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A 400-year record of disturbance history in the Bohemian Forest Ecosystem: Lessons from unique transboundary tree-rings chronicles

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Abstract

Considering the increasing frequency of disturbance events under accelerating global change, detailed knowledge about past forest dynamics forms a crucial foundation for conservation management of national parks. As sufficiently unexplored so far, our research shed light on disturbance history of the Bohemian Forest Ecosystem, comprising the Šumava Mountains and the Bavarian Forest. With a robust dendrochronological dataset of more than 6 000 trees, this is the first cross-border study dating back into the early modern era. Our aim was to compare the age structure and disturbance history on the Czech and Bavarian sides of the border using unified approach. The forest stands originated in the 17th and 18th century, with the most intense regeneration waves during the second half of the 19th century. Trees sampled on the Czech side reached significantly higher age than the Bavarian side. Despite disturbance synchronicity in the second half of the 19th century, summary disturbance histories revealed temporal variability between the Bavarian and Czech side of the border for most centuries, indicating that local storms with biotic outbreaks shaped the forest structure. Explaining the large spatial disturbance variability is challenging, suggesting different past forest management or geographic and climatic conditions as the most likely factors.

Key words: dendrochronology, disturbance dynamics, tree-rings, windstorm, bark beetle outbreak

INTRODUCTION

The Bohemian Forest Ecosystem stands as one of the largest continuous forested regions without human intervention in Central Europe, earning it the moniker of the “Green Roof of Europe”. Encompassing both the Šumava National Park in the Czech Republic and the Bavarian Forest National Park in Germany, this region has sparked extensive discussion regarding the origin and historical species composition of its forest ecosystems, crucial for formulating effective conservation management strategies. Compared to most other mountain landscapes in Central Europe, the harsh climate, remoteness and the acid and shallow soils have protected this area from extensive human deforestation activities for centuries. Despite recent archaeological and paleoecological evidence indicating local human habitation dating back to the Mesolithic period, as well as the Bronze and Iron Ages (DRESLEROVÁ et al. 2020, KOZÁKOVÁ et al. 2020, VAN DER KNAAP et al. 2020), intensive human colonization of the Bohemian Forest Ecosystem was relatively delayed, emerging predominantly during the high medieval era in the 12th century (BENEŠ 1996). More extensive exploitation activities occurred during the 18th century until the mid-19th century connected with the culminating glasswork industry. However, in the 1860s a substantial part of the mountains, predominantly more remote and inaccessible regions, still consisted of largely untouched stands, considered as pristine forest (KLOSTERMANN 1894, BRŮNA et al. 2013). Therefore, until the nineteenth century, the Bohemian Forest Ecosystem harbored naturally preserved extensive forested areas protected from direct interventions. It wasn't until the mid-19th century that forests in the higher elevations began to be intensively exploited by their owners for timber extraction, implementing practices such as clear-cutting and artificial forest regeneration. Forest management intensified from the end of the 19th century, especially on the Bavarian side, favouring spruce at the cost of deciduous tree species (HEURICH & ENGLMAIER 2010).

To a certain extent, changes driven by human activities are still visible in the landscape today, in the form of agricultural and pastoral land, glasswork settlements, and altered forest species composition. Nevertheless, what remains largely beyond the scope of current generations, is the impact and expanse of past natural disturbance events, which have been unprecedentedly changing the picture of the Bohemian Forest Ecosystem over the centuries. Acting simultaneously in interaction with bark beetle outbreaks, severe windstorms have caused large early successional areas in European mountain spruce forests (MÜLLER 2008). The most exceptional, stand-replacing events in the whole Central European context were the windstorms on 7th December 1868 and 26th October 1870, resulting in 40% at least partly disturbed area of the Bohemian Forest together with a subsequent severe bark beetle outbreak (*Ips typographus* (L.)) (BRŮNA et al. 2013). The temporal distribution of the most important wind events, triggered following bark beetle infestations, is concentrated in the 1740s, 1830s, 1870s, and 1930s–1940s (BRÁZDIL et al. 2017a, 2018a, 2022). During the last 30 years, accelerated by several drought episodes, large windthrow events resulted in stand-replacing bark beetle outbreaks, creating widespread disturbed areas (LAUSCH et al. 2011, ZEPPENFELD et al. 2015). While these disturbances were extensively documented through chronicles, newspapers, forestry, and meteorological records, determining the intensity and spatial extent of these phenomena from these sources is still challenging. From this perspective, dendrochronology (i.e. annual tree-ring analysis) serves as an appropriate retrospective tool to obtain reliable information on characteristics of disturbances and combined with tree-age structure analysis to describe the post-disturbance forest development, including changes in tree-species composition (MARTÍN-BENITO 2022).

Much progress has been made over the past years to shed light on disturbance dynamics throughout the Šumava Mts. (SVOBODA et al. 2012, JANDA et al. 2014, ČADA et al. 2016, KAŠPAR et al. 2020, VAŠÍČKOVÁ et al. 2021). Based on tree-ring analysis, ecosystems were periodically affected by extensive disturbances every 10–50 years (ČADA et al. 2013) and even more frequently in wind-exposed locations such as mountain ridges and flatter terrain (ČADA et al. 2016). As far as we know, no dendroecological or disturbance study exists for the Bavarian Forest National Park. Generally, tree-ring-related studies are very scarce on the Bavarian side of the mountains, targeted primarily on the climate response of Norway spruce or fir's growth decline (WILSON & HOPFMUELLER 2001, HEER et al. 2018). The disturbance history of the Bavarian Forest was revealed from fossil pollen lake sediment data, describing past vegetation and bark beetle dynamics (VAN DER KNAAP et al. 2020). Based on a historical cross-boundary database of forest management maps, BRŮNA et al. (2013) described the effect of the large-scale windthrow event during the years 1868–1870 in the Bohemian Forest Ecosystem. Thus, these studies provided just a piece of a "puzzle" into the complex picture as they focused only on specific ecosystems or disturbance drivers. Therefore, we present a unique dendroecological transboundary study throughout the entire Bohemian Forest Ecosystem, across the Šumava and Bavarian Forest National Park covering large altitudinal and ecological gradients as well as past human disturbance. This is the first study using the robust dendrochronological dataset derived from the forest inventory in the Bavarian Forest National Park. The present study aims to: i) reconstruct the past development of forest ecosystems throughout the Bohemian Forest, and ii) compare the age structure and disturbance history on the Czech and Bavarian sides of the border.

MATERIAL AND METHODS

Study sites

Our study covers a wide range of localities across the Šumava National Park (NP) and Protected Landscape Area (PLA) and the Bavarian Forest National Park (Fig. 1A). On the Czech side (Šumava Mts.) we used a robust dataset sampled by the Forest Ecology Department (VÚKOZ) resolving different research questions (partly published by KAŠPAR et al. 2020, 2021, VAŠÍČKOVÁ et al. 2021, 2022). These sites are scattered throughout the whole mountain range, spanning from 672 to 1 169 m a.s.l. In the Bavarian Forest, we used a unique, yet unpublished, dendrochronological material sampled in 1991, covering the Rachel-Lusen area of the national park. From this material, the most perspective sites in a sense of naturalness were selected, spanning from 697 m a.s.l. to 1 408 m a.s.l. (Fig. 1B). While some locations are considered to be primary forests with no direct human impact in the past (e.g. Boubin Primeval Forest in the Šumava PLA under strict protection since 1858), we still cannot exclude historical human interventions at certain locations (in the sense of logging or grazing).

The geological substrate belongs to the Bohemian massive, a very old crystalline complex, formed in particular by gneisses and granites. Mean annual temperatures vary widely, from 3–4 °C at ridges to 5–6 °C at low elevation. Annual precipitation ranges between approximately 1 000 mm and 1 600 mm (TOLASZ et al. 2007). Forest biotopes can be classified as *Luzulo-Fagetum*, *Asperulo-Fagetum*, *Vaccinio-Piceetea* and *Tilio-Acerion* (CHYTRÝ et al. 2010). The forest composition is dominated by Norway spruce (*Picea abies* (L.) Karst.), creating pure spruce forests of upper mountain zone above 1 100 m a.s.l. or waterlogged and peat bog forests of lower elevation. Below, Norway spruce plays only a subordinate role in mixed forests with European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.), which represent the most significant habitat. Forests on fertile steep slopes, frequently in ravines, allow a higher proportion of sycamore and maple (*Acer pseudoplatanus* L., *A. platanoides* L.) and small- and large-leaved lime (*Tilia cordata* Mill., *T. platyphyllos* Scop.). The original tree species composition has been dramatically altered since the beginning of modern forestry due to glass manufacturing and shelterwood forest management, promoting an increase in the proportion of Norway spruce at the cost of European beech and silver fir (HEURICH & ENGLMAIER 2010). Generally, original forests have been replaced by Norway spruce on the Czech side of the border in a more extensive way than on the Bavarian side; thus the species composition of the forests on the Bavarian side indicates a higher representation of fir and beech nowadays. While the proportion of tree species is 65.9% Norway spruce, 23.5% European beech and 3.2% silver fir in the Rachel-Lusen area of the

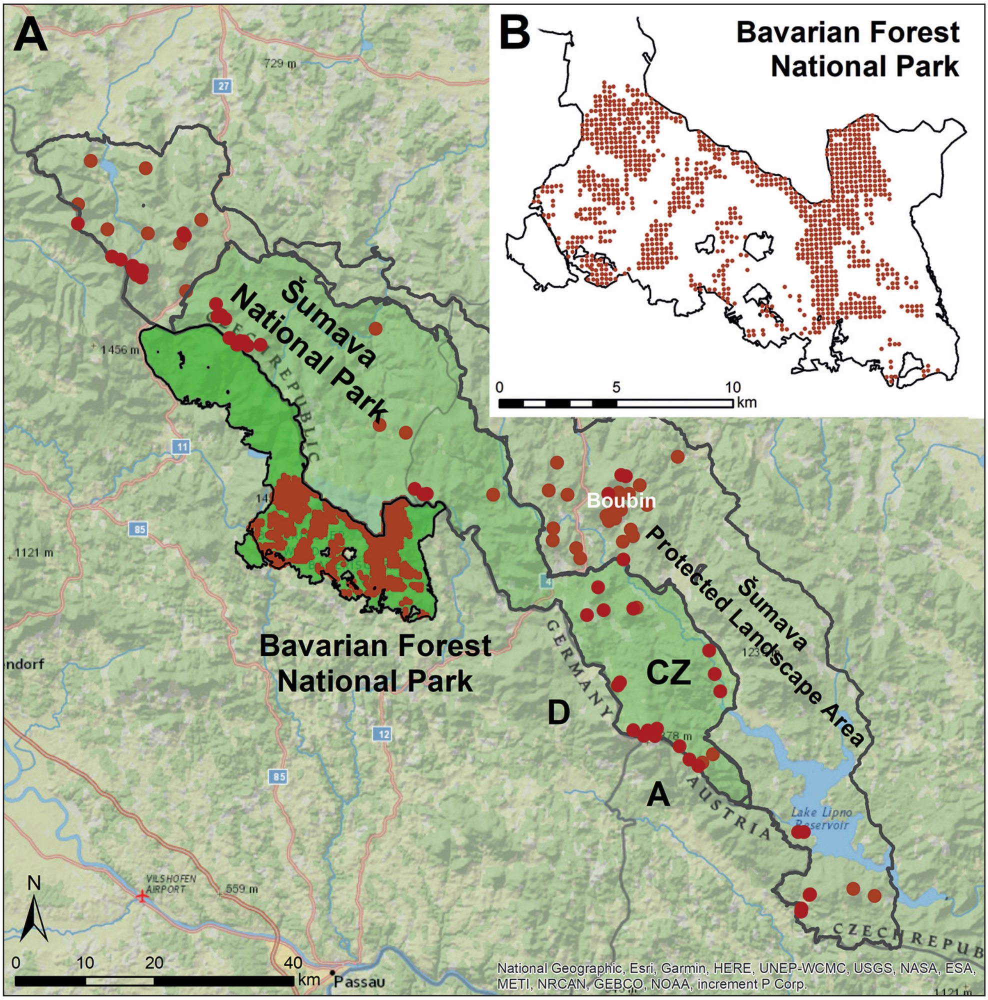


Fig. 1. Locations of all study sites (A) and the detail of inventory plots within the Bavarian Forest NP (B). Brown circle represents study sites. The size of the circles does not correspond to the size of the research plots and was chosen for better illustration.

Bavarian Forest National Park (HEURICH & ENGLMAIER 2010), in the Šumava National Park it is 74% Norway spruce, 9% European beech and 3% silver fir (HUBENÝ et al. 2022).

Data collection

Analyses are based on a robust dataset containing more than 6 000 trees (N = 3 085 on the Bavarian side and N = 3 038 on the Czech side). In 1991, an extensive dendrochronological sampling was conducted within the forest inventory covering the Rachel-Lusen area of Bavarian Forest National Park. Dendrochronological cores were taken from approximately 3 000 inventory plots in a regular square grid of 200×200 m. For each tree species, a maximum of 3 trees of variable diameter classes (0–20 cm, 20–40 cm, and >40 cm DBH) were sampled on each plot. Sample collection was carried out using Pressler's increment borer at a height of 1.3 m above the ground, allowing for comparison with the Czech side of the mountains, where analogous samples were collected at an average height of about 1 m (0.5–1.3 m) between 2012 and 2021. The sampling design in the Šumava Mts. was variable, depending on the purpose of the study. On the contrary to the Bavarian Forest, selection of plots was not schematic, as we aimed on sites of long primeval forest continuity and biological legacy. Most of the increment cores (N = 1 830) originate from the 685-ha remnant of the Boubin Primeval Forest Reserve, where randomly selected individuals with an exposed tree crown were sampled. In addition, the rest of plots were sampled in a 0.2 ha circular design, with the selection of 35 both exposed and suppressed trees per one plot. The details regarding sampling strategy were described by KAŠPAR et al. (2020) and VAŠÍČKOVÁ et al. (2021, 2022).

Data processing

Dried increment cores were treated following standard dendrochronological procedures (SCHWEINGRUBER et al. 1990), including mounting into a wooden lath, sanding and smoothing using 600 grit finest sandpaper to reveal wood structure. Subsequently, samples were scanned using an Epson LA2400 scanner at 1600 DPI resolution, and tree-ring widths were then measured in WinDENDRO software (RÉGENT INSTRUMENTS 2022), which allows for automatic detection and quantification of ring widths with an accuracy of 0.01 mm. This was followed by a process called cross-dating using the marker year method (YAMAGUCHI 1991), in which the measured tree-ring series were compared to each other and a standard chronology using PAST 5 software (SCIEM 2007) to eliminate 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). The obtained dated tree-ring series were used as a basis for evaluating the age structure and reconstructing the disturbance history on the Bavarian and the Czech sides of the Bohemian Forest Ecosystem.

To achieve maximally comparable results, we applied identical techniques and criteria of disturbance history calculation, with the exception of high-elevated (above 1 000 m a.s.l.) spruce forests with specific growth dynamics, where different criteria were used. First, it was necessary to compute the number of tree rings to the centre for cores that missed the pith using a pith locator (APPLEQUIST 1958), as the calculation of disturbance history allows only for samples reaching a distance ≤3 cm from the tree's centre. At the same time, calculations were carried out only for spruce, beech, fir and maple trees, i.e. species with existing determination criteria. Thus, only trees meeting these prerequisites were included in the subsequent analyses (N = 2 283 on the Bavarian side and N = 2 375 on the Czech side).

Two types of evidences of past canopy disturbances were considered in the tree-ring series: (i) gap origin (LORIMER et al. 1988), indicating the presence of a canopy gap of unknown age based on accelerated initial juvenile growth rate; and (ii) release (FRELICH 2002), which directly shows the occurrence of disturbance during subsequent growth as a reaction to the death of adjacent tree in the form of abrupt changes in tree radial growth. To estimate the probability that the sampled tree germinated inside the canopy gap, average juvenile growth for five consecutive tree rings in the time for a tree to reach 6 cm DBH was calculated, assuming that a tree germinated in a canopy gap exceeding a predefined threshold. The threshold we used had been calculated by KAŠPAR et al. (2020) according to the standard approach by LORIMER et al. (1988): 1.60 mm for conifers and 1.53 mm for broadleaves.

To detect growth releases in radial growth, we applied the boundary line technique (BL, BLACK & ABRAMS 2003). This method is based on a comparison of the percent growth change (PGC, %) between two 10-year intervals (NOWACKI & ABRAMS 1997) with the average prior radial growth over the previous ten years (PG, mm), taking into account individual factors of a tree (such as species, social status, age, dimensions). Separately, we constructed negative exponential curves for every tree species, i.e. boundary lines expressing maximum growth plasticity. Our robust dataset allowed for the construction of new regional boundary lines that represent the diverse gradient of forest ecosystems throughout the Bohemian Forest Ecosystem. In total, we used 632 637 and 193 837 tree rings for *P. abies* and *F. sylvatica*, respectively, which more than exceed the requirements of BLACK et al. (2009). As for *A. alba*, we did not reach the recommended minimum dataset of 50 000 tree rings (N = 38 255 tree rings), and thus a higher uncertainty in release detection must be taken into account. The same curve was used for maple as for beech.

In the first step, it was necessary to calculate the values of PG and PGC for all tree rings. PG values were then divided into 0.50 mm intervals, except for the first centimetre segment, which was classified into 0.25 mm intervals (SPLECHTNA et al. 2005). Therefore, the 1% highest values of GC in each PG interval were averaged and fitted by a negative exponential function in R software (R DEVELOPMENT CORE TEAM 2023). The best fit was estimated on the basis of the coefficient of determination (R^2). Species-specific equations as well as model fit statistics are shown in Table 1. Finally, the local maxima of PGC were scaled with this boundary line and considered as a weak, moderate or major release from suppression if exceeding 25%, 50% and 100% BL, respectively. We excluded short-term growth changes by retaining only growth changes sustaining minimally 7 years.

To prevent false events associated with the reaction of exposed canopy trees, the calculation of disturbance history was limited purely to tree-ring sequences that had not reached the canopy. For mixed and beech-dominated forests 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 the Boubin Primeval Forest. For deciduous trees, the threshold diameter was 56 cm, while for conifers, this criterion was approximated to 55 cm. The threshold diameter for higher elevated spruce forest was calculated based on the methodology of LORIMER & FRELICH (1989). To this purpose, the social status of 838 randomly selected Norway spruce individuals of various diameter classes was assessed. The determined threshold diameter was found to be 43 cm.

Table 1. Boundary line equations including basic statistics of model fit.

Species	Boundary line equation	No. tree rings	R^2	AIC
PIAB	$pgc = 2.5374866 \times \exp(-0.41305 \times pg) + 17.1163960 \times \exp(-4.31798 \times pg)$	632 637	0.99917	118.0947
FASY	$pgc = 2.8856725 \times \exp(-0.50665 \times pg) + 18.7468906 \times \exp(-4.53121 \times pg)$	193 837	0.99967	83.1272
ABAL	$pgc = 1.759399 - 0.364697 \times pg + 13.493284 \times \exp(-2.3221 \times pg)$	38 255	0.99845	90.8759

Tree codes: PIAB - *Picea abies* (L.) Karsten, FASY - *Fagus sylvatica* L., ABAL - *Abies alba* Mill.

As a measure of the release severity, the proportion of canopy disturbed area (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); for conifers this was 0.5869091 × DBH; and for broadleaves 1.424909 × DBH. To prevent from overestimation of crown area, we calculated separately this relationship for higher elevated spruce forests based on measured crown areas and DBH of 93 randomly selected individuals. The relationship was modeled using linear, quadratic, power and exponential functions. The best model was selected based on the Akaike Information Criterion (AIC), and it was determined as power function in the form $y = 0.47164 \times DBH^{1.18097}$ (AIC = 710.70).

Based on the knowledge of the canopy area of the disturbed trees and the 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 the proportion of gap-originating trees (bottom part) for each decade. These discrete features thus provide a complex picture of past disturbance dynamics, describing both the origin of the stands as well as the occurrence of important disturbance events. To maximize the credibility of the results, the chronology was truncated if the sample size dropped below 1%. The calculation of disturbance history was conducted using a customized script in R software (R DEVELOPMENT CORE TEAM 2023) and applying the TRADER package (ALTMAN et al. 2014).

RESULTS

Age and tree-species structure

Tree-species composition exhibits a very similar structure in both regions based on the dendrochronological datasets and thus, are fully comparable (Fig. 2). Norway spruce dominates tree-species structure with cca 65%. European beech and silver fir account for cca 24% and 5%, respectively. Maples contribute only a few percentage points to the composition (1.4–2.5%). In the Bavarian Forest, only mountain ash (*Sorbus aucuparia* L.) reaches more than 1%. The other auxiliary tree species are regionally variable, occurring in minor proportions below 1%: white birch (*Betula pendula* Roth), small- and large-leaved lime (*Tilia cordata*, *T. platyphyllos*), wych elm (*Ulmus glabra* Huds.), European ash (*Fraxinus*

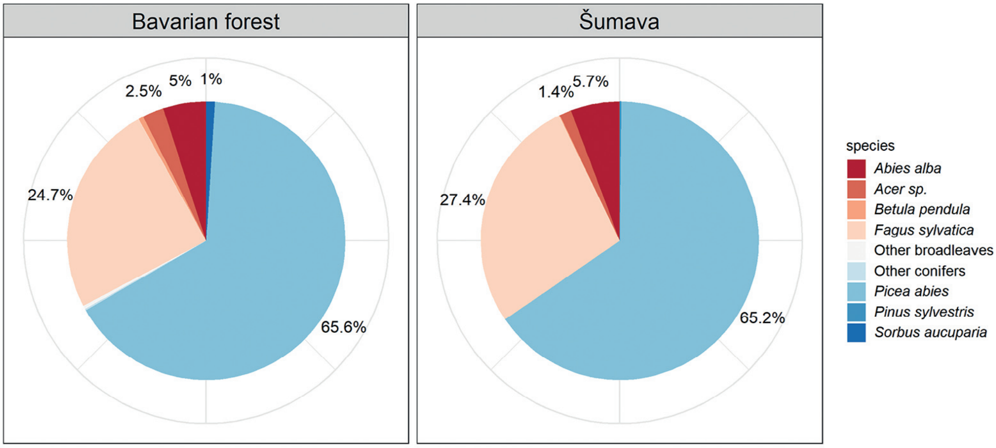


Fig. 2. Tree-species composition of the dendrochronological datasets in the Bavarian Forest and the Šumava Mts.

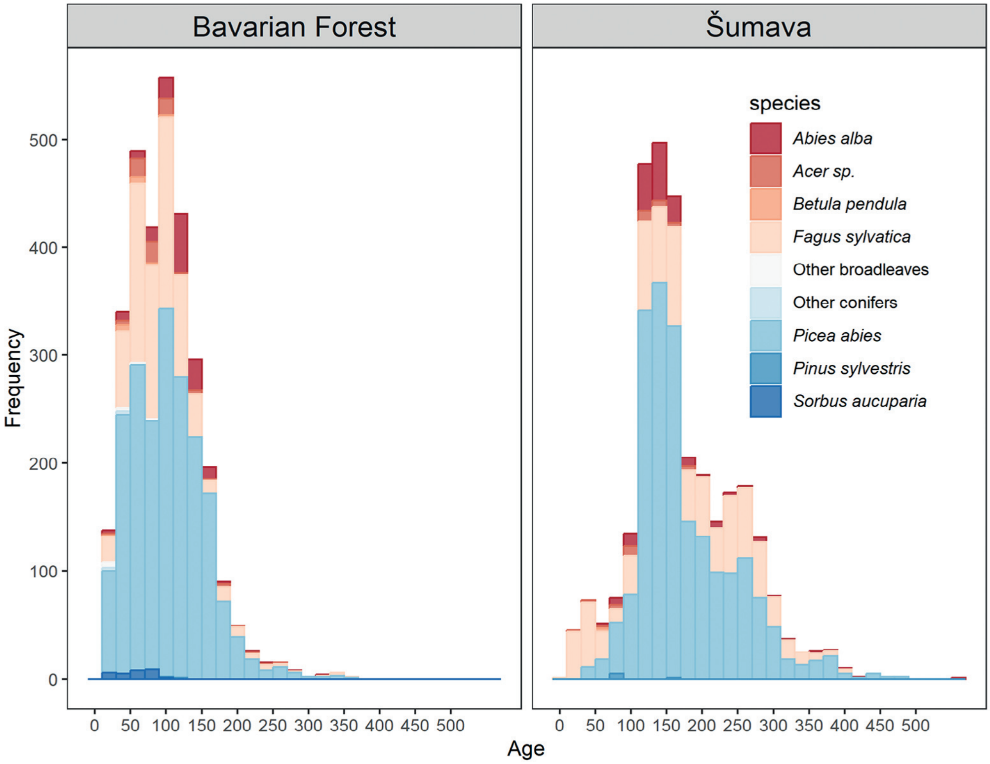
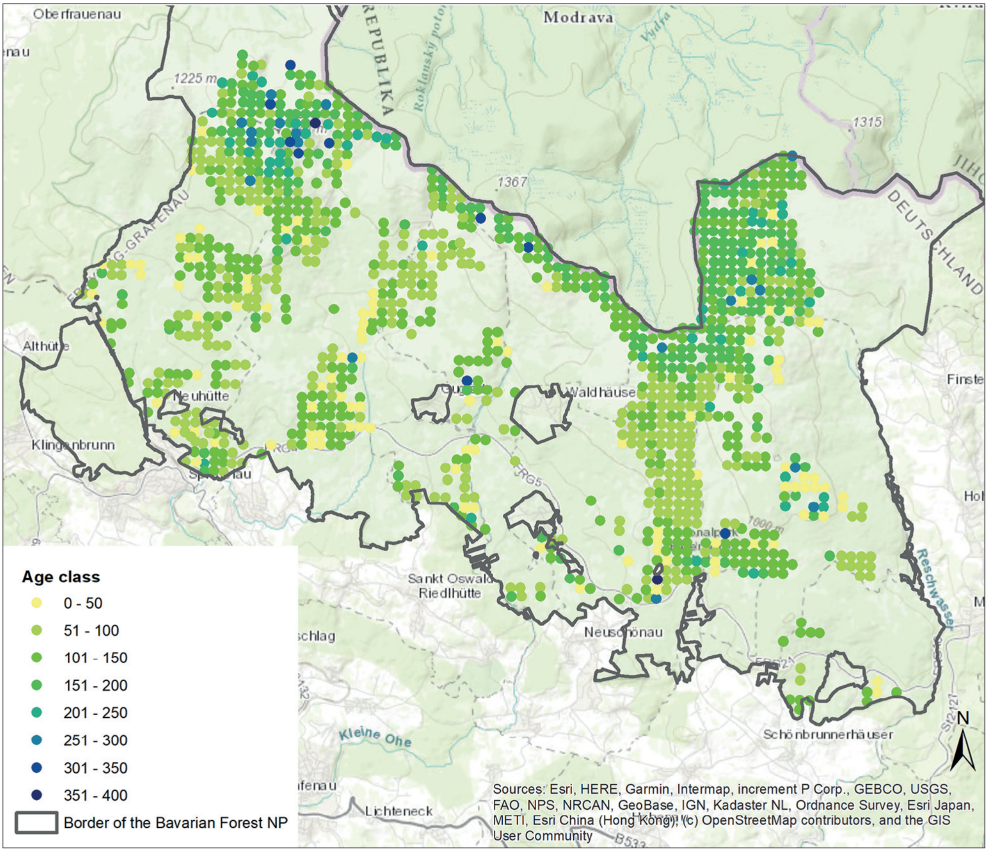


Fig. 3. Age structure based on dendrochronological datasets in the Bavarian Forest and the Šumava.

excelsior L.), black alder (*Alnus glutinosa* (L.)), Eurasian aspen (*Populus tremula* L.), scots pine (*Pinus sylvestris* L.), European larch (*Larix decidua* Mill.), Douglas fir (*Psudotsuga menziesii* (Mirb.) Franco) and the various willows (*Salix* spp.).

In the age structure of the Bavarian Forest (N = 3 085), trees aged 60–130 years dominate (25% quartile = 62 yrs, median = 96 yrs, 75% quartile = 128 yrs) (Fig. 3). This corresponds to the largest regeneration wave (i.e. establishment of a majority of the stands) between the years 1860–1930. At the same time, we expect most stands to be regenerated much earlier as the absolute ages of trees are likely even higher due to the sampling height and missing tree centre of some increment cores. However, older individuals can also be found in the dataset (the oldest *F. sylvatica* reached 370 tree rings). 3% of trees were older than 200 yrs and ten individuals exceeded up to 300 yrs. The average age differed significantly among species ($p<0.05$). The highest age was recorded for silver fir (median = 121 yrs), followed by Norway spruce (median = 101 yrs) and European beech (median = 89 yrs). The other species were much younger. We also found spatial variability in tree age among different sites, with the oldest trees coming from the Großer and Kleiner Rachel and Rachelsee and also from vicinity of the Lusen and the Moorberg (Velká Mokrůvka) (Fig. 4).



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community

Fig. 4. Age distribution based on dendrochronological dataset in the Bavarian Forest NP.

Trees sampled in the Šumava Mts. (N = 3 038) reach a significantly higher age (25% quartile = 128 years, median = 157 years, 75% quartile = 222 years) (Fig. 3), suggesting that the main body of the stands originated during the nineteenth century, with the most intense regeneration wave after the 1840. The highest average ages were reached by beech trees (median = 168 years), spruces (median = 158 years), and firs (median = 139 years). About 30% of trees are more than 200 years old. The oldest part of the datasets came from the Boubin Primeval Forest, as most trees regenerated in the 17th and 18th centuries. Fig. 5 shows map of age distribution in the Šumava Mts., based on maximum age reached within the stands. It should be noted that while data collection on the Czech side of the mountain range targeted stands with the potential for older trees, on the German side of the mountain range, data collection was schematic, covering a wide range of habitats.

Disturbance history

Summary disturbance histories revealed temporal variability between the Bavarian and Czech sides of the border. In the Bavarian Forest, 5.6% of trees were released per decade on average

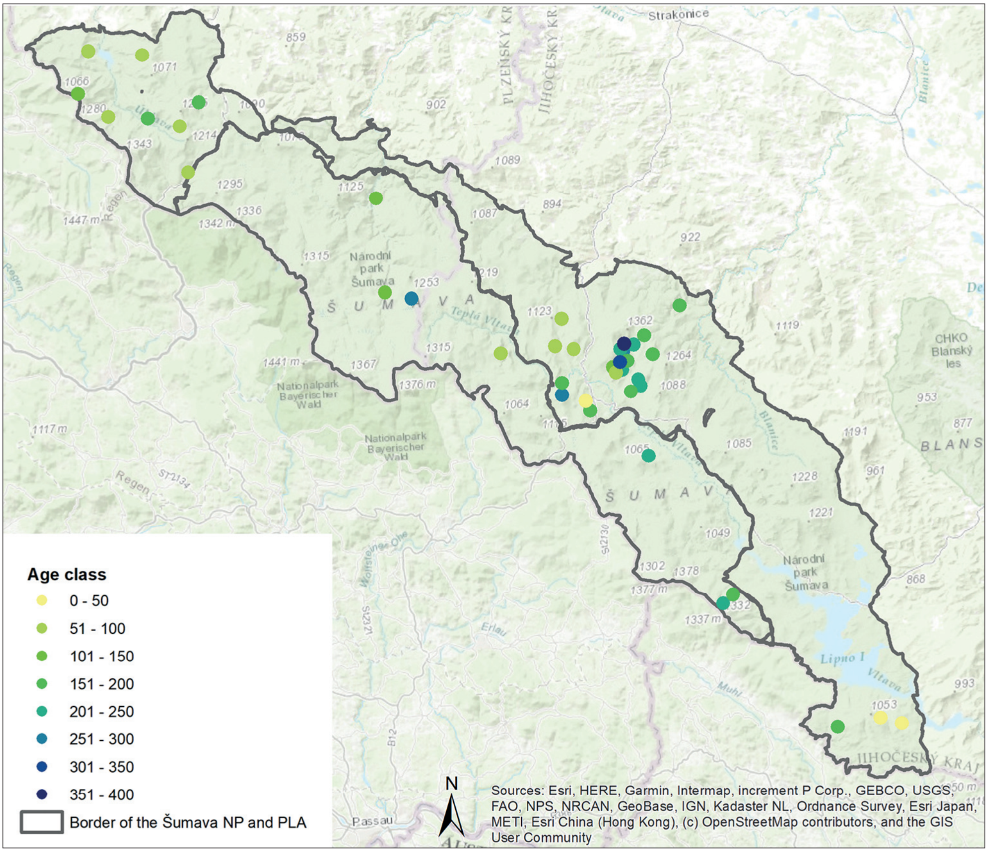


Fig. 5. Age distribution based on dendrochronological dataset in the Šumava NP and PLO.

(Fig. 6A, upper part). The most severe disturbances from the point of view of severity (i.e. proportion of canopy removal) occurred during the decades 1750s, 1770s, 1870s and 1950s. In terms of intensity (i.e. tree-growth response), our analysis of summary disturbance history revealed periods with high release magnitude during the decades 1800s and 1820s. Stands rejuvenated gradually over the 19th century, both under the canopy and inside the gaps (Fig. 6A, bottom part). On average, 3.2% of trees were recruited per decade inside the canopy gap. The evident gap-recruitment waves indicating severe disturbances occurred during the 1760s, 1780s, 1820–1840s and 1890–1900s, i.e. successive decades in which strong release events were captured in tree-ring sequences. During the 20th century, significant regeneration waves did not occur despite strong releases in the mid-20th century.

When comparing the disturbance history from the Bavarian Forest with the disturbance chronology from the Šumava (Fig. 6B), the average decadal disturbance rate on the Czech side (6.2%) does not differ significantly from the German side of the mountains. However, the overall picture highlights a specific disturbance history on both sides of the mountains. Strong disturbances of the second half of the 19th century dominate the tree-ring records from the Šumava, especially the periods 1840–1859 and 1870–1889, which resulted in the removal of up to 50% of the canopy layer in total (Fig. 6B, upper part). The increased release period during the decade 1690s is also worth mentioning; however, it is missing in the disturbance chronology of the Bavarian Forest due to shorter sample depth. The backbone of the forests has been gradually established from the early 17th century, primarily under the canopy (Fig. 6B, bottom part). With the exception of the decade 1740s, the tree-ring record does not

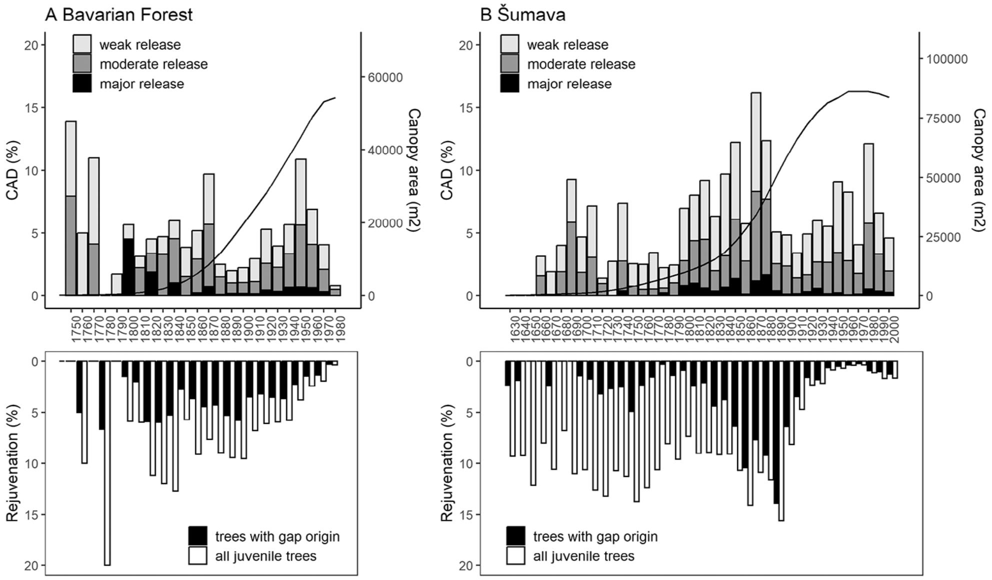


Fig. 6. Summary of disturbance histories developed for A: Bavarian Forest NP and B: Šumava Mts. The upper charts show canopy area disturbed (CAD, %) from the total sum of canopy area (sample depth, m^2) for particular decades, categorized according to release intensity. The bottom charts represent the proportion of trees with gap origin (black colour).

suggest that there was a significant regeneration wave in the gaps (i.e., disturbance) over the next 200 years. Intensive rejuvenation, on the contrary, is evident after strong disturbance events in the second half of the 19th century (1850s–1890s). On average, 2.8% of trees were recruited per decade inside the canopy gap.

DISCUSSION

Although the same region and unified methodology, historical forest trajectories mostly differ on the Czech and Bavarian sides of the mountains. The data were processed identically, but the sampling design still impacts the observed results to a certain extent as older stands were preferentially selected on the Czech side (including a randomization process). Despite these differences, which need to be considered when interpreting the results, the datasets contain valuable information deserving comparison. Among the drivers of this divergence could be geographic and climatic factors such as slope exposure, elevation, precipitation levels as well as soil conditions (MITCHELL et al. 2008, ŠAMONIL et al. 2014), varying between the Czech and German sides. Furthermore, differences in past forest management practices can also play a role.

It should be also pointed out that mortality dynamics could be driven by tree-species composition as well, determing different disturbance regimes. While frequent high-severity disturbances shape mountain conifer forests (PANAYOTOV et al. 2011, ČADA et al. 2016), mixed or low-elevated beech forests are not predisposed to experience such a dramatic wind and biotic disturbances (SPLECHTNA 2005, NAGEL et al. 2007, FRANKOVIČ et al. 2021). Unlike the Šumava Mts., schematic sampling design applied in the Bavarian Forest allowed for sampling of spuce upper mountain zone elevated above 1 100 m a.s.l. On the other hand, on the Czech side, water-affected and bog forests with spruce dominance or ravine forests are characterised by distinct mortality dynamics. Therefore, specific disturbance regimes within the Bohemian Forest Ecosystem with respect to habitat and ecological gradients should be taken into account, however this issue is beyond the scope of this study.

Results of age structure showed that the main bodies of forests on both sides of the mountains originated during the nineteenth century. Nevertheless, on the Czech side, the largest regeneration wave occurred primarily after intense disturbance events from 1840s to 1880s, while on the Bavarian side, the origin of the majority of stands can be dated from 1860 until the first half of the 20th century. In comparison to other montane spruce forests without human intervention within the region of Šumava Mts., largely originating between the beginning of the 18th century and the end of the 19th century (JANDA et al. 2010, ČADA & SVOBODA 2011, ČADA et al. 2013, JANDA et al. 2014), the main stand structure in the Bavarian Forest was established later. Nevertheless, the age structure of the forests is comparable to some near-natural beech-spruce forest stands in the Šumava Mts., that were human affected to some extent in past (VAŠÍČKOVÁ et al. 2022, KAŠPAR et al. 2020). At the same time, the presence of older trees within stands indicates that stand structures were established much earlier, in the 17th and 18th centuries, surviving large disturbances of the 19th century. 3% of trees on the Bavarian side and 30% on the Czech side are older than 200 years, consistent with KAŠPAR et al. (2020), considering these individuals as relicts of primeval forests. The oldest part of the datasets came from the Boubin Primeval Forest (mean age of *F. sylvatica* = 243 yrs and *P. abies* = 222 yrs) (KAŠPAR et al. 2020). On the Bavarian side, examples of such forests include the areas around the Rachel and Lusen, i.e. stands largely replaced by a young cohort following bark beetle outbreak during the 1990s. It should be taken into account that we are presenting lower ages of analysed trees within the current study, i.e. number of tree rings in the sampling height. In fact, trees could be even older if we consider their distance to the stem centre as well as sampling height since the average time that trees need to reach the height of 1–1.3 m spans from 8 to 14 years, depending on the tree species (ŠAMONIL et al. 2009, 2013, TROTSIUK et al. 2012). Especially for trees on the Bavarian side of the border, they were more often sampled out of the range of 3 cm tolerance and thus, higher uncertainty as well as higher ”real“ age of individuals must be assumed.

Forest dynamics was predominantly driven by natural disturbances, associated with known windstorm and bark beetle events. Except for the events of the 19th century, disturbance chronologies obtained on the contrasting sides of the border revealed substantial temporal variability for most of the centuries. While a relatively calm period without major disturbance events on the Czech side, the second half of the 18th century represented a very dynamic period in the Bavarian Forest. The increased disturbance rate during the 1750s can be explained by extreme storms in 1740 (BRÁZDIL et al. 2017a) and subsequently in 1752 (PLOCHMANN & HIEKE 1986). The explanation of the most noticeable peak in canopy removal during the 1770s is quite challenging; however, NOŽIČKA (1957) stated that the Bohemian Forest Ecosystem was affected by a massive storm in 1778. Nevertheless, a drop in sampling depth toward the past and thus, higher uncertainty must be taken into consideration at the beginning of the chronology. PLOCHMANN & HIEKE (1986) also mention an extensive black arches (*Lymantria monacha* (L.)) and spruce bark beetle outbreak in Germany, escalating in Bavaria during 1797–1798, which can explain the high-intensity releases in the 1800s.

In the tree-ring record from both sides of the mountain range, stand-replacing synchronized disturbances of the second half of the 19th century dominate, especially that during the periods of 1840–1859 and 1870–1889, with a higher severity on the Czech side. The main population waves were initiated with these severe disturbances. The significant canopy release during 1840–1849 may be attributed to severe windstorms in 1833–1834, which, together with subsequent drought, led to extensive bark beetle infestation (NOŽIČKA 1957, BRÁZDIL et al. 2022). Not only in the Bohemian Forest Ecosystem, but also in whole Central Europe, one of the most exceptional disturbances was a series of storms during 1868–1870, followed by an unprecedented bark beetle outbreak (BRÁZDIL et al. 2017b, 2018b). The timing of the most severe disturbances also corresponds to peaks in disturbance chronologies previously described for the region of the Bohemian Forest Ecosystem, e.g. the 1750s–1760s (JANDA et al. 2014), 1840s–1850s (SVOBODA et al. 2012), 1860s–1870s (ČADA et al. 2013). However, severe wind and biotic events of the 19th century were significant within the whole Central European region. In the same period as in the current study (e.g. 1840s–1850s and 1860s–1880s), large-scale disturbances were reported for primary beech-fir-spruce forests throughout the broader landscape of Novohradské Mountains (ŠAMONIL et al. 2013), Western and Eastern Carpathians (FRANKOVIČ et al. 2021, TROTSIUK et al. 2012, 2014) and Dinaric Alps (NAGEL et al. 2007). Against expectations, one of the most extensive canopy removal events connected with several wind events during the 1810s–1830s, as depicted in ČADA et al. (2016), JANDA et al. (2014) and SVOBODA et al. (2012), was not as pronounced in our data.

The most probable explanation of the lack of this period in our data could be the fact that these events were typical for wind-exposed, higher-elevated mountain spruce forests that are sporadically represented in our dataset on the Czech side.

Along with synchronised disturbances in the second half of the 19th century, early 20th century is characterized by an absence of such a strong wind events. Nevertheless, two remarkable disturbance events, asynchronous across the border, are worth mentioning. Significant canopy disturbances of the 1950s coincide with intensive post-war logging in the Bavarian Forest, accelerated by several wind events (HEURICH & ENGLMAIER 2010). On the contrary, the forests of the Czech side of the border were profoundly affected by atmospheric pollution that culminated in whole Central European region in the 1980s. As a result, substantial canopy removal during this period is connected with releases due to the dieback of neighbouring trees, primarily *Abies alba*, as well as a post-pollution recovery favouring the growth of silver fir (ELLING et al. 2009, OULEHLE et al. 2010).

While the average decadal disturbance rate is relatively low (5.6–6.2%), "fade out" effect of the bark-beetle outbreaks following wind events must be taken into account when interpreting the amount of canopy loss. It extends tree-mortality duration into several consecutive decades, thus reaching up to 40% canopy removal during the most intensive disturbance period 1870–1899.

CONCLUSION

Our results indicate that periodic wind disturbance events and biotic outbreaks are an important component of the disturbance regime in mountain forests of the Bohemian Forest Ecosystem. Despite dramatic changes due to post-war logging, pollution and severe disturbances during the 2000s, the windstorms from the 19th century (especially 1868 and 1870) and subsequent bark beetle infestation still remain the most significant events in the Šumava Mts, shaping the current structure. These events triggered large-scale canopy removal, facilitating the germination and growth of forest regeneration, leading to the initiation of most stands. However, the main bodies of the recent forest were established much earlier, in the 17th and 18th centuries, surviving the large disturbances of the 19th century. Despite the same region and similar tree-species composition, our findings reveal differences across the Czech-German border. Trees sampled on the Czech side of the mountains reached significantly higher age. Along with the large-scale synchronized disturbance of the 19th century, local thunderstorms formed the forest structure for most of the centuries, with a specific impact on the Czech and Bavarian sides of the mountain range. Among the drivers of this divergence geographic and climatic factors as well as past forest management are suggested.

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