Integration of dendrochronological and palaeoecological disturbance reconstructions in temperate mountain forests

Niina Kuosmanen, Vojtěch Čada, Karen Halsall, Richard C. Chiverrell, Nick Schafstall, Petr Kuneš, John F. Boyle, Miloš Knížek, Peter G. Appleby, Miroslav Svoboda, Jennifer L. Clear

Published article is available here https://doi.org/10.1016/j.foreco.2020.118413

Highlights

• Integration of dendrochronological and palaeoecological disturbance reconstructions.

• Increase in disturbances in temperate mountain spruce forests from 1600s.

• The concurrent occurrence of disturbance agents create a complex disturbance regime.

• Management and conservation strategies should consider the multiple disturbance agents.

Abstract

Disentangling the long-term changes in forest disturbance dynamics provides a basis for predicting the forest responses to changing environmental conditions. The combination of multidisciplinary records can offer more robust reconstructions of past forest disturbance dynamics. Here we link disturbance histories of the central European mountain spruce forest obtained from dendrochronological and palaeoecological records (fossil pollen, sedimentary charcoal, bark beetle remains and geochemistry) using a small glacial lake and the surrounding forest in the Šumava National Park (Czech Republic). Dendrochronological reconstructions of disturbance were created for 300-year-long records from 6 study plots with a minimum of 35 trees analyzed for the abrupt growth increases (releases) and rapid early growth rates, both indicative of disturbance events. High-resolution analysis of lake sediments were used to reconstruct 800-year long changes in forest composition and landscape openness (fossil pollen), past fire events (micro- and macroscopic charcoal), bark beetle occurrence (fossil bark beetle remains), and erosion episodes (geochemical signals in the sediment) potentially resulting from disturbance events.

Tree-ring data indicate that disturbances occurred regularly through the last three centuries and identify a most intensive period of disturbances between 1780 and 1830 CE. Geochemical erosion markers (e.g. K, Zr, % inorganic) show greater flux of catchment sediment and soils in the periods 1250–1400 and 1450–1500 CE, before a substantial shift to a more erosive regime 1600–1850 and 1900 CE onwards. Pollen records demonstrate relatively small changes in forest composition during the last 800 years until the beginning of the 20th century, when there was decrease in Picea. Fossil bark beetle remains indicate continuous presence of bark beetles from 1620s to 1800s, and charcoal records suggest that more frequent fires occurred during the 18th century. Each of the dendrochronological, palaeoecological and sedimentological records provide a unique perspective on forest disturbance dynamics, and combined offer a more robust and complete record of disturbance history. We demonstrate that sedimentary proxies originating from the lake catchment mirror the forest disturbance dynamics recorded in the tree-rings. The multidisciplinary records likely record forest disturbances at different spatial and temporal scales revealing different disturbance characteristics. Integrating these multidisciplinary datasets demonstrates a promising way to obtain more complete understanding of long-term disturbance dynamics. However, integrating datasets with variable spatial and temporal influence remains challenging. Our results indicated that multiple disturbance factors, such as windstorms, bark beetle outbeaks and fires, may occur simultaneously creating a complex disturbance regime in mountain forests, which should be considered in forest management and conservation strategies.

Keywords: Disturbance, Forest dynamics, Bark beetles, Fire, Pollen, Geochemistry, Tree-rings, Picea abies

1. Introduction

Natural disturbances such as windthrows, insect outbreaks, droughts and fires maintain the high diversity and structural characteristics of natural temperate forest ecosystems (Kulakowski et al., 2017). In recent years, natural disturbances have intensified and the changing climate, together with increasing anthropogenic influence, have put temperate mountain forests under increasing pressure that may affect the resilience of these forests (Reyer et al., 2015, Thom et al., 2017). In central European temperate mountain forests, insect outbreaks and windthrow events have caused large disturbances during the last few decades (e.g. Schelhaas et al., 2003, Čada et al., 2013, Čada et al., 2016, Holeksa et al., 2017). Windstorms and insect outbreaks are considered as the main disturbance agents in these mountain ecosystems. However, there is an increasing number of studies demonstrating the importance of fire as a disturbance agent in temperate forest ecosystems (e.g. Niklasson et al., 2010, Feurdean et al., 2017, Bobek et al., 2018, Carter et al., 2018) and predictions of increasing climate extremes, such as droughts, may increase the future risk of fires in central European ecosystems (IPCC). As it is uncertain how forest ecosystems will respond to the future changes, knowledge of long-term changes of natural and human-induced disturbances, and understanding the processes behind them is crucial to apply the best management practices to maintain the ecological diversity and ecosystem services.

Dendrochronology has been widely used to reconstruct stand-scale disturbance dynamics and their impact on forest ecosystems. These disturbance reconstructions from tree-rings can extend a few hundred years back in time and provide valuable information about disturbance frequency and severity (e.g. Svoboda et al., 2013, Čada et al., 2016, Holeksa et al., 2017, Janda et al., 2017). However, it is problematic to assess the long-term changes in disturbance history based on dendrochronological records alone, because these records usually span just one tree generation. It is also impossible to identify the disturbance agent, because prevailing agents such as windstorms, bark beetle outbreaks, and logging are not recorded in tree-rings by any specific feature. Palaeoecological data, such as pollen, macrofossils, and charcoal, derived from sedimentary archives provide information of past disturbance history over millennial scale and can provide means to assess the possible disturbance agents in long-term perspective. Where dendrochronological data is accurate at the spatial (single tree) and temporal (annual) scale, this accuracy is limited to km’s and decades in palaeoecological records, respectively. In addition to dendrochronological and palaeoecological records, physical properties of lake sediments, measured using the sediment geochemistry and grain size, reflect erosion events (e.g. floods) and change in the baseline erosion regime of the catchment (Davies et al., 2015). Physical properties thereby provide means for identifying potential landscape responses to forest disturbances. These multidisciplinary approaches used to reconstruct disturbances reveal different spatial and temporal aspects of disturbance regimes, and highlight the effects that disturbances can have on forest ecosystems. This highlights the importance of integrating multidisciplinary records to enable us to understand the complex processes behind the mountain forest dynamics. The integration of dendrochronological, palaeoecological and sedimentological records in disturbance reconstructions provide a more robust and complete record of disturbance history, and are essential to identify the impact of disturbances on forest ecosystems with changing climate dynamics.

There have been previous studies including both dendrochronological and palaeoecological methods to reconstruct for example past climate (e.g. Edwards and Dunwiddie, 1985, Helama et al., 2012), natural and anthropogenic environmental change (e.g. McLachlan et al., 2000) and past fire dynamics from fire scars (e.g. Niklasson et al., 2002, Drobyshev et al., 2004, Higuera et al., 2005, Stivrins et al., 2019). Here we link, for the first time to our knowledge, dendrochronological (300-years long) disturbance reconstruction based on changes in tree-ring width with multiproxy sedimentological and palaeoecological (800-years long) datasets from a central European mountain spruce forest, in which windthrows and bark beetle outbreaks are expected to be the prevailing disturbance agents. Precise dendrochronological disturbance reconstruction based on trees' growth rate changes is coupled with; (1) high-resolution fossil pollen records to reconstruct the changes in forests composition and landscape openness, (2) sedimentary charcoal to reveal the past fire events, (3) fossil bark beetle remains to identify insect outbreaks, and (4) variations in sediment geochemistry and grains size to detect changes in the catchment erosion regime associated with disturbance events in the lake catchment. The main objectives are to (i) produce a long-term (800 years) disturbance history in the mountain spruce forest, (ii) to assess the possible disturbance agents and the impacts in the lake catchment and (iii) to evaluate the integration of dendrochronological, palaeoecological and sedimentologicaldata in providing a multidisciplinary reconstruction of forest disturbance history.

2. Methods

2.1. Study area

The study area is located in the temperate vegetation zone in Bohemian Forest, Šumava National Park (NP), Czech Republic, central Europe (Fig. 1). Bedrock of the lake catchment belongs to the crystalline complex of the Bohemian massive and consists of gneisses (Cháb et al., 2007). Soils are shallow and poor, dominated by podsols and stony soils (Kozák, 2010). Climate is cold with mean annual temperature of 4 °C, and a mean annual precipitation of 1200 mm (Tolasz et al., 2007). The mountain glacier in the area was deglaciated ~14,000 cal yr BP (Mentlík et al., 2010). The study site, Laka is a shallow (maximum depth 4 m) mesotrophic lake located at 1096 m.a.s.l. being at the highest elevation of the eight glacial lakes formed in the glacial cirques in the Bohemian Forest. It is also the smallest with surface area of circa 2.8 ha, a catchment area of 1,35 km2 and catchment:lake area ratio at 48:1, which is conducive for recording catchment processes.

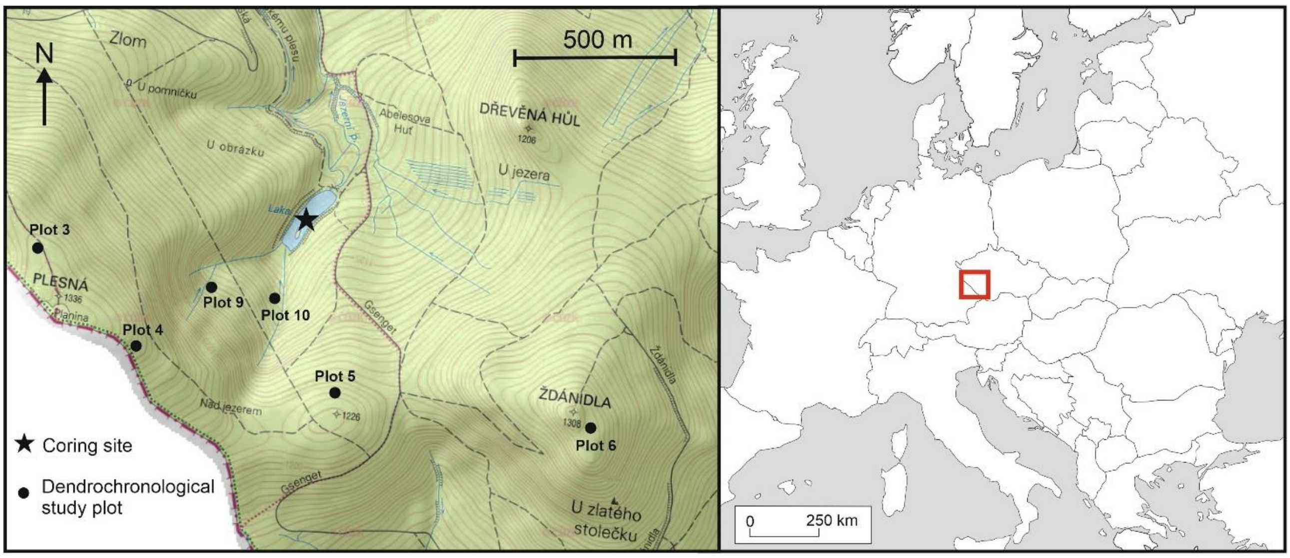

Fig. 1. Research area in Bohemian/Bavarian forest is marked in the map on the right with red square and map in left shows the study area with coring site (star) and dendrochronological study plots (dots).

The present vegetation in the Laka catchment is composed of the nearly monospecific Norway spruce (Picea abies) forests, with minor components of rowan (Sorbus aucuparia), Sycamore maple (Acer pseudoplatanus), fir (Abies alba), and beech (Fagus sylvatica) (Neuhäuslová and Moravec, 1998). The vegetation community is mostly comprised of grass species Calamagrostio villosae-Piceetum; with patches dominated by Calamagrostis villosa (Chaix), Deschampsia flexuosa, and blueberry (Vaccinium myrtillus) growing on more stony soils (Neuhäuslová and Moravec, 1998).

The Mountain regions in Šumava NP have remained in relatively natural conditions until fairly recently. Intensive colonization of the foothills and logging of the Bohemian Forest linked to the glass and metallurgy industries occurred during the 14th century. However, the higher parts of the Bohemian forests were not colonized until the 18th century onwards (Kozáková et al., 2015). Old growth forest with minimal human disturbance during last centuries (Čada et al., 2016a) characterizes the mountain spruce forests surrounding the lake catchment, which provides valuable opportunity to assess the natural processes behind the disturbance history.

2.2. Dendrchronological analyses

Six plots used for the dendrochronological analysis is located circa 0.2–1.6 km from the lake (Fig. 1). Four of these plots were already published in landscape level study of Čada et al. (2016a) and two plots were additionally sampled for this study using the same method. The plot size was 1000 m2 to obtain increment cores from at least 35 trees within the plot. The ring width measurement and cross dating of increment cores were conducted using standard techniques. In accordance to traditional dendrochronological approach, individual tree-ring series were analyzed for two ring-width patterns that indicate past disturbance events: abrupt and sustained growth increases (releases from suppression) and rapid early growth rates (Lorimer and Frelich, 1989). In order to classify annual tree-ring growth as a release, the absolute growth increase between subsequent 10-year means had to exceed 0.55 mm. In case there were multiple subsequent years exceeding the 0.55 mm release threshold, the maximum growth year within a 20-year interval (±10 years) was identified as a release year. The average ring width of 6th–15th ring had to exceed 1.0 mm to classify the first year of the series as a year of rapid early growth rate (Čada et al., 2016a). The threshold values specific for Norway spruce were obtained from the literature and have been verified during our previous studies using extensive tree-ring data and our experience with growth variation of the species (see; Čada et al., 2016a). The stand-level disturbance chronology was based on the number of trees that indicated a disturbance event at each decade relative to the number of trees available within a given decade. The beginning of the chronology was set to 1720s, when the number of available trees and plots was 5 and 3, respectively. The number of samples and the robustness of dendrochronological disturbance estimations increased dramatically after 1800s (87 and 6 available trees and plots, respectively).

2.3. Sediment sampling

A 1.5 m sediment profile (Laka 15-1) was collected from 1.6 m depth of water and sampled from a floating platform using a Russian-style (1.5 × 0.075 m) corer. The sediment-water interface was collected using a gravity corer (Laka 15-1GC) (Boyle, 1995). The cores were taken to the laboratory in the University of Liverpool for wet sediment geochemical analysis (Olympus Delta XRF) and high-resolution (15 µm) photography under uniform lighting with a Linescan Camera on a Geotek Multi-sensor Core logger and subsampling. Sediment core were stored at +4 °C for further analysis. Subsamples were taken at 1 cm intervals to analyse fossil pollen and non-pollen-palynomorphs, micro- and macroscopic charcoal, fossil beetles, particle size, near-infrared spectrometry and dry mass specific geochemistry using an energy dispersive X-ray Florescence (ED-XRF) analyser.

2.4. Sediment chronology

Independent age control for the top 10 cm of the sediment profile at Laka was determined using records of the fallout radionuclides Pb-210, Cs-137 and Am-241 (Appleby and Oldfield, 1978, Appleby et al., 1991) (Table 1). Measurements of these radionuclides were carried out by direct gamma spectrometry using Ortec HPGe GWL series well-type coaxial low background intrinsic germanium detectors (Appleby et al., 1986) at the Environmental Radioactivity Research Centre in Liverpool, UK (See more detailed description from APPENDIX A.1).

Table 1. Radiocarbon results for the long-core Laka-15 and lead 210 dating results for core LAK 15-1GC.

Depth	**Laboratory**	**^{14}CAge±**	**Assigned^{210}Pb**	**Assigned age**	**Material**
(cm)	**ID**		**(YearCE)**	**(calyrBP)**	
163	Pb210_1		2015 ± 0	−65	
164.5	Pb210_2		2009 ± 1	−59	
165.5	Pb210_3		1996 ± 2	−48	
166.5	Pb210_4		1981 ± 3	−31	
167.5	Pb210_5		1965 ± 4	−15	
168.5	Pb210_6		1948 ± 5	2	
169.5	Pb210_7		1933 ± 6	17	
170.5	Pb210_8		1925 ± 7	25	
171.5	Pb210_9		1925 ± 7	25	
172.5	Pb210_10		1915	35	
173.5	Pb210_11		1899	51	
193.5	Poz-81584	130 ± 30			Plantmaterial
207.5	Poz-94514	340 ± 30			Plantmaterial
220.5	Poz-84784	195 ± 30			Plantmaterial
244.5	Poz-84785	150 ± 30			Plantmaterial
274.5	Poz-85123	310 ± 30			Plantmaterial
305.5	Poz-85124	630 ± 30			Plantmaterial
325.5	Poz-94517	880 ± 30			Plantmaterial

The stratigraphy of the long-core was secured by 10 AMS C-14 dates (Table 1) targeting hand-picked terrestrial-sourced plant macrofossils (e.g. Picea abies needles) measured at the Poznań Radiocarbon Laboratory, Poland. All the geochronological data (Table 1) including the sediment surface (2015) were integrated within a Bayesian age-depth modelling routine 'BACON' (Blaauw and Christen, 2011) using a Student-t distribution that considers scatter in the 14C measurements and allows for statistical outliers. The Bayesian analysis (Christen and Perez, 2009) partitioned the core into 36 sections (0.05 m thick) estimating the accumulation rate for each segment using a Markov Chain Monte Carlo (MCMC) approach. The modelling was constrained by a prior model of sediment accumulation rate (a gamma distribution with mean 5-year cm-1 and shape 1.5) and its variability (memory, a beta distribution with mean 0.32 and shape 18). All 14C ages were calibrated and modelled in 'BACON' using the IntCal13 curve (Reimer et al., 2013) (Fig. 2).

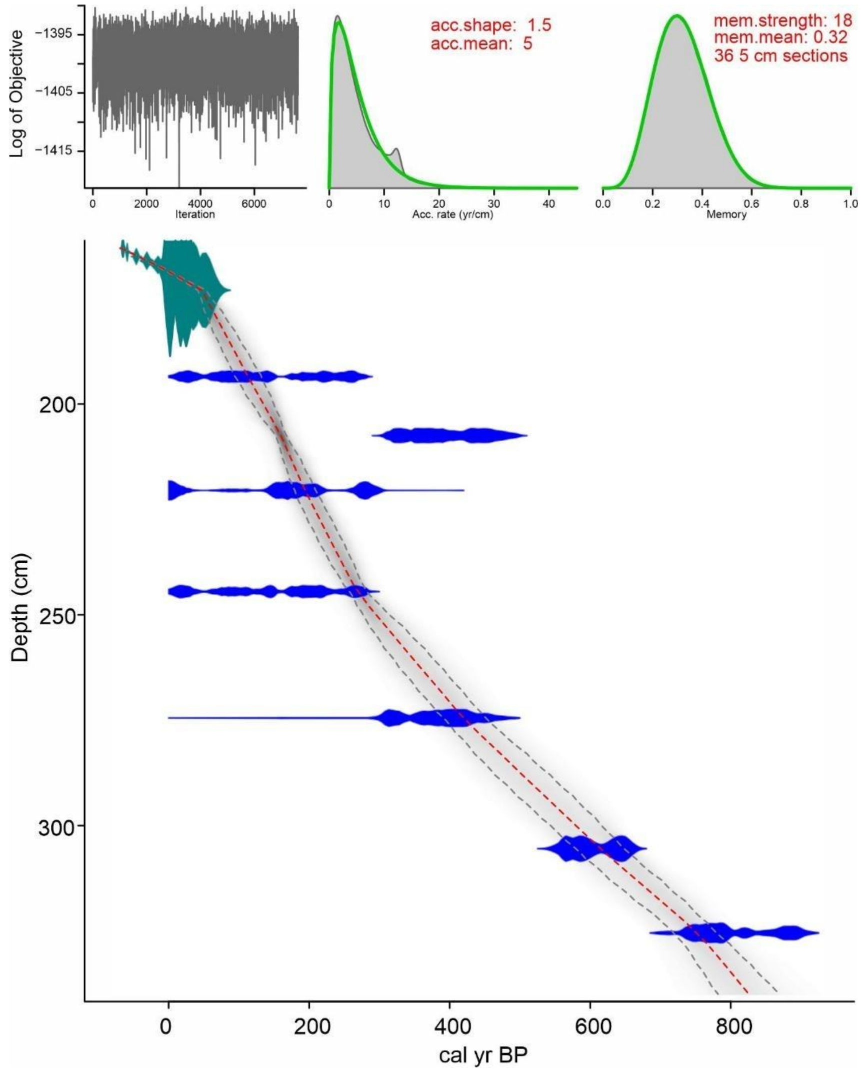

Fig. 2. 'Bacon' age-depth model for the integrated Laka core based on seven radiocarbon ages and the 210Pb and 137Cs radionuclide dating series.

2.5. Sedimentary analyses

2.5.1. Physical properties and geochemistry

The long and gravity cores were subsampled at 1 cm intervals and freeze dried for 48–60 h to collect water content data (%). Major and trace element concentrations were determined using a Bruker S2 Ranger ED-XRF for the gravity core and Spectro XEPOS 3 ED-XRF for the long core. For both ED-XRF, the samples were hand pressed and measured under a He atmosphere under combined Pd and Co excitation radiation and using a high resolution, low spectral interference silicon drift detector. Daily standardisation procedures provide a system check on both ED-XRF and they have comparable accuracies verified using 18 certified reference materials (Boyle et al., 2015). Particle size distributions (PSD) were measured for all samples across the range 0.375–2000 µm using a Coulter LS 13 320 Single-Wavelength Laser Diffraction Particle Size Analyser. Hot H2O2 pretreatment removed organic matter from the PSD samples, with samples dispersed Na6O18P6, sonicated and run under sonicating measurement conditions. Results are the average of three repeats following elimination of outliers. The Coulter LS320 undergoes regular calibration checks using samples with known size distributions and particle size frequency statistics were calculated using standard geometric formulae using the GRADISTAT 8.0 software (Blott and Pye, 2001).

Near Infrared Spectrometry (NIRS) by diffuse reflectance were measured for all sediment samples using a Bruker MPA Fourier-Transform NIRS using an integrating sphere. All samples were homogenised by grinding and were lightly hand pressed, with the NIR spectra produced from 64 scans at an 8 cm^{-1} interval across the range 3595–12,500 cm^{-1}. We used multiple regression of the NIR spectra for a selection known composition end-member materials (EMS-MR, Russell et al., 2019) to interpret the unknown composition lake sediment samples from Lake Laka. The EMS-RC provides simultaneous quantification of major sediment components; here these were end member spectra for local bedrock, biogenic silica (diatoms) and organic matter (see Russell et al., 2019). The end members were minerogenic late glacial muds from nearby Prášilské lake, which we regard as representative of the catchment bedrock. A marine diatom sample treated with H_2O_2 to remove any organic material to reflect the proportion of biogenic silica. The organic component of the lake sediment were rationalised to an ombrotrophic peat sample including less decomposed plant remains and humic compounds. The fitting of these end member materials included sensitivity analysis using other end member selections for all three components across a wider library of materials to obtain the overall best fitting performance, defined by high R^2 of the sample multiple regressions (>0.85).

The catchment-lake area ratio (48:1) for Laka is conducive to efficient flux of detrital materials from catchment to the lake, and so the down core patterns of major geochemical elements are likely to reflect changes in the erosion regime. Geochemical ratios for Si:Al and Zr:Rb provide information on indications of biogenic silica and the presence of coarser grain sizes, respectively (Davies et al., 2015). Changes sediment sources, availability and the energy in the catchment most likely guided changing in properties like the mean grain size, the coarsest grains (e.g. 90th percentile) and degree of sorting. The NIR spectra provide parallel reconstructions of the proportions mineral, biogenic silica (diatom) and organic matter in the sediments. Principal components analysis (PCA) was used to explore the relationships between geochemical, grain size and NIRS down-core patterns. A stratigraphically constrained cluster analysis for all these parameters, after standardisation to ± one standard deviation unit length, produced dendrograms that identify the major changes in the stratigraphy.

2.5.2. Pollen and non-pollen palynomorph analysis

Subsamples of 0.5 cm^3 were extracted in 1 cm resolution and processed standard procedures of KOH-, acetolysis- and HF-treatment (Faegri et al., 1989). In order to calculate microfossil concentrations (grains cm^{-3}) and accumulation rates (PAR; grains cm^{-2} yr) Lycopodium marker spores were added into the subsamples (Stockmarr, 1972) prior-to the sample preparation. The samples were mounted in glycerine and a minimum of 500 terrestrial pollen grains were identified using a 400x magnification. Pollen identification is based on Beug, 2004, Moore et al., 1991, and a reference collection at Charles University in Prague. Results are presented as a proportion of each pollen taxon from the total sum of terrestrial taxa. The pollen ratio between the sum of arboreal pollen (AP) taxa and the sum of non-arboreal pollen (NAP) taxa indicating more open landscape were used to detect opening of forest canopy related to disturbance events. The summed percentage of Cerealia-type, Secale cereale, Centaurea cyanus-type, Fagopyrum, Plantago sp., Rumex sp. and Urtica were used as an indicator of anthropogenic activity.

In addition to pollen, non-pollen palynomorphs (NPP: microfossil remains of fungi, insect, algae and cyanobacteria) were analyzed simultaneously with pollen from microscopic slides. NPPs provide valuable additional proxy information for past disturbances and changes in the lake catchment (Van Geel, 2002).

Identification of NPPs was based on van Geel (1998). Pollen and NPP data were plotted using the C2 program (Juggins, 2003).

2.5.3. Fossil bark beetle analysis

For the analysis of bark beetles (Coleoptera: Curculionidae: Scolytinae), sediment was sieved over 100 µm mesh in order to retain all insect and botanical macro fossils (Hofmann, 1986, Birks, 2007). Beetle remains were picked under a stereomicroscope with 15x magnification and bark beetles were identified with the help of a small collection of Scolytinae species and an identification key of Scolytinae of Czechoslovakia (Pfeffer, 1989). Primary (species feeding on healthy trees) and secondary (species feeding on dying or dead trees) bark beetles were identified and their remains were used for the reconstruction of the minimum number of individuals (MNI) per sample.

2.5.4. Charcoal analysis and detection of fire events

Macroscopic charcoal particles (>200 µm) were used to detect local fires, where microscopic charcoal provides a signal of regional fire history (Whitlock and Larsen, 2001). For the reconstruction of regional fires, microscopic charcoal was analyzed concurrently from the same microscopic slides used for pollen and NPP identification. Opaque, sharp-edged particles (>5 µm) were identified as charcoal (Scott, 2010). The total concentrations (particles cm−3) and influx (particles cm−2 yr) of microscopic charcoal fragments were calculated for each sample. For the reconstruction of local fire events, macroscopic charcoal was analyzed following the method adapted from Mooney and Tinner (2011). Subsamples of 0.5–1 cm3 were soaked in a 20 ml solution of sodium hexametaphosphate ((NaPO3)6) and 10 ml of potassium hydroxide (KOH; 5%). Samples were carefully sieved through a 250 µm mesh, and then bleached using a solution of 1 or 2 ml of NaOCl (8%). After bleaching samples were once more sieved through a 125 µm mesh. Macroscopic charcoal particles were first recorded under a binocular microscope and then ImageJ (https://imagej.nih.gov/ij/) software was employed for analyzing charcoal area measurements and counts using 8-bit images at a threshold of 137 greyscale units (ie 137–255 greyscale units) following Halsall et al. (2018). The total concentrations and influx of macroscopic charcoal area and counts were calculated for each sample.

CharAnalysis software, applying a signal-to-noise index (SNI) to separate peaks in the charcoal record from background variability (Higuera et al., 2009, Higuera et al., 2010, Kelly et al., 2011) were used for assessing the regional and local fire events. Microscopic charcoal concentrations (particles cm−3) were used to determine regional fires. Macroscopic charcoal concentrations (particles cm−3) were used to assess the local fire history. First both records were interpolated to mean temporal samples resolution and then separated into a low-frequency background component (BCHAR) and a peak component using the CharAnalysis software (Higuera et al., 2009). In both cases smoothing with LOWESS regression within a 100-year moving-window was applied to determine the background component. The peak component was calculated as residuals between interpolated charcoal records and BCHAR (Cpeak = CHARint-BCHAR) and evaluated using the 99th percentile of a Gaussian mixture model in order to separate fire events reflected by charcoal peaks from the background noise. Furthermore, detected peaks in microscopic charcoal records were screened using minimum-count peak (p = 0.05) test in CharAnalysis.

Determination of the macroscopic charcoal area has proven to be a reliable method for detection of local fires, when the number of charcoal particle counts is low (Ali et al., 2009, Halsall et al., 2018). Therefore macroscopic charcoal area measurements (the area of particles mm2 cm−2 yr), were used as additional proxy to assess local fires.

2.5.5. Comparison of dendrochronological and palaeoecological data

To compare the palaeoecological records and the disturbance history based on dendrochronological records, all palaeoecological data (pollen, Glomus spores, sedimentary charcoal, bark beetles) were combined to 10-year bins corresponding the decadal resolution used in tree-ring based disturbance reconstruction (e.g. 1710–1720, 1720–1730, 1730–1740 etc.) and plotted using C2 – program (Juggins, 2003).

3. Results

3.1. Disturbance signal from dendrochronological data

The dendrochronological disturbance signal indicates that the most extensive disturbances occurred during the period of 1780–1830 CE (Fig. 3). The extensive, frequent disturbances affected all of the study plots within this period and removed most of the canopy cover on at least four of the six available plots (Appendix A.2). Two plots (plot 3 and 10) also experienced severe disturbance during the period of 1830–1860 CE. Other less severe (loss of ≥10%), localized disturbance events occurred regularly within the study period (e.g. in 1720s, 1740–1760, 1870s, 1900s, 1920s and 1980–1990s). The accuracy of the dendrochronological record is questionable before the 1760s due to the limited number of records available, however regional reconstruction from Šumava NP identifies regional disturbances during the 1690s, 1720s and 1740s (Čada et al., 2016a; see the paper for more detailed description of tree-ring based disturbance history).

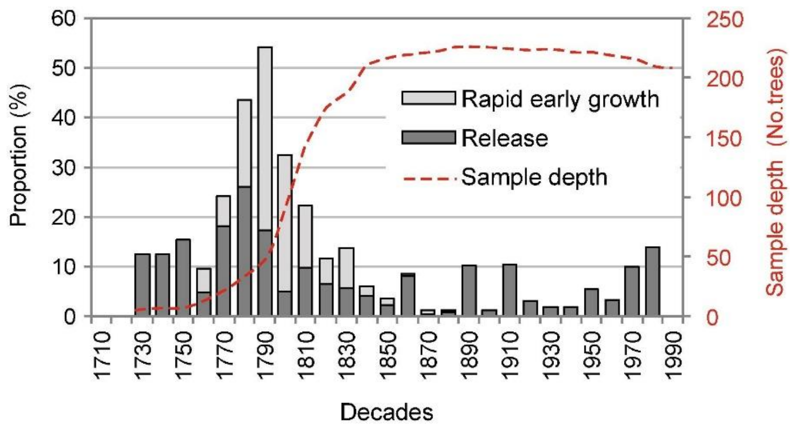

Fig. 3. Tree-ring based disturbance history of the forest stand in the catchment of Laka, Šumava NP, Czech Republic. Decadal resolved disturbance rate (columns) showing the proportion of affected trees was compiled from 6 study plots with 224 trees located throughout the catchment. The trend in number of available individual tree-ring series (tree age-structure) is shown with red dashed line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Disturbance signals from the lake sediments

3.2.1. Trends in the physical properties and geochemistry

In the physical properties measured for the Laka sediments 68.5% of the variation in a Principal Components Analysis (PCA) is summarised on the first two components (Fig. 4). The geochemistry, NIRS end member components and grain size parameters (d90, d50 and sorting) form three distinct groupings in the PCA. Group 1 includes organic content and elements that strongly associate with organic matter (Br, S and Cl). Group 2 associates NIRS-inferred biogenic silica with Si (mg m-1) measured by XRF, which suggests firstly that biogenic silica dominates these samples and second the Si:Al ratio (Davies et al., 2015) should be a strong measure of biogenic silica that is independent of NIRS-inferred biogenic silica. Coarser grain size and poor sorting also associate in part with biogenic silica indicating that larger diatoms may be affecting grain size measurements for more organic older samples. Group 3 (a + b) includes a large number of primarily minerogenic indicators including NIRS-inferred mineral content and a series of lithogenic elements (e.g. Al, K, Zr, Ca and Ti).

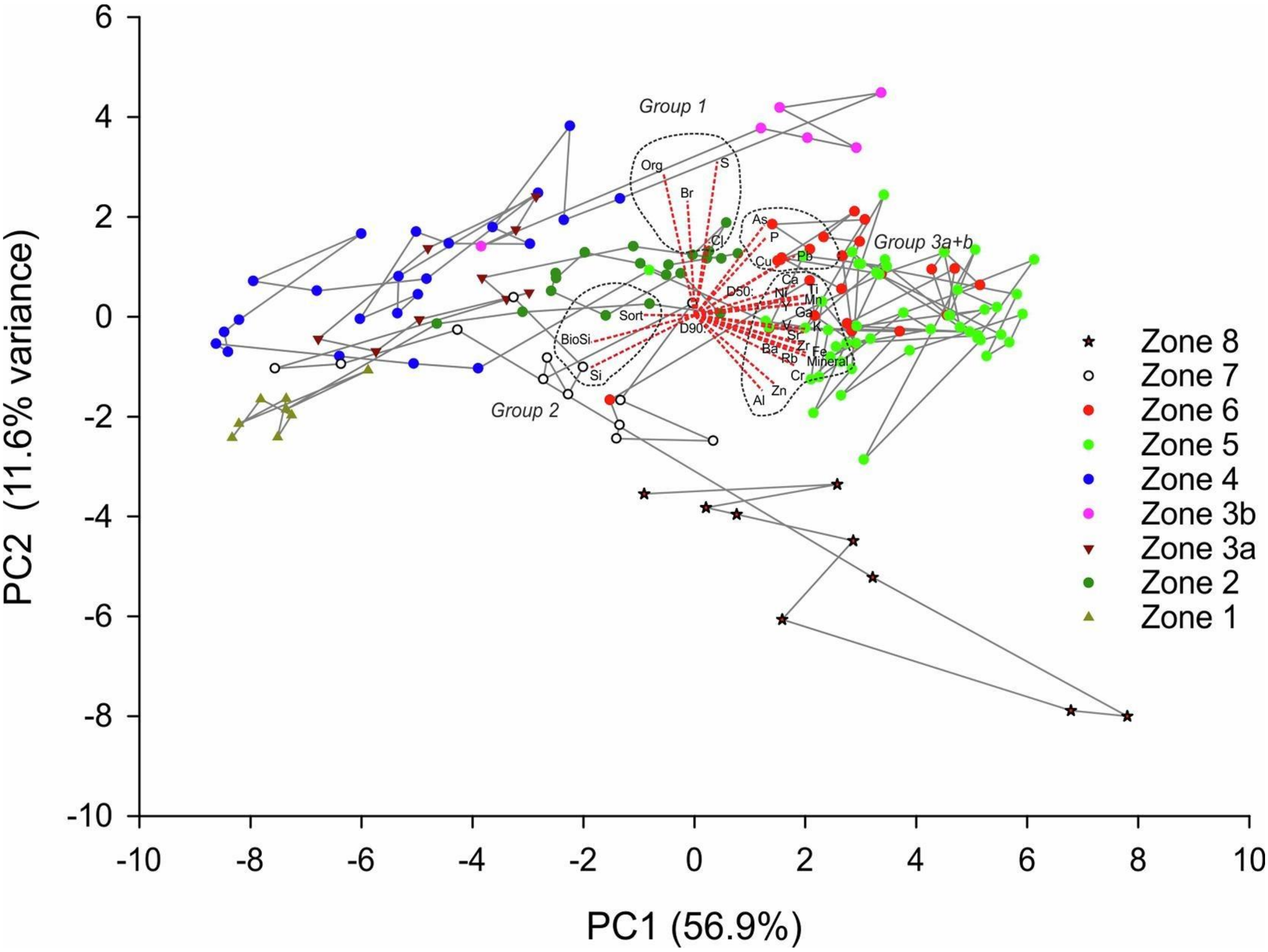

Fig. 4. Biplot of Principal Component Analysis axes 1 and 2 calculating for geochemical, NIRS end member components and grain size parameters (d90, d50 and sorting) showing three distinct groupings of parameters. Sample PCA coordinates are colored by zones delimited using a stratigraphical cluster analysis for all variables.

The cluster analysis of the physical properties highlights a series of major stratigraphical changes through the last 800 years and provides a basis for zoning the sediment sequence (Fig. 5). There is some separation with Group 3 with elements Cu, Pb, P and As plotting higher on PC2 closer to the organic Group 1, the more easily remobilized elements (Al, Zn and Cr) plot lower on PC2, with the more stable elements in the middle (Ti, Zr, K). There is a strong stratigraphical order to the distribution of samples within the PCA progressing between the organic Zones 1, 3a and 4 with abundant biogenic silica, and Zones 2 and 3b a mix of organic and mineral matter (Fig. 5). The transition to Zones 5 and 6 reflects a substantial shift in the erosion regime in the catchment producing limnic muds composed dominantly of minerogenic sediment and containing less organic and diatomaceous material. Zone 7 shows evidence for a reduction in minerogenic material with more diatom-rich sediments. Zone 8, the most recent sediments, plot as outliers in the PCA with fluctuations in concentrations of biogenic silica, and a switch to lithogenic elements of the more easily mobilized variety (Al, Zn and Cr).

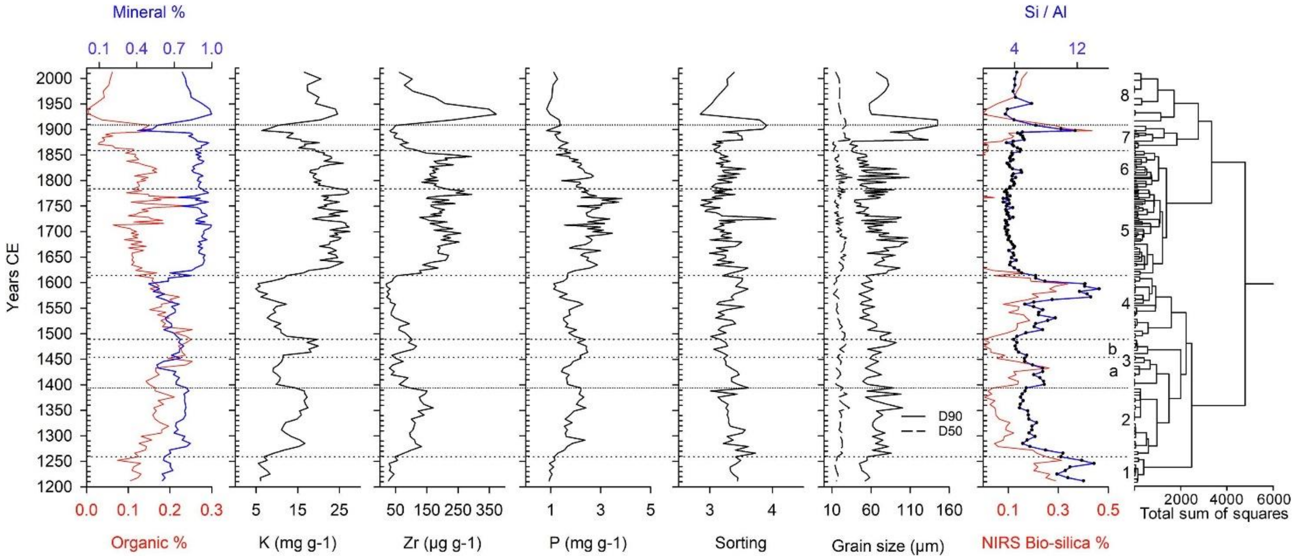

Fig. 5. Physical properties for the Laka sediment profile plotted against the age-depth model (cal. years CE) showing the relative proportions of NIRS-inferred mineral and organic content, element concentrations (ED-XRF) for K, Zr and P, degree of sorting, d90 and d90 of the grain size distributions, and NIRS inferred biogenic silica alongside the Si:Al element ratio. The dendrogram reports a stratigraphical cluster analysis for all variables standardized to mean = 0 and ±1 standard deviation, which informed the zone boundaries (1–8).

3.2.2. Physical properties and geochemistry

Zone 1 (1200–1265 CE): has moderately low minerogenic content, but without being particularly inorganic. Interpretation of the NIRS and Si:Al ratios reflect high concentrations of biogenic silica (Fig. 5). Laka appears quite productive and has a relatively stable catchment limiting the flux of minerogenic materials. Zone 2 (1265–1395 CE): begins with a sharp increase in mineral and organic content, with sharp declines in biogenic silica. Concentrations of the detrital lithogenic elements all increase mirrored by increases in grain size. The d90 (µm) displays a series of peaks showing coarse in-wash events that resemble flood or similar high-energy events. The catchment-lake area ratio is large and flood in-wash is a plausible mechanism (Schillereff et al., 2015). Lithogenic elements are not uniform in their concentration, with broad multi-decade peaks early and late in zone 2. Organic content for the most part varies inversely with the lithogenic elements. Zone 3 (1395–1490 CE): comprises two stages, an early 3a with abundant biogenic silica content which increases at the expense of both mineral and organic content. This relationship reverses with 3b comprising a pronounced minerogenic layer. Lithogenic elements follow the trends in the total mineral content. Sediment grain size fluctuates reflecting a continued contribution of higher energy in- wash events. Declines in the degree of sorting, however resemble patterns in biogenic silica indicating a possible contribution from diatoms to the grain size spectra. Zone 4 (1490–1610 CE): is dominated by peaks in the Si:Al ratio and biogenic silica increasing to >30% of the sediment initially and latterly climbing to maxima close to 50%. These increases are at the expense of sharp declines in mineral content and lithogenic elements. There is no inverse relationship with patterns in organic content, which declines by 10% through the zone. The sediment reflects a relatively stable catchment limiting the flux of minerogenic materials to the lake and the lake is very productive. Zone 5 (1610–1785 CE): is marked by the most substantial changes in the sequence, with organic content falling to <10% and mineral content increasing to >90%. NIRS-inferred biogenic silica and the Si:Al ratio suggest either an absence of algae or dissolution of diatoms. We exclude masking of a diatom signal by the increased flux of mineral matter, because Si and Al are in ratio.

There is an increase in lithogenic elements throughout the zone. Higher energy in-wash event (~18 layers) are represented by d90 peaks that extend into the fine sand and by poorer sorting of these coarse units. In summary, the catchment has shifted to a more erodible condition, and higher energy flows drove the sharper peaks in coarser minerogenic influx. Zone 6 (1785–1860 CE): begins with declines in concentrations of lithogenic elements and a minor dip in the total mineral content. These changes reflect greater organic content, with little or no change in the proportion of biogenic silica. This recovery or increasing catchment stability required to reduce the supply of lithogenic elements is short-lived and followed by further layer of coarse sediment enriched with K, Zr and P denoting a further erosion episode. Zone 7 (1860–1910 CE): is unusual in commencing with falls in all lithogenic elements except for Si, a phenomenon often associated with diatom rich sediments, but here NIRS-inferred diatoms and Si:Al ratio are both low. Grain size increases sharply and so the unit comprises of relatively pure quartz sand. Latterly, the mineral content falls sharply, lithogenic elements continue at low concentrations, there is increased organic content and a spike in biogenic silica, which is perhaps a lagged response by algal communities in the lake to the influx of quartz sand to the lake. Zone 8 (1910–2015 CE): is marked by relatively slow rates of sediment accumulation and in the early part a sharp in-wash layer dominated by increases in all lithogenic elements. The product of greater erosion in the catchment, this layer contains finer grain sizes than the Zone 7 quartz-dominated event, and it suppresses both the biogenic silica and organic content. The last 50 years show a stabilization of the catchment reflected by declines across all lithogenic elements, increasing the organic and biogenic silica content. There is a minor mineral-rich layer near the top of the core profile.

The physical properties show substantial shifts in the flux of materials from catchment to the lake. These take the form of shifts in the baseline chemistry and grain size, but also differing event scale dynamics with greater frequency of in-wash layers/spikes, probably floods, during the extreme erosive episode 1600–1790 CE. Together the physical properties show short-lived erosive episodes 1250–1300, 1340–1400, 1450–1500 and around 1550 CE, before a major regime change 1600–1790 and 1825–1860 CE. The peaks in minerogenic sediment supply reflect some form of catchment disturbance, most likely perturbation of the forest cover; with the intervening lulls in minerogenic sediment reflect system recovery. The last century shows slower rates of sediment accumulation but includes a further minerogenic unit 1900–1950 CE before some recovery and a further minerogenic influx event towards the top of the core.

3.2.3. Palynological records

Spruce was the dominant tree taxa in the forest vegetation during the last 800 years, with beech and fir as minor components. Forest composition remained relatively constant during 1200–1900 CE and most notable changes occurred during the 20th century. Pollen record demonstrates the highest average proportion (30%) of Picea pollen from 1500 to 1610 CE (Fig. 6). There is circa 10% momentarily drop around 1630 CE, after which the values stay roughly at 25% until the end of the 19th century. During the last 100 years of the record the proportion of Picea pollen fluctuated between 18 and 30 %, with lowest values at 1920s, 1930s and 1990s and highest values at 1900s and 1960s. Fagus pollen had the second highest values of an average of 15% proportion of the forest composition during 1500–1900 CE. Most notable changes in Fagus pollen record occurred during the last 100 years, when the highest Fagus pollen values (12–14%) coincided with the decline in Picea pollen around 1930–40 s. The highest values (8–10%) of Abies pollen occurred during the first half of the record from 13th to 16th century, followed by a gradual decline towards the present, especially during the last 100 years of the record. The increase in the pollen proportion of light demanding early successional taxa, such as Acer, Populus, Salix, Sorbus, Epilobium, and Pteridium coincides with the decrease in the main tree taxa during the last 100 years indicating forest openness. Proportions of herbs and human indicator taxa, such as Cerealia-type, Secale cereale, Rumex sp.

and Plantago sp., increased slightly from the 16th century with a clear increase during the 20th century, indicating the opening of the landscape. More detailed pollen diagram can be found in Appendix A.3.

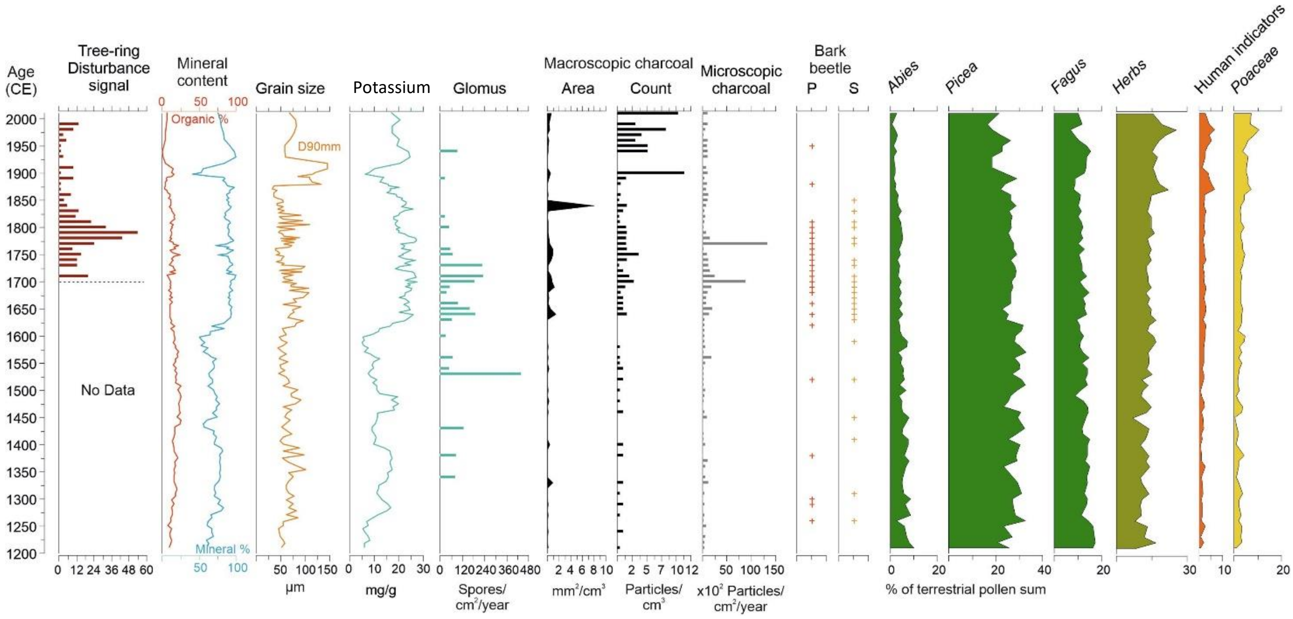

Fig. 6. Diagram showing tree-ring based disturbance signal in decadal resolution, mineral content (%), grain size (µm) and Potassium (mg/g) as sedimentological proxies for erosion in the lake catchment and palaeoecological proxies Glomus fungal spore influx, macroscopic charcoal concentrations (particles cm−3) and area measurements (mm2 cm−3), microscopic charcoal influx, presence of primary (P) and secondary (S) bark beetles, pollen curves for main forest forming tree taxa Abies, Picea and Fagus, sum of herbaceous pollen taxa sum of human indicator pollen taxa (Cerealia sp., Secale, Plantago sp. Rumex) and Poaceae in 10 year temporal resolution.

Glomus fungal spores were used as an additional indicator of soil erosion, possibly caused by disturbances in lake catchment (Van Geel, 2002). Increase in influx of Glomus fungal spores indicating enhanced soil erosion of topsoil in the lake catchment occur at 1350–1400, 1450s, 1520s, between 1600 and 1780s, 1860s and 1950s (Fig. 6).

3.2.4. Bark beetles

The number of insect remains is typically low due to the small volume samples analyzed throughout the lake sediment record resulting in mostly one or zero individuals of Scolytinae per sample. Both primary and secondary bark beetle remains were found throughout the core. The top part of the core from 1620 CE to the present (0–255 cm) contained notably higher amounts of beetle remains than the lower part (255–322 cm) of the core. Remains of Ips typographus, the species causing the most extensive mortality of Norway spruce, were found at 1270, 1290, 1630, 1700, 1800, 1880 and 1950 CE (Fig. 6). Remains from other primary bark beetles feeding on Norway spruce, Pityogenes chalcographus, Pityogenes conjunctus, Polygraphus poligraphus and Polygraphus subopacus, were found throughout the core but mainly between 1620 and 1820 CE. The highest occurrence of primary bark beetles in single samples was found during the 1800s, where Ips typographus appeared together with Polygraphus poligraphus and P. subopacus. Remains of secondary bark beetles consisted of a variety of genera, attacking dead or dying conifer trees. In general, occurrences of secondary bark beetles coincided with primary bark beetles or shortly after. A detailed list of the identified Scolytinae species can be found in Appendix A.4.

3.2.5. Fire history

The amount of sedimentary charcoal is relatively low in both micro- and macroscopic charcoal records, and in the macroscopic area measurements during the last 800 years (Fig. 6). All records show increasing values from 1600s onwards. Results from CharAnalysis show that average SNI values were above 3.0 for both micro- and macroscopic charcoal count records demonstrating the suitability of both records to the peak detection analysis. Ten significant peaks in the microscopic charcoal were recorded in Šumava NP during the last 800 years. Highest peak magnitude in microscopic charcoal was recorded at 1710 and 1770 CE indicating more extensive regional (longer distance from the lake) fire events. In macroscopic charcoal record four significant charcoal peaks were recorded indicating possible fire events at 1710, 1750, 1900 and 1980 CE in the vicinity of the Laka. The macroscopic charcoal area measurements show an slight increase around 1700 and 1750 CE and between 1900 and 1910 CE corresponding with the peaks in macroscopic charcoal counts. However, there is a peak in macroscopic charcoal area measurements at 1840 CE that is not detected in the macroscopic charcoal particle concentrations. A more detailed reconstruction of fire history and the results of CharAnalysis can be found in Appendix A.5.

4. Discussion

4.1. Increasing disturbances from 1600s

Multidisciplinary dataset of palaeoecological and dendrochronological records demonstrated reoccurring disturbances in central European mountain spruce forest during the last 800 years (Fig. 6). Increases in Glomus spores together with the increase in lithogenic elements from 1600s suggest changes to the catchment erosion regime. Coarse laminations in the more minerogenic episodes reflect that higher flows (floods) are interacting with a landscape that is in general more susceptible to erosion. This change coincides with the increase in sedimentary charcoal records and with the continuous occurrence of fossil bark beetle remains. Therefore, the change in the erosion regime is most likely triggered by an increase in disturbance rate in the study area from 1600s. Tree-ring records demonstrate a period of severe disturbances in the lake surroundings between 1780 and 1820 CE. Sedimentary records reveal that the period of more severe and/or frequent disturbances started at the beginning of the 17th century. There is no local tree-ring data for the 17th century, but the regional disturbance reconstruction from whole Šumava region demonstrated potentially extensive disturbance event around 1620s (Čada et al., 2016a). While disturbance reconstruction based on tree-ring records and physical proxies reflecting the erosional events give an indication of the occurrence and timing of the disturbance events around the lake catchment, fossil bark beetle remains, and charcoal records provide insights for the possible causes of the disturbances.

Morris et al. (2015) suggested that even low numbers of fossil bark beetle remains in lake sediments may indicate disturbances and it is plausible that the continuous presence of fossil bark beetle remains, although in low numbers, from 1600s is linked to increasing frequency of bark beetle disturbances. Presence of three different species of primary and two species of secondary bark beetles in the fossil record between 1700 and 1720 CE coincides with the historical documents recording insect outbreaks in the area around 1720s (Zatloukal, 1998, Brázdil et al., 2004, Jelínek, 2005). The highest number of different primary and secondary bark beetle species around 1800s coincide with the period of maximum disturbance indicated in the tree-ring based disturbance signal and sedimentary records. It is plausible that disturbances in the early 1800s might have resulted from the joint effect of insect outbreak indicated in the fossil record and windthrows documented in the archival documents (see Čada et al., 2016a). The effect of outbreaks on the amount of fossil bark beetle remains accumulating into lake sedimentary basin is still unknown. Therefore, it could be only speculated that the presence of fossil bark beetles during the disturbance events at 1380–1400 and 1510–1530 CE, indicated by the soil erosion (increased flux of lithogenic elements and

Glomus spores), could have been at least partly caused by bark beetle outbreaks. The periods of absence of bark beetle fossils before 1600s, coincide with the periods of low disturbance rate indicated by both tree-ring and sedimentary records. Bark beetle population were probably smaller during these periods and did not cause more extensive tree mortality. This may be, because bark beetle outbreaks are not only triggered by favorable climatic conditions, such as warm and dry weather, but also by stand structural characteristics (older and bigger trees are more sensitive to bark beetles) and related windthrows (Seidl et al., 2011, Thom et al., 2013). In general, these results suggest that bark beetle outbreaks have been an important part of the disturbance regime in mountain spruce forests for a long time and that windstorms and insect outbreaks are the main and intimately related disturbance agents in central European mountain spruce forests (e.g. Svoboda et al., 2013, Seidl et al., 2014, Čada et al., 2016). We also found that these disturbance agents may produce a substantial response in erosion regime of the affected areas. Comparison of the fossil bark beetle remains together with dendrochronological reconstruction is promising and may provide more exact information about past bark beetle outbreaks, but further development of the method with more extensive dataset is needed.

Compared to windthrows and bark beetle outbreaks, fire disturbances have not been studied intensively in central European mountain spruce forest probably because there are very few known recent natural fires in these forests (Feurdean et al., 2017). Our sedimentary disturbance record revealed the presence of fires in the history of the studied area and it suggests increased fire activity from the 1600 CE onwards. The more pronounced increase in microscopic charcoal compared to macroscopic charcoal most probably indicates regional fires, rather than local fires in the lake catchment. However, macroscopic charcoal records suggest four local fire events in the lake catchment from which the significant peak around 1800 CE is recorded in both micro- and macroscopic charcoal records, and coincides with the period of the most severe disturbances indicated by tree-ring records, with erosional indicators and with the highest number of bark beetle taxa. As there are no significant changes in forest composition in connection to these events, it is likely that no substantial stand-replacing fires, but rather small and very local fires occurred in the study area. Fires may have been connected to the increasing fuel load from windthrows and bark beetle infested dying trees. Similar co-occurrence of bark beetle outbreak and fires were observed after the severe windthrow at 2004 in Tatra mountains (Fleischer et al., 2017). However, it is important to note that these fires may have been also connected to the increased human influence in the area. Although, fires have been scarce around the study site during the last millennia, our results together with a recent study by Carter et al. (2018) demonstrated that fires have been part of the long-term disturbance dynamics in Šumava NP. Furthermore, the recent report of European commission EIP-AGRI focus group (2019) identified the increasing fire risk in temperate continental zone and mountain forests as one of the probable climate change impacts. Therefore, it is vital to acknowledge the role of fires in the past disturbance history and the probable future role of fires in the management plans of the temperate mountain spruce forests.

In general, the long-term disturbance dynamics derived from both denrochronological and palaeoecological records demonstrate the co-occurrence of multiple disturbance factors such as windthrows, bark beetles and fires. Similar interaction of different disturbance agents has been reported also in previous studies (e.g. Brunelle et al., 2008, Holeksa et al., 2016, Nagel et al., 2017, Šoltés et al., 2010). Hence, the future forest management and conservation strategies should acknowledge that multiple disturbance factors, such as windthrows, bark beetles, and fires, may occur simultaneously creating a complex disturbance regime in mountain forests affecting the forests composition and structure.

4.2. Stable forest composition until the end of the 20th century

Despite the fact that the studied spruce forest was subjected to relatively extensive disturbances during 1600–1900 CE, only minor changes in the pollen composition were recorded in this period. However, the most notable changes in pollen composition that could relate to forest disturbances were recorded at the beginning of the 20th century, when only small disturbance events were indicated by dendrochronological analyses. The decline in Picea pollen during the 1930s and 1970s together with an increase of landscape openness indicators may be connected to the windstorms recorded in historical documents (Brázdil et al., 2004).

More intensive and/or proximal anthropogenic disturbance near the lake during last 100 years could also explain the shift in pollen composition. Current forest structure indicates localized clearings and management in the surrounding forest and along the lake shore, this coincides with an increase of cultivated plants observed in the pollen taxa during the 20th century. It is also plausible that human induced air pollution peaked in the region during the 1950–1980s affected the physiology of the mature trees (Kopácek et al., 2001, Čada et al., 2016), which may have resulted in lower pollen production and hence more notable changes in the pollen records corresponding to disturbance events during the last 100 years.

4.3. Integration of dendrochronological and sedimentary data

In the integration of tree-ring and sedimentary data, the biggest challenge lies in the unambiguous temporal and spatial correlation of these two different datasets. We expected that the disturbance-related mortality of mature trees, indicated by tree-ring records and resulting in a likely decrease in spruce trees, would be accompanied by a decrease in the proportion of spruce pollen in the sedimentary pollen record. However, pollen records of the main tree taxa did not indicate substantial compositional changes during the major disturbance events revealed by dendrochronology around 1800s. There are multiple reasons for this discrepancy. It is probable that although Laka is a small lake, the relative source area of pollen extends beyond the lake catchment due to the strong upscaling winds in the mountain region that may bring regional rather than local pollen signals (e.g. Bunting et al., 2008, van der Knaap et al., 2010), whereas the disturbance signal from tree-rings is very local. The relatively high proportion of Corylus pollen supports this notion, as the closest hazel population is located at a lower elevation circa 1–2 km from the study site. Whereas the pollen record reflects the vegetation from all directions surrounding Laka, the tree-ring record based on 6 study plots is highly localized and all plots are located on the slope above the southern edge of the lake in the old-growth stand. Therefore, the source area for the pollen record derived from a lake sediments and the disturbance signal from individual tree-ring study plots may have notably different spatial scale.

Other explanations for the lack of any clear response between the pollen record and the extensive disturbance events based on tree-ring data may be related to pollen production. It is possible that the canopy opening was only moderate, when the whole canopy area is considered and that the pollen production in remaining trees increased in response to disturbance due to increased light and nutrient availability, or that the trees in the closest proximity of the lake might have survived disturbance events and subsequently influence the pollen record. Furthermore, as windthrows and bark beetle outbreaks kill mainly the mature trees, the younger, surviving trees continue or quickly start to produce pollen and hence there may be a weaker signal in the pollen records compared to e.g. notable changes in the pollen composition seen after severe stand-replacing fire event. It is therefore probable that patchy forest disturbances driven primarily by wind and insect outbreaks (Čada et al., 2016a) are not necessarily reflected in the main tree pollen taxa derived from lake sediments.

From our knowledge, this is the first study to compare tree-ring based and sedimentary disturbance records in order to construct more precise disturbance reconstruction. Although, integration of these two different data sets can be challenging, the information derived from both records are complementing and when combined can provide valuable insights into the cause, extent and consequences of the disturbance events. It is noteworthy that sedimentary records that most likely have originated from the lake catchment, such as fossil beetle remains indicating bark beetle outbreaks, macroscopic charcoal indicating local fires, high values of Glomus spores together with increase in physical and geochemical properties indicating soil erosion, demonstrate similar trends to those reconstructed using tree-ring data. This allows the interpretation of possible causes behind the disturbance events indicated by tree-ring record. Furthermore, comparison of sedimentary records to the tree-ring records demonstrated that all disturbances are not necessarily visible in the pollen record, but may still have important impact on the forest structure, especially when caused by disturbance agents that affect just specific age cohorts, such as windstorms or insect outbreaks. Finally, with the palaeoecological and sedimentological records we were able to extend the disturbance reconstruction beyond the length of the tree-ring chronology (age of tree generation) and demonstrate changes in the disturbance regime, which were not detectable in the dendrochronological records. In future, the challenges in the integration of multidisciplinary data that have different spatial and temporal limitation could be overcome with using more local sampling sites (e.g. small hollows) for palaeoecological data or more regional set of dendrochronological study plots. To overcome the offset in the temporal resolution of the different records would require even more high-resolution sedimentary records and high chronological control of the samples.

5. Conclusions

Comparison of disturbance records from multidisciplinary data can provide important insight into the disturbance agents and the changes in forest composition. Multidisciplinary data demonstrate more frequent disturbance events and heightened catchment erosion from the 1600s in the study area. This suggests that there has been long-term shift in disturbance history, that could not have been detected solely with dendrochronological record. Although, windstorms and insect outbreaks are considered as main disturbance factors in the mountain spruce forest, the role of fires should not be ignored in the future forest management and conservation strategies.

This study highlights the importance of spatial and temporal consideration when integrating multidisciplinary datasets. We demonstrated that sedimentary proxies that originate from the lake catchment appear to mirror patterns in the tree-ring based disturbance signal. As the spatial scale of the datasets used may largely explain the discrepancies between palynological and tree-ring records, there is need for developing more precise analytical methods to integrate dendrochronological, sedimentological and palaeoecological data from spatially more constrained sites as from small forest hollows or if lake sediment is used comparison should be conducted with more larger dendrochronological data set.

Authors’ contributions

NK, JLC (PI) and VČ conceived the idea and designed the study; NK, VČ, KH, NS, MK, RCC, JFB, JLC collected and produced the data. NK, VČ, RC and JLC did the data analysis. All authors participated to the interpretation of data. NK led the writing of the manuscript. All authors contributed to the drafts and gave approval for the publication of the final manuscript.

CRediT authorship contribution statement

Niina Kuosmanen: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing - original draft, Data curation, Project administration. Vojtěch Čada: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing - review & editing. Karen Halsall: Investigation, Writing - review & editing. Richard C. Chiverrell: Investigation, Formal analysis, Visualization, Writing - review & editing. Nick B. Schafstall: Investigation, Writing - review & editing. Petr Kuneš: Investigation, Writing - review & editing. John F. Boyle: Investigation, Writing - review & editing. Milos Knížek: Investigation, Writing - review & editing. Peter G. Appleby: Investigation, Writing - review & editing. Miroslav Svoboda: Writing - review & editing. Jennifer L. Clear: Conceptualization, Methodology, Investigation, Formal analysis, Writing - review & editing, Funding acquisition, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

In regards the coring and processing the sedimentary data we want to thank John Boyle, Lauren Boyle, Daniel Schillereff, Fiona Russell, Isaac Clear, Daniel Vondrák, Tereza Opravilová, and Jolana Tátosová. In regard to dendrochronological records we would like to thank Tomáš and Bohuslav Koutecký for field sample collection, Jonny F. Pena and others for laboratory measurement. We would also like to thank the Šumava National Park authorities for research permission in the national park and allowing us to retrieve sediment core from Lake Laka.

Funding

Financial support for this research was provided by the PEDECO project (number 16-23183Y) funded by the Czech Science Foundation (GAČR). The involvement of Miloš Knížek was supported by the Ministry of Agriculture of the Czech Republic, institutional support MZE-RO0118.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Ali, A.A., Higuera, P.E., Bergeron, Y., Carcaillet, C., 2009. Comparing fire-history interpretations based on area, number and estimated volume of macroscopic charcoal in lake sediments. Quaternary Res. 72, 462–468. https://doi.org/10.1016/j.yqres.2009.07.002.

Appleby, P.G., Nolan, P.J., Gifford, D.W., Godfrey, M.J., Oldfield, F., Anderson, N.J., Battarbee, R.W., 1986. 210Pb dating by low background gamma counting. Hydrobiologia 141, 21–27. https://doi.org/10.1007/BF00026640.

Appleby, P.G., Oldfield, F., 1978. The calculation of 210Pb dates assuming a constant rateof supply of unsupported 210Pb to the sediment. Catena 5, 1–8. https://doi.org/10.1016/S0341-8162(78)80002-2.

Appleby, P.G., Richardson, N., Nolan, P.J., 1991. 241Am dating of lake sediments. Hydrobiologia 214, 35–42. https://doi.org/10.1007/BF00050929.

Beug, H.-J., 2004. Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Friedrich Pfeil, German, pp. 542.

Birks, H.H., 2007. Plant macrofossil introduction. In: Elias, S.A. (Ed.), Encyclopedia of Quaternary Science, Elsevier, vol. 3, pp. 2266–2288. https://doi.org/10.1016/B0-44-452747-8/00215-5.

Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Anal. 6, 457–474. https://doi.org/10.1214/11-BA618.

Blott, S.J., Pye, K̇., 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surf. Process. 26, 1237–1248. https://doi.org/10.1002/esp.261.

Bobek, P., Šamonil, P., Jamrichová, E., 2018. Biotic controls on Holocene fire frequency in a temperate mountain forest, Czech Republic. J. Quat. Sci. 33 (8), 892–904. https://doi.org/10.1002/jqs.3067.

Boyle, J.F., 1995. A simple closure mechanism for a compact, large-diameter, gravity corer. J. Paleolimnol. 13 (1), 85–87. https://doi.org/10.1007/BF00678113.

Boyle, J.F., Chiverrell, R.C., Schillereff, D., 2015. Approaches to water content correction and calibration for μXRF core scanning: comparing X-ray scattering with simple regression of elemental concentrations. Micro-XRF Stud. Sediment Cores 373–390. https://doi.org/10.1007/978-94-017-9849-5_14.

Brázdil, R., Dobrovolný, P., Štekl, J., Kotyza, O., Valášek, H., Jež, J., 2004. History of Weather and Climate in the Czech Lands VI: Strong Winds. Masaryk University, Brno.

Brunelle, A.R., Rehfeldt, J., Bentz, B.J., Munson, A.S., 2008. Holocene records of Dendroctonus bark beetles in high elevation pine forests of Idaho and Montana USA.For. Ecol. Manag. 255, 836–846. https://doi.org/10.1016/j.foreco.2007.10.008.

Bunting, M.J., Twiddle, C.L., Middleton, R., 2008. Using models of pollen dispersal and deposition in hilly landscapes: some possible approaches. Palaeogeogr. Palaeoclimatol. Palaeoecol. 259, 77–91. https://doi.org/10.1016/j.palaeo.2007.03.051.

Čada, V., Svoboda, M., Janda, P., 2013. Dendrochronological reconstruction of the disturbance history and past development of the mountain Norway spruce in the Bohemian Forest, central Europe. For. Ecol. Manag. 295, 59–68. https://doi.org/10.1016/j.foreco.2012.12.037.

Čada, V., Morrissey, R.C., Michalova, Z., Bacě, R., Janda, P., Svoboda, M., 2016. Frequent severe natural disturbances and non-equilibrium landscape dynamics shaped the mountain spruce forest in central Europe. For. Ecol. Manag. 363, 169–178. https://doi.org/10.1016/j.foreco.2015.12.023.

Čada, V., Šantrůčková, H., Šantrůček, J., Kubištová, L., Seedre, M., Svoboda, M., 2016.Complex physiological response of Norway spruce to atmospheric pollution decreased carbon isotope discrimination and unchanged tree biomass increment. Front. Plant Sci. 7, 805. https://doi.org/10.3389/fpls.2016.00805.

Carter, V.A., Moravcová, A., Chiverrell, R.C., Clear, J.L., Finsinger, W., Dreslerová, D.,Halsall, K., Kuneš, P., 2018. Holocene-scale fire dynamics of central European temperate spruce-beech forests. Quat. Sci. Rev. 191, 15–30. https://doi.org/10.1016/j.quascirev.2018.05.001.

Cháb, J., Stráník, Z., Eliáš, M., 2007. Geological Map of the Czech Republic 1:500,000.Czech Geological Survey, Prague.

Christen, J.A., Perez, S.E., 2009. A new robust statistical model for radiocarbon data. Radiocarbon 51, 1047–1059. https://doi.org/10.1017/S003382220003410X.

Davies, S., Lamb, H., Roberts, S., 2015. Micro-XRF Core Scanning in Palaeolimnology: Recent Developments. In: Croudace, I., Rothwell, R. (Eds.). Micro-XRF Studies of Sediment Cores. Developments in Paleoenvironmental Research, vol. 17. Springer, Dordrecht. https://doi.org/10.1007/978-94-017-9849-5_7.

Drobyshev, I., Niklasson, M., Angelstam, P., 2004. Contrasting tree-ring data with fire record in a pine-dominated landscape in the Komi Republic (Eastern European Russia): recovering a common climate signal. Silva Fenn. 38 (1), 43–53. https://doi.org/10.14214/sf.434.

Edwards, M.E., Dunwiddie, P.W., 1985. Dendrochronological and palynological observations on populus balsamifera in Northern Alaska, U.S.A. Arct. Antarct. Alp. Res.17 (3), 271–277. https://doi.org/10.1080/00040851.1985.12004035.

Faegri, K., Kaland, P.E., Kzywinski, K., 1989. Textbook of Pollen Analysis. Wiley, NewYork.Feurdean, A., Florescu, G., Vannière, B., Tanţău, I., O'Hara, R.B., Pfeiffer, M., Hutchinson,S.M., Mariusz Gałka, M., Moskal-del Hoyo, M., Hickler, T., 2017. Fire has been an important driver of forest dynamics in the Carpathian Mountains during the Holocene. For. Ecol. Manag. 389, 15–26. https://doi.org/10.1016/j.foreco.2016.11.046.

Fleischer, P., Pichler, V., Fleischer Jr, P., Holko, L., Máli, F., Gömöryová, E., Cudlín, P.,Holeksa, J., Michalová, Z., Homolová, Z., Střelcová, K., Hlaváč, P., 2017. Forest ecosystem services affected by natural disturbances, climate and land-use changes in the Tatra Mountains. Clim. Res. 73, 57–71. https://doi.org/10.3354/cr01461.

Van Geel, B., 1998. A Study of Non-Pollen Objects in Pollen Slides. Utrecht.Van Geel, B., 2002. Non-pollen palynomorphs. In: Smol, J.P., Birks, H.J.B., Last, W.M.,(Eds.). Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial,Algal, and Siliceous indicators. Kluwer Academic Publishers, Dordrecht, TheNetherlands. https://doi.org/10.1007/0-306-47668-1_6.N.

Halsall, K.M., Ellingsen, V.M., Asplund, J., Bradshaw, R.H.W., Ohlson, M., 2018. Fossil charcoal quantification using manual and image analysis approaches. The Holocene 28, 1345–353. https://doi.org/10.1177/0959683618771488.

Helama, S., Seppä, H., Bjune, A.E., Birks, H.J.B., 2012. Fusing pollen-stratigraphic and dendroclimatic proxy data to reconstruct summer temperature variability during the past 7.5 ka in subarctic Fennoscandia. J. Paleolimnol. 48, 275–286. https://doi.org/10.1007/s10933-012-9598-1.

Higuera, P.E., Sprugel, D.G., Brubaker, L.B., 2005. Reconstructing fire regimes with charcoal from small-hollow sediments: a calibration with tree-ring. The Holocene 15,238–251. https://doi.org/10.1191/0959683605hl789rp.

Higuera, P.E., Brubaker, L.B., Anderson, P.M., Hu, F.S., Brown, T.A., 2009. Vegetation mediated the impacts of postglacial climatic change on fire regimes in the south-central Brooks Range. Alaska. Ecol. Monog. 79, 201–219. https://doi.org/10.1890/07-2019.1.

Higuera, P.E., Gavin, D.G., Bartlein, P.J., Hallet, D.J., 2010. Peak detection in sediment-charcoal records: impacts of alternative data analysis methods on fire-history interpretation. Int. J. Wildland Fire 19, 996–1014. https://doi.org/10.1071/WF09134.

Hofmann, W., 1986. Chironomid analysis. In: Berglund, B. (Ed.), Handbook of Holocene Palaeoecology and Palaeoecology. New York, Wiley, pp 715–727.

Holeksa, J., Jaloviar, P., Kucbel, S., Saniga, M., Svoboda, M., Szewczyk, J., JerzySzwagrzyk, J., Zielonka, T., Żywiec, M., 2017. Models of disturbance driven dynamics in the West Carpathian spruce Forests. For. Ecol. Manag. 388, 79–89. https://doi.org/10.1016/j.foreco.2016.08.026.

Holeksa, J., Zielonka, T., Żywiec, M., Fleischer, P., 2016. Identifying the disturbance history over a large area of larch–spruce mountain forest in Central Europe. For. Ecol. Manag. 361, 318–327. https://doi.org/10.1016/j.foreco.2015.11.031.

Janda, P., Trotsiuk, V., Mikoláš, M., Bače, R., Nagel, T.A., Seidl, R., Seedre, M., Morrissey,R.C., Kucbel, S., Paloviar, P., Jasík, M., Vysoký, J., l Šamonil, P., Čada, V., Mrhalová,H., Lábusová, J., Nováková, M.H., Rydval, M., Matějů, L., Svoboda, M., 2017. The historical disturbance regime of mountain Norway spruce forests in the Western Carpathians and its influence on current forest structure and composition. For. Ecol. Manag. 388, 67–78. https://doi.org/10.1016/j.foreco.2016.08.014.

Jelínek, J., 2005. Od jihočeských pralesůk hospodářským lesům Šumavy. MZe Č R, ÚHÚL,Brandýs nad Labem.

Juggins, S., 2003. C2 User Guide. Software for Ecological and Palaeoecological Data Analysis and Visualization. University of Newcastle upon Tyne, Newcastle.

Kelly, R., Higuera, P.E., Barrett, C.M., Hu, F.S., 2011. A signal-to-noise index to quantify the potential for peak detection in sediment-charcoal records. Quaternary Res. 75,11–17. https://doi.org/10.1016/j.yqres.2010.07.011.

van der Knaap, W.O., van Leeuwen, J.F.N., Svitavská-Svobodová, H., Pidek, I.A.,Kvavadze, E., Chichinadze, M., Giesecke, T., Kaszewski, B.M., Oberli, F., Kalniņa, L.,Pardoe, H.S., Tinner, W., Ammann, B., 2010. Annual pollen traps reveal the com-plexity of climatic control on pollen productivity in Europe and the Caucasus. VegetHist Archaeobot 19, 285–307. https://doi.org/10.1007/s00334-010-0250-6.

Kopácek, J., Veselý, J., Evzen Stuchlík, E., 2001. Sulphur and nitrogen fluxes and budgets in the Bohemian Forest and Tatra Mountains during the Industrial Revolution (1850–2000). Hydrol. Earth Syst. Sci. 5 (3), 391–405.

Kozák, J., 2010. Soil Atlas of the Czech Republic. Czech University of Life Sciences, Prague, Prague.

Kozáková, R., Pokorný, P., Peša, V., Danielisová, A., Čuláková, K., Svitavská Svobodová, H., 2015. Prehistoric human impact in the mountains of Bohemia. Do pollen and archaeological data support the traditional scenario of a prehistoric “wilderness”? Rev Palaeobot Palyno 220, 29–43. https://doi.org/10.1016/j.revpalbo.2015.04.008.

Kulakowski, D., Seidl, R., Holeksa, J., Kuuluvainen, T., Nagel, T.A., Panayotov, M.,Svoboda, M., Thorn, S., Vacchiano, G., Whitlock, C., Wohlgemuth, T., Bebi, P., 2017.A walk on the wild side: disturbance dynamics and the conservation and management of European mountain forest ecosystems. For. Ecol. Manag. 388, 120–131. https://doi.org/10.1016/j.foreco.2016.07.037.

Lorimer, C., Frelich, L., 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Can. J. For. Res. 19, 651–663. https://doi.org/10.1139/x89-102.

McLachlan, J.S., Foster, D.R., Menalled, F., 2000. Anthropogenic ties to late-successional structure and composition in four New England hemlock stands. Ecology 81 (3),717–733. https://doi.org/10.1890/0012-9658(2000)081[0717:ATTLSS]2.0.CO;2.

Mentlík, P., Minár, J., Břízová, E., Lisá, L., Tábořík, P., Stacke, V., 2010. Glaciation in the surroundings of Prásilské Lake (Bohemian Forest, Czech Republic). Geomorphology117, 181–194. https://doi.org/10.1016/j.geomorph.2009.12.001.

Mooney, S.D., Tinner, W., 2011. The analysis of charcoal in peat and organic sediments. Mire Peat 7, 1–18.

Moore, P.D., Webb, J.A., Collinson, M.E., 1991. Pollen Analysis. Blackwell Scientific Publications, Oxford.

Morris, J.L., Courtney Mustaphi, C.J., Carter, V.A., Watt, J., Derr, K., Pisaric, M.F.J., Scott Anderson, R., Brunelle, A.R., 2015. Do bark beetle remains in lake sediments correspond to severe outbreaks? A review of published and ongoing research. Quat. Int.387, 72–86. https://doi.org/10.1016/j.quaint.2014.03.022.

Nagel, T.A., Mikac, S., Dolinar, M., Klopcic, M., Keren, S., Svoboda, M., Diaci, J., Andrej Boncina, A., Paulic, V., 2017. The natural disturbance regime in forests of the Dinaric Mountains: a synthesis of evidence. For. Ecol. Manag. 388, 29–42. https://doi.org/10.1016/j.foreco.2016.07.047.

Neuhäuslová, Z., Moravec, J., 1998. Map of Potential Natural Vegetation of the Czech Republic. Academia, Prague.

Niklasson, M., Lindbladh, M., Björkman, L., 2002. A long-term record of Quercus decline, logging and fires in a southern Swedish Fagus-Picea forest. J. Veg. Sci. 13, 765–774. https://doi.org/10.1111/j.1654-1103.2002.tb02106.x.

Niklasson, M., Zin, E., Zielonka, T., Feijen, M., Korczyk, A.F., Churski, M., Samojlik, T.,drzejewska, B., Gutowski, J.M., Brzeziecki, B., 2010. A 350-year tree-ring fire record from Białowieza Primeval Forest, Poland: implications for Central European lowland fire history. J. Ecol. 98, 1319–1329. https://doi.org/10.1111/j.1365-2745.2010.01710.x.

Pfeffer, A., 1989. Kůrovcovití (Scolytidae) a jádrohlodovití (Platypodidae). Praha,Academia: 137.

Reimer, P., Bard, E., Bayliss, A., Beck, J., Blackwell, P., Ramsey, C., Van der Plicht, J.,2013. Selection and treatment of data for radiocarbon calibration: an update to the international calibration (IntCal) criteria. Radiocarbon 55 (4), 1923–1945. https://doi.org/10.2458/azu_js_rc.55.16955.

Reyer, C.P.O., Brouwers, N., Rammig, A., Brook, B.W., Epila, J., Grant, R.F., Holmgren,M., Langerwisch, F., Leuzinger, S., Lucht, W., Medlyn, B., Pfeifer, M., Steinkamp, J.,Vanderwel, M.C., Verbeeck, H., Villela, D.M., 2015. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. J. Ecol. 103,5–15. https://doi.org/10.1111/1365-2745.12337.

Russell, F.E., Boyle, J.F., Chiverrell, R.C., 2019. NIRS quantification of lake sediment composition by multiple regression using end-member spectra. J. Paleolimnol. 62,73–88. https://doi.org/10.1007/s10933-019-00076-2.

Schelhaas, M.J., Nabuurs, G.J., Schuck, A., 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Glob. Change Biol. 9, 1620–1633. https://doi.org/10.1046/j.1365-2486.2003.00684.x.

Scott, A.C., 2010. Charcoal recognition, taphonomy and uses in palaeoenvironmental analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 291, 11–39. https://doi.org/10.1016/j.palaeo.2009.12.012.

Schillereff, D.N, Chiverell, R.C., Croudace, I.W., Boyle, J.F., 2015. An Inter-comparison of µXRF Scanning Analytical Methods for Lake Sediments. In: Croudace, I., Rothwell, R.,(Eds.), Micro-XRF Studies of Sediment Cores. Developments in Paleoenvironmental Research, vol. 17. Dordrecht: Springer. https://doi.org/10.1007/978-94-017-9849-5_24.

Seidl, R., Schelhaas, M.-J., Lexer, M.J., 2011. Unraveling the drivers of intensifying forest disturbance regimes in Europe. Glob. Change Biol. 17, 2842–2852. https://doi.org/10.1111/j.1365-2486.2011.02452.x.

Seidl, R., Schelhaas, M.-J., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. Nat. Clim. Change 4,806–810. https://doi.org/10.1038/nclimate2318.

Šoltés, R., Školek, J., Homolová, Z., Kyselová, Z., 2010. Early successional pathways in the Tatra Mountains (Slovakia) forest ecosystems following natural disturbances. Biologia 65 (6), 958–964. https://doi.org/10.2478/s11756-010-0110-y.

Stivrins, N., Aakala, T., Ilvonen, L., Pasanen, L., Kuuluvainen, T., Vasander, H., Gałka, M.,Disbrey, H.R., Janis Liepins, J., Holmström, L., Seppä, H., 2019. Integrating fire-scar, charcoal and fungal spore data to study fire events in the boreal forest of northern Europe. The Holocene 29 (9), 1480–1490. https://doi.org/10.1177/0959683619854524.

Stockmarr, J., 1972. Tablets with spores used in absolute pollen analysis. Pollen Spores13, 614–621.

Svoboda, M., Janda, P., Báce, R., Shawn Fraver, S., Nagel, T.A., Jan Rejzek, J., Mikoláš,M., Douda, J., Boublík, K., Šamonil, P., Čada, V., Trotsiuk, V., Teodosiu, M.,Bouriaud, O., Biriş, A.I., Sýkora, O., Uzel, P., Zelenka, J., Sedlák, V., Lehejček, J.,2013. Landscape-level variability in historical disturbance in primary Picea abies mountain forests of the Eastern Carpathians. Romania. J. Veg. Sci. 25 (2), 386–401. https://doi.org/10.1111/jvs.12109.

Thom, D., Seidl, R., Steyrer, G., Krehan, H., Formayer, H., 2013. Slow and fast drivers of the natural disturbance regime in Central European forest ecosystems. For. Ecol. Manag. 307, 293–302. https://doi.org/10.1016/j.foreco.2013.07.017.

Thom, D., Rammer, W., Seidl, R., 2017. Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. Glob. Change Biol. 23, 269–282. https://doi.org/10.1111/gcb.13506.

Tolasz, R., Míková, T., Valeriánová, A., Voženílek, V., 2007. Climate Atlas of Czechia. ČHMÚ/Palacký University, Prague/Olomouc.

Zatloukal, V., 1998. Historické a současné příčiny k rovcové kalamity v Národnímparku Šumava. Silva Gabreta 2, 327–357.

Whitlock, C., Larsen, C., 2001. Charcoal as a fire proxy. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), Tracking Environmental Change Using Lake Sediments. Springer, pp.75–97. https://doi.org/10.1007/0-306-47668-1_5.