lower research plot (2) is further away, the upper plot (1) lies at the border of this past pasture. Although its establishment might be seemingly seen in the disturbance history in the form of disturbed canopy during the 1820s (Fig. 4E), at the same time we cannot ignore the fact that this decade is considered as the most severe disturbance period over the 550 years in the Bohemian Forest (ČADA et al. 2016) and this effect could also be reflected in disturbance chronology in the upper plot. Lacking evidence of regeneration wave in disturbance history after abandonment of the pasture supports this statement. On the other hand, Fig. 5A indicate that forest was not completely deforested due to grazing purposes, instead many trees might have survived the grazing era in the form of disperse woody vegetation, provided for rapid spruce rejuvenation following the disturbance during consecutive decades (1830–1849). Thus, although the evidence of grazing history at Smrčina is undisputed based on historical sources, we cannot unequivocally claim that disturbance history revealed establishment of the pasture, probably as a result of the fact that research plot is situated at the border of past pasture area. Nevertheless, we regarded this explanation as the most probable clarifying the increased disturbance rate in the first half of the 19th century. Interestingly, research plot no. 2, situated in the lower part of Smrčina Mountain, experienced a completely different development (described in detail later).

The evidence of grazing history was also noticed at Vlasatá, situated in the neighbourhood of the former village Neu Busk, a renowned glass-making settlement. The surrounding forested landscape began to be successively replaced by pastures and meadows with disperse vegetation from the mid 19th century (Fig. 5B). Thus, the disturbance detected in the tree-ring data lead to the question of whether this event reflects windstorms in the 1870s or rather the establishment of the pasture. Nevertheless, the presence of characteristic windthrow features (Fig. 5C), i.e. evidence of past natural disturbance, as well as the occurrence of trees of typical pasture habitus indicate a joint effect of natural and human disturbance in the past. Unfortunately, only a fragment of the original forest has remained as a result of ongoing human interventions in the form of clear-cuttings in the vicinity of the research plot, detected in the summary disturbance history as well as aerial photographs from the 1960s and 1980s.

The factor of the specific disturbance history at lower beech-dominated research plot of the Smrčina massif is questionable. One of the probable explanation of the severe canopy disturbance during the 1850s (Fig. 4F) could be connected with the drifting of wood, that was traditionally an important method to transport timber from forests via a system of water channels. The Schwarzenberg Canal was among the longest, floating logs from 1793 to 1962

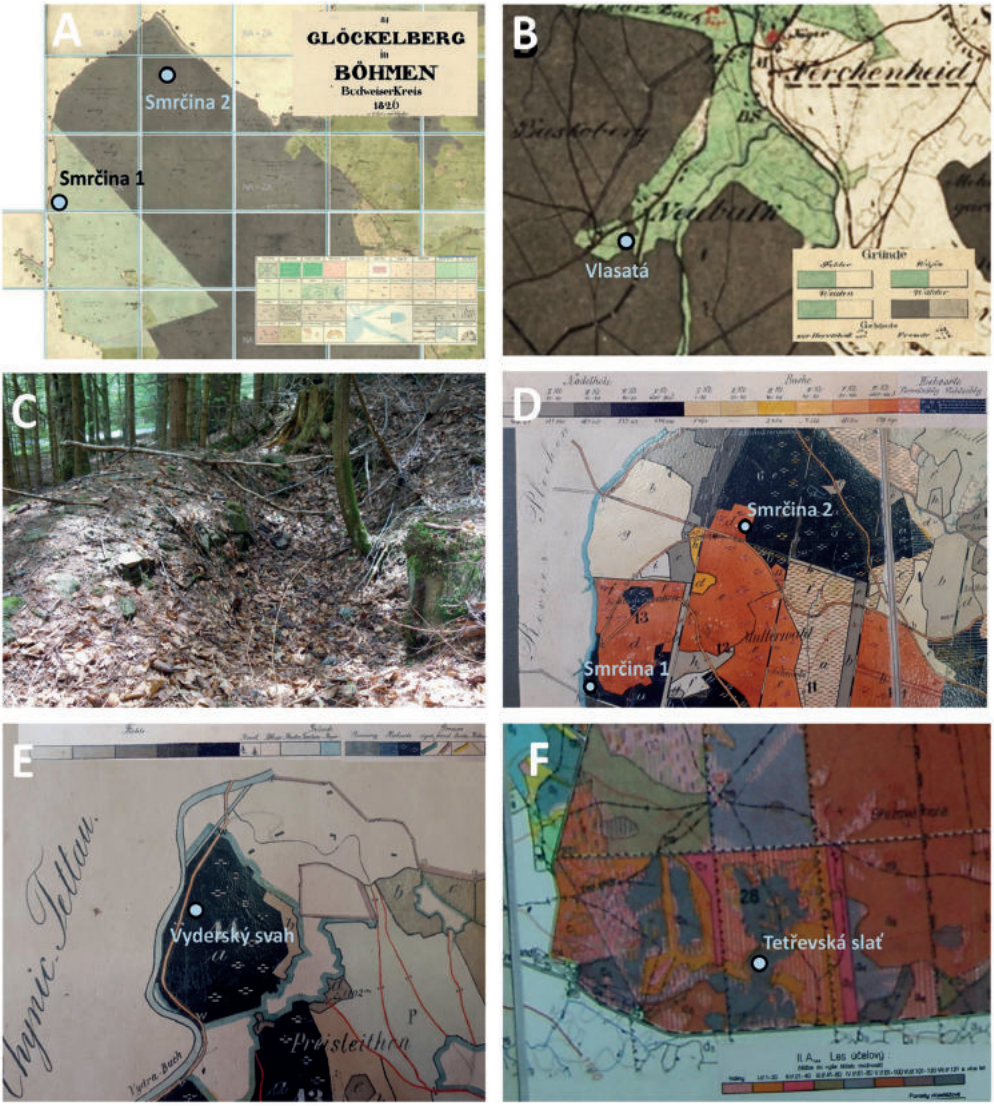

Fig. 5. Historical evidences of anthropogenic vs. natural disturbances: A – Indicatory sketch of the Stable Cadastre with research plots of Smrčina 1 and 2 (Indikationsskizze der Gemeinde Glöckelberg, 1826), source: https://ags.cuzk.cz/archiv. B – Administrative map of the Vimperk manor and goods of Přečín and the municipal forests of Volary and Prachatice with research plot Vlasatá (Administrativní mapa panství Vimperk a zboží Přečín a volarských a prachatických městských lesů, 1833), source: https://www.starelesnimapy.cz. C – picture of a characteristic windthrow feature (pit and mound) at the Vlasatá plot. D – Forest management map of the Vorderstift district with research plots Smrčina 1 and 2 (Přehledová mapa revíru Bližší Lhota, 1922/23), source: State District Archive in Český Krumlov. E – Forest management map of the Phillipshütte district with the Vyderský svah research plot (Přehledová mapa revíru Filipova Huť, 1921/22), source: State District Archive in Český Krumlov. F – Growing stock map of the Modrava forest district with the Tetřevská slať research plot (Porostní mapa Polesí Modrava, 1974).

and connecting the Vltava catchment with the Danube River. As a result, the increased demand for timber in Vienna led to the overharvesting of neighbouring forests, including the Smrčina massif, situated above this canal SAITZ (1898). He also described the original forests on Smrčina as spruce-dominated, with admixtures of fir and beech. Nowadays, however, the forests of the Smrčina massif are regarded as the largest beech forests of the Šumava region. On the other hand, high-severity disturbances identified during the 1850–1870s period in some plots in the Šumava Mts. (ČADA et al. 2013) coincide with our disturbance chronology and might be also be a contributing factor explaining intensive canopy accession events at Smrčina. At the same time, our data do not completely support the perspective on tree-species transition of SAITZ (1898), as beech trees dominated in the higher age classes (Fig. 3), suggesting the presence of beech or mixed forest even before the canal construction. This finding well corresponds with dendrochronological study in the Ukraine Carpathians, where beech trees were observed (ŠAMONIL unpubl.) despite they had been overlooked in earlier studies from the same sites (ZLATNÍK et al. 1938). Similarly, a higher share of European beech in the past throughout the Šumava Mts. was inferred by HUBENÝ et al. (2022) based on historical forestry surveys. Based on the historical forest management maps it is evident that primeval forests have never been completely logged in this area, but were instead managed by the Femelschlag system (Fig. 5D), a historical German shelterwood forestry practice, emulating natural disturbances. Under this management system, most trees are cut with the exception of several high-quality reserved trees that are left in the stand as seed trees.

The map of the forest district of Filipova Huť from 1921–1922 indicates that Femelschlag management was also applied at Vyderský svah (Fig. 5E). A severe canopy disturbance during the 1910s detected in the summary disturbance history might be linked with harvesting using this system. Further, smaller clear cuts are obvious from aerial photographs during the period 1965–1999. Historical documents demonstrate past human interventions even at Tetřevská slať. Despite a 150 year period with no evidence of stronger canopy disturbances until the beginning of the 20th century, an aerial photograph from 1949 documents scattered clear cuts in the vicinity of the research plot, likely related to severe events from 1930–1949 in the disturbance history. The extent of past interventions is also clear from the forest management map of the Modrava district from 1974 (Fig. 5F), demonstrating a 120 year old forest fragment inside the young forest stand. Undoubtedly, past drainage, one of the most serious interventions into peat-bogs and mires in the Šumava (BUFKOVÁ 2013), might have impacted increasing disturbance rate in the 1930s and 1940s through a drop in the groundwater level. Drainage ditches in the vicinity of the locality are still detectable from aerial photographs, however an exact time period of their building remains unknown.

As we did not find appropriate archival material documenting the past development at Dračí skály, we might only assume that a massive die-off of *Abies alba* is responsible for severe disturbances during the 1970s as a consequence of air pollution in Central Europe.

CONCLUSION

Our results demonstrate that the simultaneous use of tree-rings, maps and written records is a very effective tool for studying the past development of natural forest ecosystems. In comparison to other primary spruce or mixed forest stands in the Bohemian Forest, our studied stands experienced rather simplified natural disturbance histories, apparently attributed to the lower age of the stands. These forest stands were largely rejuvenated after severe disturbances during the 1870s or were not exposed to winds due to their young age. Despite this, 13% of tree individuals were older than 200 years, and thus a significant proportion of the stand structure was established much earlier than severe disturbances in the 19th century, retaining the legacy of primeval forests. Nevertheless, based on historical documents and maps, all examined stands were probably affected by human activities in the past to a certain extent in the form of cattle grazing, timber logging and atmospheric pollution. The occurrence of anthropogenic disturbances is also the main factor explaining the differences in summary disturbance histories across the localities. Despite the past human influence in the region, the primeval forest continuity was not entirely disrupted and is still present at most of stands in the form of ancient trees as well as high deadwood volume. From this perspective, we conclude that all the localities might be considered as being first generation after primeval forests, with the occurrence of some trees surviving the human interventions. From the point of view of the presence of very old trees, the most valuable forest stands were found at Tetřevská slať and higher elevated parts of the Smrčina Mountain. Evaluation of the importance of these sites for species biodiversity preservation would be valuable.

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