Quaternary Science Reviews 229 (2020) 106137

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Towards the understanding the impact of fire on the lower montane forest in the Polish Western Carpathians during the Holocene

Piotr Kołaczek [a, *], Włodzimierz Margielewski [b], Mariusz Gałka [c], Monika Karpińska-Kołaczek [a, d, e], Krzysztof Buczek [b], Mariusz Lamentowicz [a, d], Aleksandra Borek [a], Valentina Zernitskaya [f], Katarzyna Marcisz [a, d, g]

[a] Department of Biogeography and Palaeoecology, Faculty of Geographical and Geological Sciences, Adam Mickiewicz University, Poznań, Bogumiła Krygowskiego 10, 61-680 Poznań, Poland
[b] Institute of Nature Conservation Polish Academy of Sciences, Adama Mickiewicza Ave. 33, 31-120, Kraków, Poland
[c] University of Lodz, Faculty of Biology and Environmental Protection, Department of Geobotany and Plant Ecology, Banacha 12/16, 90-237 Łódz, Poland
[d] Laboratory of Wetland Ecology and Monitoring, Faculty of Geographical and Geological Sciences, Adam Mickiewicz University, Poznań, Bogumiła Krygowskiego 10, 61-680 Poznań, Poland
[e] Centre for the Study of Demographic and Economic Structures in Preindustrial Central and Eastern Europe, University of Bialystok, Plac NZS 1, 15-420 Białystok, Poland
[f] Institute of Nature Management, National Academy of Sciences of Belarus, F. Skorynu Str. 10, 220114 Minsk, Belarus
[g] Institute of Plant Sciences and Oeschger Centre for Climate Change Research, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland

ARTICLE INFO

Article history:
Received 4 September 2019
Received in revised form
12 December 2019
Accepted 12 December 2019
Available online 5 January 2020

Keywords:
Pollen
Charcoal
Fire regime
4.2 ka. BP event
Fagus sylvatica
Abies alba
Wallachians
Central Europe

ABSTRACT

In this article, we aim to decipher the effect of fire on the changes in the forest composition during the past ca. 10,700 years in the lower montane zone of the Polish Western Carpathians (Beskid Makowski Mountains, Central Europe). The results revealed that during the Early Holocene, the *Ulmus* population (a fire-intolerant taxon) was well-established under high fire activity, induced by the prominent presence of *Pinus sylvestris*. *Ulmus* probably was only slightly affected by fire because it occurred in wetter habitats, whereas *P. sylvestris* occupied drier ones. The final disruption of *Pinus sylvestris*–*Betula* woodlands were linked to a declining trend in fire activity but stable fire frequency, combined with the rapid expansion of *Corylus avellana* at ca. 9680 cal. BP. A low magnitude of fire disturbance with an increasing fire frequency supported the expansion of *Tilia cordata* (a fire-sensitive species) and *C. avellana* (a fire-adapted species) against *Picea abies* during ca. 7650–7270 cal. BP. Cooler and wetter conditions during the 4.2 and 2.8 ka. BP climatic events probably forced humans to migrate to higher altitudes, which contributed to fire-induced deforestation of a small area, which in turn, together with climatic changes, stimulated the expansion of *Abies alba* and *Fagus sylvatica* (both are fire-intolerant taxa). The discontinuities in the deposits of mire might be related to the global climatic changes of the 8.2 and 4.2 ka. BP events and extended deforestations linked to the Wallachian colonisation during the Middle Ages. Such depositional gaps, when remaining undetected during palaeoecological studies, may distort the reconstruction process of fire–vegetation relationships. In this study, we unequivocally show that small disturbances in fire may be an advantageous factor for the expansion of tree taxa devoid of morphological–physiological fire traits.

© 2020 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

1. Introduction

Worldwide, fire is a crucial component of many natural ecosystems and biogeochemical cycles (Randerson et al., 2006; Archibald et al., 2013), which is closely linked to the climate (Daniau et al., 2012; Marlon et al., 2013), serving as an important tool for human-induced land cover changes across the globe (Bowman et al., 2011; Vannière et al., 2016; Dietze et al., 2018; Feurdean et al., 2019). The understanding of past trajectories of changes in fire regime and their variability, supported by the palaeoecological data, is the key to finding proper strategies related to forest management, conservation of forest ecosystem, and

* Corresponding author.
E-mail address: pkolacz@amu.edu.pl (P. Kołaczek).

https://doi.org/10.1016/j.quascirev.2019.106137
0277-3791/© 2020 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

restoration activities (e.g. Finsinger et al., 2017, 2018; Marcisz et al., 2018; Słowiński et al., 2019). Hence, in the last few decades, there has been an increase in the interest in palaeoecological studies on past fire regimes (Conedera et al., 2009; Marlon et al., 2013). However, the data on palaeofires are not equally distributed; hence, various areas of the world remain underexplored (https://www.paleofire.org/index.php).

Burning of biomass delays competitive exclusion, increases landscape heterogeneity, and generates new ecological niches; thus, it may contribute to maintenance or increase in the biodiversity (Pausas and Ribeiro, 2017). Mountainous areas are habitats with great biodiversity that is linked to steep altitudinal gradients, topographical complexity, and other mosaic elements of the environment, including the availability of bedrock and nutrients, humidity, and persistence of snow cover (Mráz and Ronikier, 2016 and references therein). Therefore, reconstructing past fire regimes seems to be crucial for understanding the long-term functioning of habitat and consequently its biodiversity. In this study, we focus on the Carpathians, the largest mountain range in Central-Eastern Europe (and the second largest in Europe), covering more than 2 km in the altitudinal gradient. Despite the fact that the researchers are greatly interested in studying this mountain range (Mráz and Ronikier, 2016), vast areas, such as the Western Carpathians, still needs to be studied in regard to past fire regimes. Studies lack especially combined analyses of micro- and macrocharcoal from contiguous sampling. Nonetheless, research has been conducted on the adjacent mountain ranges, e.g. Novohradské Mountains (Bobek et al., 2018a), Šumava Mountains (Carter et al., 2018), Bohemian Switzerland (Bobek et al., 2018b), Transylvanian Plain (Feurdean et al., 2013), Rodna Mountains (Feurdean et al., 2017b), and Retezat Mountains (Finsinger et al., 2018) (Fig. 1). Moreover, review studies based on different types of charcoal data have been published with respect to the Romanian and Hungarian part of the Carpathians (Feurdean et al., 2012) and adjacent areas in Czech Republic (Bobek et al., 2019). At the same time, the Western Carpathians are well recognised in terms of patterns of changes in the vegetation during the postglacial period (Obidowicz, 2013a,b; Jamrichová et al., 2017). Hence, any study on past fire regime would be desired to broaden the knowledge about the long-term forest functioning and to support conservation activities in this area.

In this study, we focus on a lower montane forest zone in the northern part (Polish) of the Western Carpathians, which is a habitat mainly for *Abies alba*–*Fagus sylvatica* forests with an admixture of *Picea abies* (*Dentario glandulosae*–*Fagetum* and *Abieti*–*Piceetum* association). However, as a result of silvicultural practices, *P. abies* monocultures were introduced in many areas of this zone (Szwagrzyk and Holeksa, 2004; Mirek, 2013). In the Polish part of the Western Carpathians, only ca. 6% of all the areas are overgrown by forests characterised by the primaeval character and are protected by law (Denisiuk, 1995; Denisiuk et al., 1993). However, ca. 50% of all such protected forests belong to the *D. glandulosae*–*Fagetum* alliance (Korpel', 1995; Skrzydłowski, 2019). During the last millennium, the forests of the Western Carpathians were affected by immense human activities in which forest clearance with the use of fire was a common practice leading to major degradation of the forests (Sadowski, 2003; Jawor, 2016a,b). Hence, understanding the long-term functioning of vegetation and fire, especially before the period of acceleration of the human activity, in the lower montane zone, seems to be crucial to plan future conservation activities.

The primary aim of this study was to decipher the effect of fire disturbances on the changes in the forest composition during the past ca. 10,700 years. We also paid attention to the effect of impact of human, herbivore, pathogens, and climatic disturbance factors on the forest development. This period was chosen because it spans each of the most characteristic turnovers of forest composition, which took place in the lower montane zone in the Polish Western Carpathians (cf. Margielewski, 2006; Obidowicz, 2013b). The fire-tolerance of arboreal taxa inhabiting temperate woods is well recognised by palaeoecological (e.g. Tinner et al., 2000; Feurdean et al., 2017a; Carter et al., 2018) as well as modern ecological studies (e.g. https://www.feis-crs.org/feis/ and references therein). However, there are cases in which traces of fire poorly explain the species–fire relationship. For example, fire may promote the expansion of particular wood taxa that are devoid of fire adjustments e.g. *F. sylvatica* (Bradshaw and Lindbladh, 2005; Ascoli et al.,

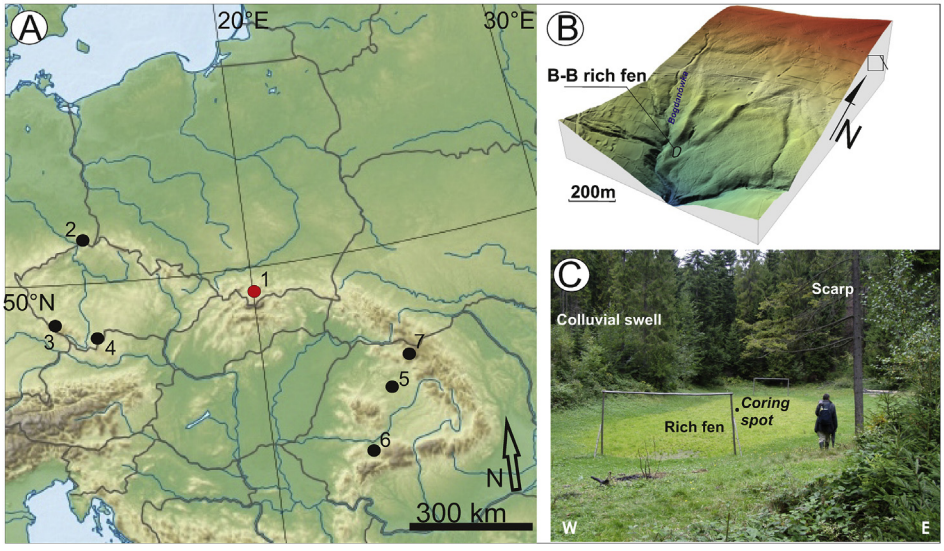


Fig. 1. Location of the Bogdanówka-Beło (B-B) site. A – B-B site location in Central Europe, the numbers express sites in which macrocharcoal analysis from contiguous sampling was carried out in the Carpathians and adjacent areas: 1 – Bogdanówka-Beło, Beskid Makowski Mountains (this study), 2 – Eustach bog, Bohemian Switzerland (Bobek et al., 2018b), 3 – Lake Prášilské (Carter et al., 2018); 4 – Žofín, Novohradské Mountains (Bobek et al., 2018a), 5 – Lake Stiucii, Transylvanian Plains (Feurdean et al., 2013), 6 – Lake Brazi and Lake Lia (Finsinger et al., 2018), 7 – Tăul Muced and Poiana Ştiol (Feurdean et al., 2017a,b); B – Morphological position of the fen on the LIDAR-derived topographical map. C – View on the fen (with a coring site; photo by W. Margielewski) (from Kołaczek et al., 2017, modified).

2015). Therefore, we hypothesize that small to moderate fires may have promoted the spread of fire-intolerant taxa during the periods of main forest transformations in the lower montane zone in the Polish Western Carpathians. As the fire activity is closely related to the climate, we also assume that the events of global climate change (e.g. Bond et al., 1997, 2001; Mayewski et al., 2004; Wanner et al., 2011) may have driven the occurrence of fire (Florescu et al., 2019) and influenced the main Holocene transformations of the forest. To solve this problem for the first time in the Polish Western Carpathians, we analysed together pollen, non-pollen palynomorphs (NPPs) (fungal tree pathogens and coprophilous fungi), plant macrofossil, and micro- and macrocharcoal from the sediment samples. The latter analysis was a basis for the first quantitative reconstruction of fires in the Polish Carpathians and the second from the area of Poland (cf. Marcisz et al., 2019).

2. Site area

The study area (Bogdanówka-Beło, B-B) is located in a fen developed in the landslide depression situated in the Bogdanówka village (southern Poland), on the southern slopes of the Mount Koskowa Góra (Beskid Makowski Mountains, Polish Outer Carpathians; Fig. 1) at an altitude of 675 m a.s.l. The landslide originated within the thick-bedded Magura Sandstones (composed mainly of quartz grains with glauconite and cemented with clayey-siliceous material) in the head area of the valley of the Bogdanówka Stream, which flows into Krzczonówka Stream, the right tributary of the Raba River. Nowadays, the landslide depression, located in the lower part of a landslide zone, which is transformed by multistage landslides, is framed by a steep scarp and colluvial swell (Fig. 1). The depression is undrained (without a superficial outflow) and recharged by a periodic stream that forms after downpours or continuous rains. The minerogenic mire that formed in the depression covers an area of ca. 0.3 ha (Fig. 1; Margielewski, 2006).

The mean year temperature is ca. 5.7 °C (Bogdanówka; https://pl.climate-data.org/) with cold and rainy springs. The local climate, despite being characterised by frequent rains, is drier in comparison with the adjacent areas, due to its location within the rain shadow (Lis and Stańczuk, 2008). The mean temperature of the warmest month (July) is 15.3 °C, whereas that of the coldest month (January) is −5.2 °C. The annual precipitation is 970 mm (Bogdanówka; https://pl.climate-data.org/), and the highest rainfall occurs in the area of the Mount Koskowa Góra and the Bogdanówka village. The growing season in valleys lasts for 200–210 days (Lis and Stańczuk, 2008).

The surface of the mire, which is stabilised by a minerogenic layer that covers organic deposits, is an open area, overgrown by fresh meadow communities (Fig. 1). The local mixed forests are typical of the modern lower mountainous forest belt (550–870 m a.s.l.) and consist of beech (*F. sylvatica*) and silver fir (*A. alba*) with an admixture of Norway spruce (*P. abies*), whereas damp sites along the streams are overgrown by alder forests with *Alnus glutinosa* and *Alnus incana* and tall-herb groundcover communities (Mirek, 2013). Nowadays, forest stands in the Tokarnia municipality (the administrative unit within which the B-B site is located) mainly consist of *A. alba* (ca. 60%), *F. sylvatica*, and *Pinus sylvestris* (Lis and Stańczuk, 2008).

The historical sources reveal that the area of Mount Koskowa Góra and the Krzczonówka Stream catchment was gradually inhabited from the 14th to 16th century AD (550–350 cal. BP) as reflected by the onset of villages: (i) Tokarnia (AD 1455, 495 cal. BP), (ii) Bieńkówka (AD 1537, 413 cal. BP), and (iii) Bogdanówka (AD 1650, 300 cal. BP) (Sadowski, 2003). Even though the area of the Bogdanówka site surroundings was probably situated north of the main area of the Wallachian settlement (Jawor, 2016a,b), their presence was mentioned at AD 1473 (477 cal. BP; Sadowski, 2003). In the past, the local presence of the Wallachian shepherds within the Mount Koskowa Góra was marked in the local geographical nomenclature originated from their language (Krukar, 2004). There was a substantial reduction of sheep flocks in the region, which took place at the end of the 16th century AD (450–350 cal. BP) and was linked to the development of wood-processing industries (Sadowski, 2003).

3. Material and methods

3.1. Core retrieval, lithology, absolute chronology, and accumulation rate

The core (B-BII/2014), 495 cm long, was retrieved from the central part of the mire (Fig. 1) using the Russian-type sampler (chamber dimension: 6 × 50 cm) from the area characterised by the highest thickness of sediments (ca. 520 cm in total, according to Margielewski, 2006; 49°45.252′N; 19°47.661′E) in November 2014. As the multi-proxy study on peat core fragment (495–400 cm) was already published (Kołaczek et al., 2017), in this study, the section between the depths of 400–0 cm was the subject of analysis. The bottom part of the deposits (495–390 m) is composed of mineral sediments (mainly sandy clayey silt with an admixture of organic matter at the top). The fen deposits were accumulated as peat intercalated with layers of mineral sediments (silty sand 283–261 cm) (Fig. 2, Table 1). Mineral cover (sandy clayey silt; 55 cm thick), was formed upon the peat sequence (Table 1, see also Margielewski, 2006).

The Bayesian age-depth model was constructed to determine the absolute chronology for the entire profile based on 24 out of 26 ^{14}C AMS dates (Table 2). The measurements of ^{14}C content were carried out at the Poznań Radiocarbon Laboratory (Poland) (Table 2). The age-depth model was constructed using the OxCal 4.3 software (Bronk Ramsey, 1995) and by applying the *P_Sequence* function with the following parameters: $k_0 = 0.8$, $\log_{10}(k/k_0) = 1$ and interpolation = 0.5 cm (Bronk Ramsey, 2008; Bronk Ramsey and Lee, 2013). The IntCal13 ^{14}C atmospheric curve was used as the calibration set (Reimer et al., 2013). Two ^{14}C dates (Poz-80166 and Poz-86394), which differ significantly from neighbouring dates (younger of ca. 840–1050 ^{14}C years), were excluded prior to the modelling. The age-depth model was constructed separately for two sections (500–55 cm and 55–0 cm) due to a significant change in the type of deposit at a depth of 55 cm (transition between peat and sandy clayey silt). To restrict the artificial decline of age in the 350.5–330.5 cm section, where the fragment of wood was found (probably a single-age piece), the date from this wood was used three times in the model for depths of 350.5, 340.5, and 330.5 cm. The sections of the profile with potential changes in the accumulation rate of deposits ($AR_{deposits}$) were introduced to the model as boundaries (*Boundary* command). In the model, for the section of depth 495–55 cm, the boundaries were placed at the following depths: (i) 495 cm—the bottom of the model, (ii) 390 cm—sandy clayey silt to peat transition, (iii) 351 cm—bottom of the wood fragment, (iv) 330 cm—top of the wood fragment, (v) 285 cm—bottom of the silty sand horizon, (vi) 261 cm—top of the silty sand horizon, (vii) 200 cm—bottom of the layer of brown decomposed peat, (viii) 81 cm—top of the layer of brown decomposed peat, and (ix) 55 cm—peat to sandy clayey silt transition. In the section of 55–0 cm, the boundaries were placed at the bottom and at the top of this section of the profile.

For better readability, in the following sections of this article, μ value is rounded to tens and was selected as the one reflecting the modelled age, which was expressed as cal. BP (a year before AD 1950). The $AR_{deposits}$ was calculated by the OxCal 4.3 software

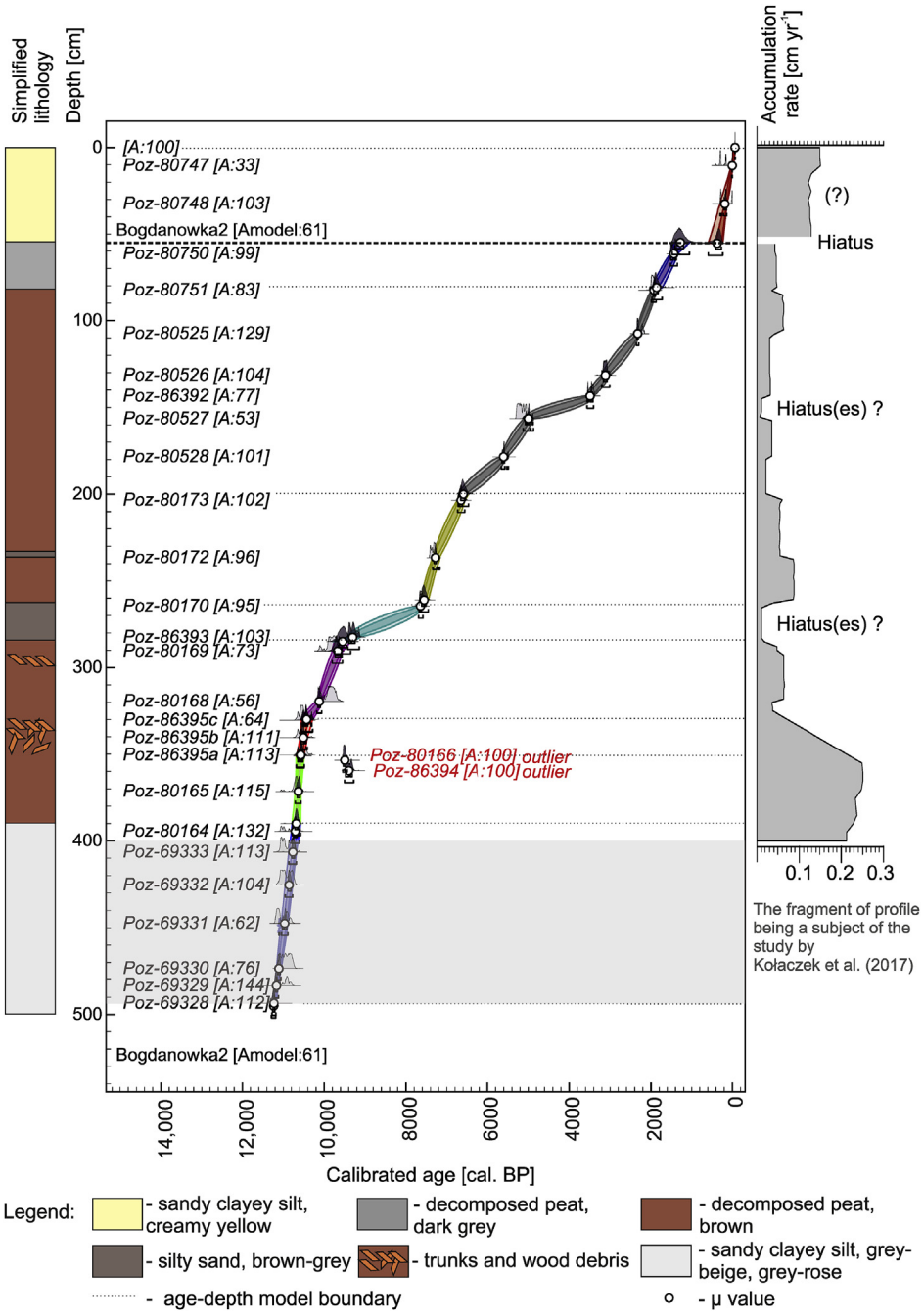


Fig. 2. Bayesian age-depth model and accumulation rate. For detailed lithology see Table 1.

(Bronk Ramsey, 1995) and presented in the unit: cm yr^{-1}.

3.2. Pollen, non-pollen palynomorphs, and micro- and macrocharcoal

A total of 122 samples (1 cm^3 in volume) were prepared for palynological analysis using the standard laboratory procedures (Berglund and Ralska-Jasiewiczowa, 1986). To remove the mineral fraction, samples were treated with 10% hydrochloric acid (to dissolve carbonates), heated in 10% potassium hydroxide (to remove humic compounds), and finally soaked in 40% hydrofluoric acid for 24 h (to remove the mineral fraction). Next, acetolysis was performed. Two *Lycopodium* tablets (Batch 3862 containing 9666 spores per tablet; produced by the Lund University) were added to each sample for the calculation of microfossil concentration during the laboratory procedures (Stockmarr, 1971). Pollen, spores, and the selected non-pollen palynomorphs (NPPs) were counted under an upright microscope until the number of total pollen sum (TPS) grains in each sample reached at least 500. Sporomorphs were identified with the assistance of atlases and keys (Moore et al., 1991; Beug, 2004; van Geel and Aptroot, 2006). The results of the palynological analysis were expressed as percentages and accumulation rates (selected taxa). Percentages of pollen grains, spores, and NPPs were calculated on the basis of the ratio of an individual taxon to the TPS, i.e., the sum of arboreal pollen (AP) and non-arboreal pollen (NAP) and by excluding aquatic and wetland

Table 1
Lithology of the B-BII/2014 profile.

Depth [cm]	Description of deposits
55–0	Sandy clayey silt, creamy yellow
81–55	Decomposed peat, dark grey
200–81	Decomposed peat, brown
233–200	Decomposed peat, brown-yellow, at depths of 217–219 cm and 229–231 cm, fragments of wood were detected
236–233	Silt, grey
250–236	Detrital peat characterised by distinct number of *Sphagnum* remains
261–250	Detrital peat characterised by distinct amount of matrix
283–261	Silty sand, brown-grey
326–283	Decomposed peat, beige-brown, wood fragment at a depth of 290–300 cm
350–326	Wood fragment
382–350	Detrital peat, brown
383–282	Silt, grey
390–383	Decomposed peat, brown-grey
391–390	Silt, grey
394–391	Decomposed peat, brown
397–394	Peat-silt layers
495–397	Sandy clayey silt, grey-beige, grey-rose

plants and by including Cyperaceae, cryptogams, and fungi. In this study, we selected only pollen of terrestrial plants and two aquatic and amphibious plants (*Callitriche palustris* t. and *Potamogeton* subgen. *Eupotamogeton*; hereafter subgen. = subgenus, t. = type) as the taxa indicative of the period of increased level of water table. Microscopic charcoal particles (hereafter ch. p. = charcoal particles) (diameter: 10–100 μm) were counted from the same slides as pollen and NPPs (Tinner and Hu, 2003).

For macroscopic charcoal analysis, a total of 400 1 cm^3 contiguous samples of deposits (each representing 1 cm slice of the profile) were prepared according to the standard procedures (Whitlock and Larsen, 2001; Conedera et al., 2009). Charcoal particles were counted in two fractions, 100–500 μm and >500 μm, under a stereomicroscope with 40× magnification. The pollen accumulation rate (PAR_{taxon}; measured as grains cm^{-2} yr^{-1}) and microscopic and macroscopic charcoal accumulation rate ($CHAR_{micro}$ and $CHAR_{macro}$) were calculated on the basis of the formula proposed by Davis and Deevey (1964) i.e. PAR_{taxon}, $CHAR_{micro}$, and $CHAR_{macro} = C_t \times AR_{deposits}$, in which C_t is the concentration of sporomorph taxon or ch. p. (unit: grains or particles cm^{-3}) and $AR_{deposits}$ is the accumulation rate of deposits.

3.3. Plant macrofossils

A total of 400 1-cm thick slices of the profile (10–14 cm^3) were investigated, which were continuously sampled. Each of the samples was gently washed and wet-sieved through 0.2 mm mesh screen under the stream of warm water. The carpological and vegetative remains (fruits, seeds, leaves, and epidermis) were identified using keys and atlases (e.g., Grosse-Brauckmann, 1974; Tobolski, 2000) under a stereomicroscope. Data are presented as the absolute number of a particular macrofossil. For the purposes of this article, only the arboreal taxa were selected (Fig. 3).

3.4. Statistical analyses and data presentation

All statistical analyses were conducted on the 399.5–55 cm section to avoid possible biases. The topmost layer (0–55 cm) was characterised by a tentative chronology (two dates from the ^{14}C plateau; Table 2), extremely high concentration of micro- and macrocharcoal, in comparison with other sections of the profile, and overrepresentation of herb pollen (see section 4 Results and interpretation).

To identify the features of fire regimes, we applied peak recognition approach by assuming that the likelihood of identifying local fires increases with an increasing value of $CHAR_{macro}$ (Conedera et al., 2009). The reconstruction of statistically significant fire peaks per episode and fire frequency was performed using contiguously analysed $CHAR_{macro}$ record in CharAnalysis (Higuera et al., 2009, 2010). The inferred fire frequencies (IFFs; fire episodes 1000 yrs^{-1}) were calculated and smoothed using a lowess smoother and a 1000-year window. Due to the lack of macrocharcoal in long sections of the profile, it was not possible to calculate a fire return interval (FRI).

To describe the relationships between the dominant forest arboreal taxa, the selected shrubs, as well as the NAP sum and changes in the fire activity ($CHAR_{micro}$, the same sampling resolution as the pollen) at the Bogdanówka site, we used the Generalized Additive Model (GAM; Hastie and Tibshirani, 1986). For GAM calculation the *mgcv* (Wood, 2006) package in R software (R Development Core Team, 2014) was used. GAM is a semi-parametric extension of the generalized linear model that uses a link function to establish a relationship between the mean response variable (i.e. the dependent variable; percentages and PAR of the selected taxa) and a smoothed predictor variable(s) (i.e. the independent variable; $CHAR_{micro}$) (Carter et al., 2018). The default setting for GAMs, Gaussian error distribution and an identity link function were used in this study.

To identify critical values of fire activity ($CHAR_{micro}$) that might have caused changes in the vegetation (palynological data expressed as percentages), we used the method of Threshold Indicator Taxa ANalysis (TITAN) to reveal sharp, non-linear transitions in the entire community data (Baker and King, 2010). Briefly, TITAN identified the optimum changing point of taxa abundance along the $CHAR_{micro}$ gradient using bootstrapping and permutation tests to assess the uncertainty of every changing point (Baker and King, 2010). TITAN detects changes in the distribution of taxa (species that increase (normalized z+ scores) or decrease (normalized z− scores) in abundance) along a gradient and assesses the synchronicity among responses by species as evidence for community thresholds. The quality and estimation of the critical tipping point area in a plant community were tested using 1000 permutations and 150 bootstrap replicates (resampling with replacement) using the *TITAN2* R package (Baker and King, 2010) in R software (R Development Core Team, 2014).

The correspondence between the selected, most frequent, arboreal taxa pollen, *Pteridium aquilinum*, and environmental variables were verified using Non-metric Multidimensional Scaling (NMDS). These variables were as follows: (i) $CHAR_{micro}$ reflecting regional fires, (ii) cultivated land—sum of pollen taxa indicating

Table 2
Radiocarbon dates from the B-BII/2014 profile.

Sample depth (value in model) [cm]	Laboratory code-number	^{14}C date [^{14}C BP]	Age [cal. BP] (2σ 95.4%)	Dated material; remarks
10–11 (10.5)	Poz-80747	240 ± 30	425–394 (5.7%) 319–269 (51.9%) 212–200 (1.3%) 189–147 (29.5%) 14 – modern (7.1%)	Charcoal
32–33 (32.5)	Poz-80748	205 ± 30	305–265 (26.9%) 220–141 (50.1%) 24–modern (18.5%)	Charcoal
61–62 (61.5)	Poz-80750	1530 ± 30	1523–1352 (95.4%)	Fragments of *Abies alba* and *Picea abies* needles and *Sphagnum* stems
82–83 (82.5)	Poz-80751	2010 ± 30	2041–2017 (4.2%) 2010–1885 (91.2%)	Fragments of *A. alba* needles
107–108 (107.5)	Poz-80525	2270 ± 30	2349–2300 (49.3%) 2253–2159 (46.1%)	Fragments of *A. alba* needles
131–132 (131.5)	Poz-80526	2955 ± 30	3209–3004 (95.4%)	Fragments of *P. abies* needles
143–144 (143.5)	Poz-86392	3230 ± 30	3557–3531 (8.2%) 3511–3381 (87.2%)	Fragments of *P. abies* and *A. alba* needles
156–157 (156.5)	Poz-80527	4480 ± 35	5291–5035 (89.4%) 5010–4978 (6%)	Fragments of *P. abies* needles
178–179 (178.5)	Poz-80528	4850 ± 35	5653–5578 (74.4%) 5530–5482 (21%)	Fragments of *P. abies* needles
203–204 (203.5)	Poz-80173	5830 ± 35	6737–6539 (95.4%)	Fragments of *P. abies* needles
236–237 (236.5)	Poz-80172	6390 ± 35	7418–7264 (95.4%)	Fragments of *P. abies* needles
264–265 (265.5)	Poz-80170	6780 ± 40	7679–7577 (95.4%)	Fragments of *P. abies* needles and two *P. abies* bud scales
282–283 (282.5)	Poz-86393	8280 ± 40	9417–9134 (95.4%)	*Carex vesicaria* fruits
290–291 (290.5)	Poz-80169	8780 ± 50	10,128–10,062 (6.1%) 10,035–10,030 (0.2%) 10,009–9993 (0.9%) 9945–9581 (87.5%) 9574–9562 (0.7%)	Two *Menyanthes trifoliata* seeds, *Rubus idaeus* seed, *Sambucus nigra* seed, *C. vesicaria* fruit
319–320 (319.5)	Poz-80168	8810 ± 50	10,155–9983 (22.3%) 9966–9671 (73.1%)	Fragments of *P. abies* needles
350.5–330.5 (350.5, 340.5, 330.5)	Poz-86395	9330 ± 50	10,694–10,394 (95%) 10,312–10,305 (0.4%)	Wood fragment
353–354 (353.5)	Poz-80166	8490 ± 50	9542–9438 (95.4%)	Fragments of needles, two bud scales, and seed of *P. abies*; outlier
359–360 (359.5)	Poz-86394	8380 ± 50	9500–9279 (95.4%)	Fragments of *P. abies* needles; outlier
371–372 (371.5)	Poz-80165	9430 ± 50	11,057–11,037 (1.1%) 10,990–10,981 (0.4%) 10,786–10,515 (93.9%)	Fragments of *P. abies* needles
Dates published by Kołaczek et al. (2017)				
394–395 (394.5)	Poz-80164	9470 ± 50	11070–10953 (16.7%) 10867–10846 (1.8%) 10821–10574 (77%)	Fragments of needles, two bud scales and seed of *P. abies*
406–407 (406.5)	Poz-69333	9530 ± 50	11091–10685 (95.4%)	One needle of *P. abies*, three fruits of *C. vesicaria* and fruits of *Scirpus sylvativus*
425–426 (425)	Poz-69332	9560 ± 50	11107–10711 (95.4%)	Fourteen bud scales, seed and needle of *P. abies*
447–448 (447.5)	Poz-69331	9660 ± 50	11204–11061 (50.5%) 11032–10988 (4.4%) 10975–10786 (40.5%)	Seven bud scales, seed and two needles of *P. abies*
473–474 (473.5)	Poz-69330	9590 ± 50	11145–10742 (95.4%)	Eleven bud scales and two seeds of *P. abies*, needle of *Pinus sylvestris*
483–484 (483.5)	Poz-69329	9690 ± 60	11232–11063 (61.2%) 11030–10995 (2.8%) 10970–10788 (31.4%)	Six bud scales and needle of *P. abies*, needle of *P. sylvestris*, fruit of *Betula* sec. *Alba*
493–494 (493.5)	Poz-69328	9850 ± 50	11390–11376 (1.5%) 11362–11190 (93.9%)	Four bud scales, seed and needle of *P. abies*

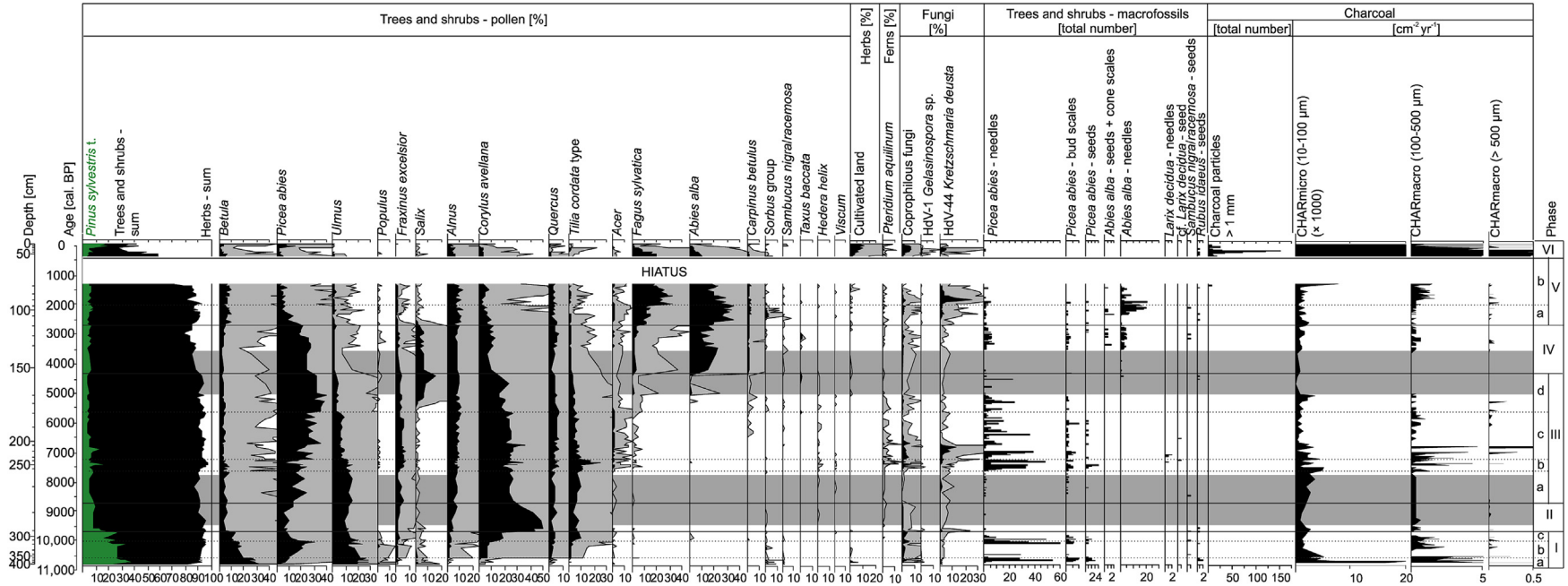


Fig. 3. Forest changes, human impact (pollen percentages) and fire activity. Curves of lighter shades present values exaggerated 10 times. The dark grey bands represent zones with probable deposition gap(s).

agricultural activity (pollen of Cerealia t., *Secale cereale*, *Triticum* t., and *Centaurea cyanus*), (iii) coprophilous fungi sum—as an indicator of grazing activity by herbivores/omnivores and/or potential human pastoral activity (HdV-55A *Sordaria* t., HdV-55B Sordariaceae, HdV-113 *Sporormiella* sp., HdV-112 *Cercophora* sp., HdV-172 *Coniochaeta lignaria*, HdV-169 *Apiosordaria* sp., HdV-205, HdV-368 *Podospora* sp., HdV-261 *Arnium* t., HdV-262 *Arnium imitans* t., and BRN-7), and (iv) *Kretzschmaria deusta*—indicator of tree fungal infections. Bray-Curtis dissimilarity was applied, and the appropriate solution was identified by comparison of the final stress quantities. Statistically significant ($p < 0.05$) environmental variables were fitted using *envfit* procedure with 999 permutations. Analyses were performed using R software (R Development Core Team, 2014) using *vegan* package (Oksanen et al., 2017).

All diagrams presenting pollen, NPPs, plant macrofossils, $CHAR_{micro}$, and $CHAR_{macro}$ (Figs. 3–7) were drawn using the TILIA software (Grimm, 1992). Diagrams were arbitrarily divided into phases based on the main AP taxa, particularly the trends of main curves, and the phases were cross-validated by the CONISS dendrogram (Grimm, 1987; Supplementary Data 1).

4. Results and interpretation

4.1. Absolute chronology and peat accumulation rate

The age-depth model was characterised by a reliable model agreement index ($A_{model} = 60.9\%$) (>60% is a recommended value for the robustness of the model; Bronk Ramsey, 2008). The results also showed that the fragment of the profile dated only by ^{14}C method (400–55 cm) spans the period of ca. 10,730 ± 60–1280 ± 110 cal. BP. The σ error of the modelled age ranged between ca. 20–30 (ca. 7670–7639, 2350–2270, and 1950–1920 cal. BP) and 210–220 years (ca. 8778–8220 cal. BP). The sections representing the period of 9500–7690 cal. BP (0.01–0.011 cm yr^{-1}) and ca. 4940–3550 cal. BP (0.008–0.009 cm yr^{-1}) demonstrated the lowest accumulation rate of deposits, in which probably sedimentary gap(s) occurred. The section representing the period of ca. 10,730–10,570 cal. BP (0.2–0.37 cm yr^{-1}) demonstrated the highest accumulation rate. The age-depth model also revealed that a potential sedimentary gap at a depth of 55 cm reached ca. 900 cal years. The topmost 55 cm of the deposits spans a period of 370–-64 cal. BP. The $AR_{deposits}$ in the topmost 55 cm of deposits ranged between 0.12 and 0.15 cm yr^{-1}. However, this value is tentative because this layer might have originated during run-off events and may represent discontinue deposition.

4.2. Forest vegetation and fire history: pollen, plant macrofossils, micro- and macrocharcoal

4.2.1. Phase I, Pinus–Betula–Ulmus, ca. 10,730–9680 cal. BP

At the beginning of Phase I (subphase Ia: 10,730–10,610 cal. BP), woodlands were dominated by *P. sylvestris* (pollen: 23–37%), *Betula* (21–32%), *Ulmus* (18–28%), and *P. abies* (1.4–9%, 410–6130 grains cm^{-2} yr^{-1}, macrofossils; Fig. 3), and a constant expansion of the latter species was observed. The presence of spruce macrofossils might have been also a result of its occurrence on the surface of the peatland. This time interval was characterised by high fire activity, proved by high values of $CHAR_{micro}$ (but a declining trend from 17,400 to 2800 ch. p. cm^{-2} yr^{-1}) and $CHAR_{macro}$. However, this period witnessed one of the highest fire frequencies in the entire Holocene (4 events/1000 years; Fig. 7). About 10,610–10,030 cal. BP (subphase Ib), *Corylus avellana* (pollen: 5.6–8.3%), *Quercus* (0.8–4.5%), *Alnus* (0.7–2.6%), and *Tilia cordata* (type: 0.5–3.8%) probably appeared in the woodlands (Huntley and Birks, 1983). *P. abies* constantly expanded (from 9 to 30%), whereas *Betula* distinctly declined simultaneously to a decrease in fire activity. *Populus* was an additional component. The period of 10,030–9680 cal. BP (subphase Ic) was characterised by the continuous expansion of *C. avellana* (up to 19%) and *T. cordata* (type: up to 10%), which might have contributed to the retreat of *P. abies*, *P. sylvestris*, and *Ulmus*. Since ca. 9890 cal. BP, *Fraxinus excelsior* probably started to expand (pollen >1%; Huntley and Birks, 1983).

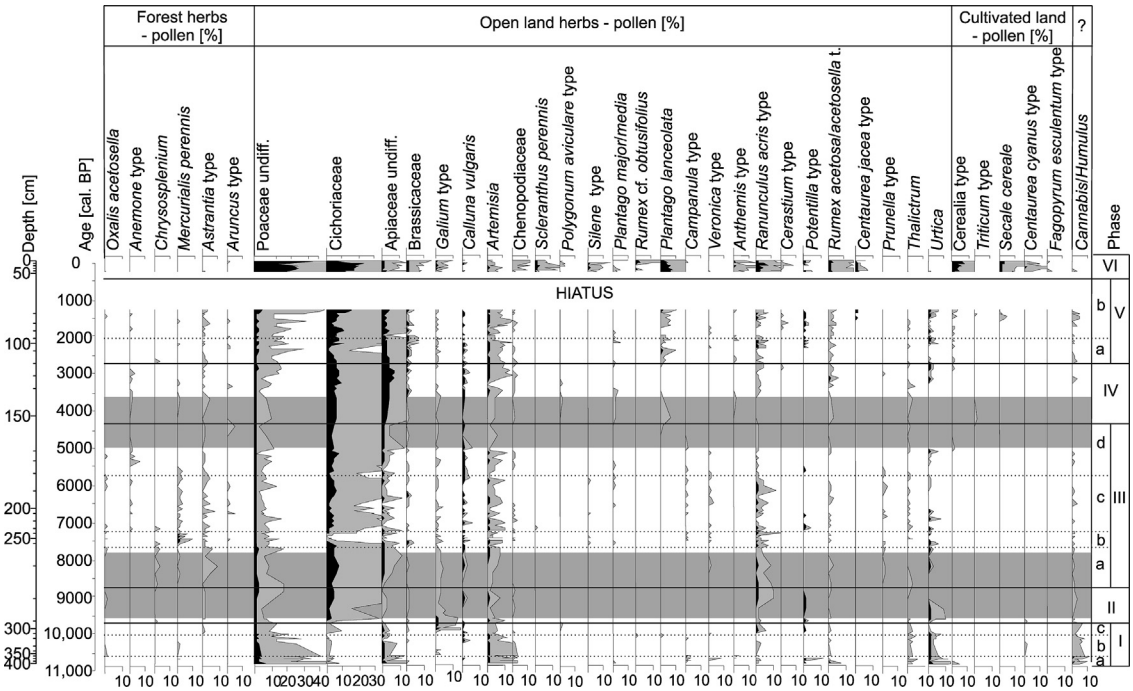


Fig. 4. Herbaceous vegetation. Curves of lighter shades present values exaggerated 10 times. The dark grey bands represent zones with probable deposition gap(s). Abbreviations: t. – type, undiff. – undifferentiated.

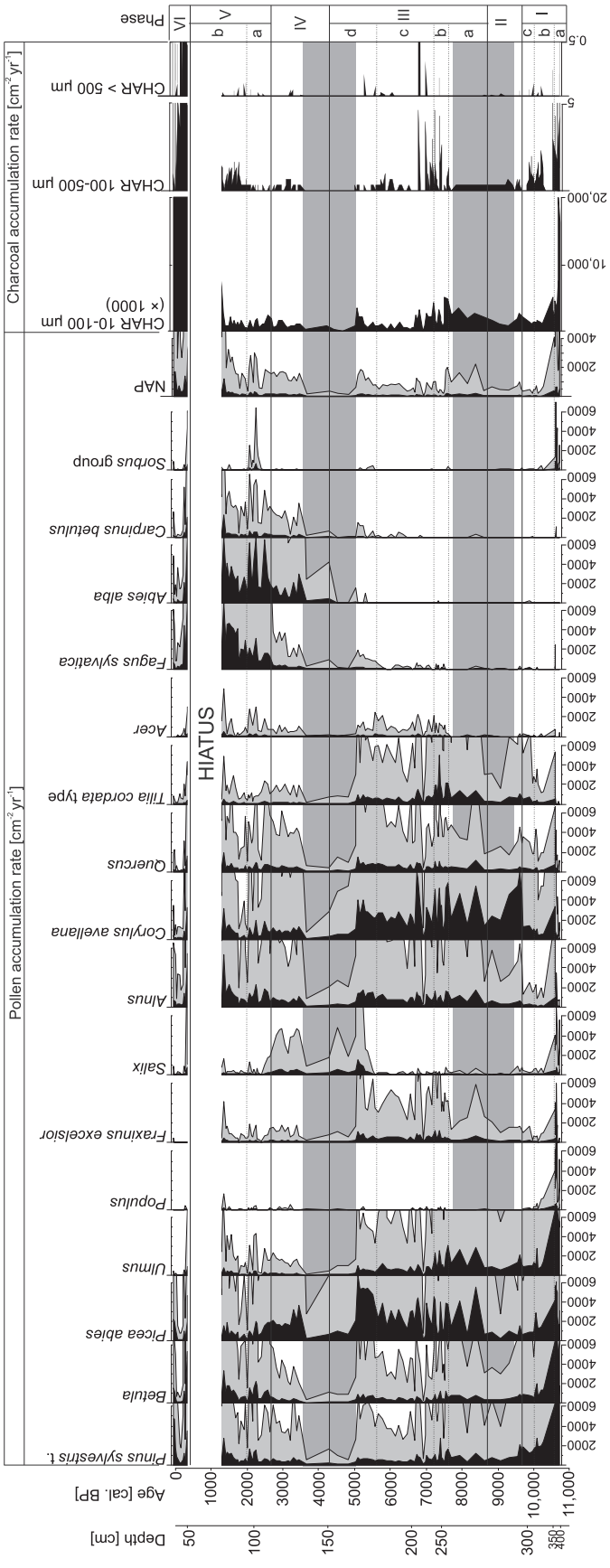


Fig. 5. Pollen accumulation rates versus fire activity. Curves of lighter shades presents values exaggerated 10 times. The dark grey belts represents zones with probable deposition gap(s).

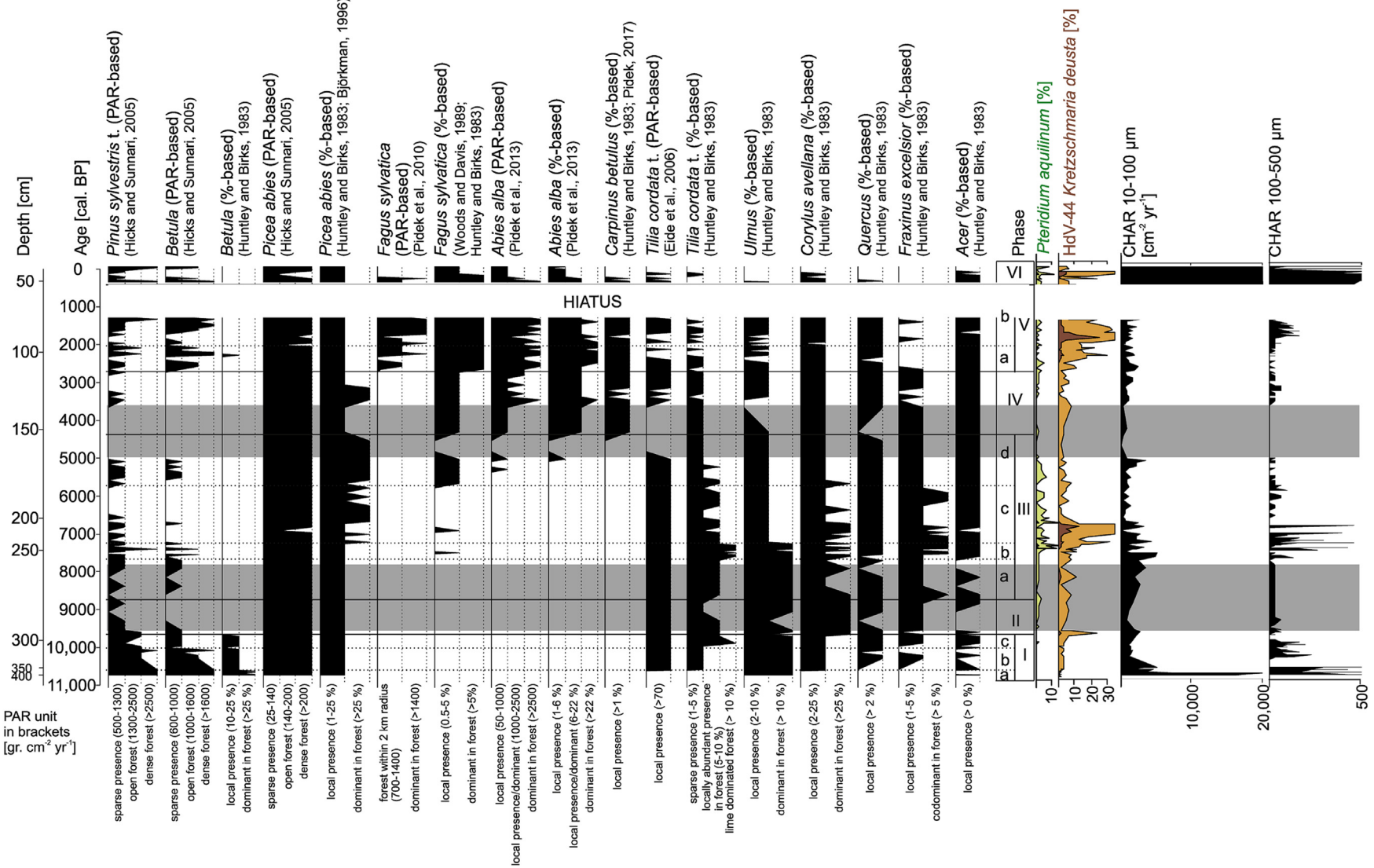


Fig. 6. The population structure selected taxa in forest structure on the basis of percentage and PAR data (Huntley and Birks, 1983; Björkman, 1996; Hicks and Sunnari, 2005; Eide et al., 2006; Pidek, 2017; Pidek et al., 2013). Threshold values are presented in the brackets in the bottom section of the diagram. The dark grey bands represent zones with probable deposition gap(s). Abbreviation: gr. - grains.

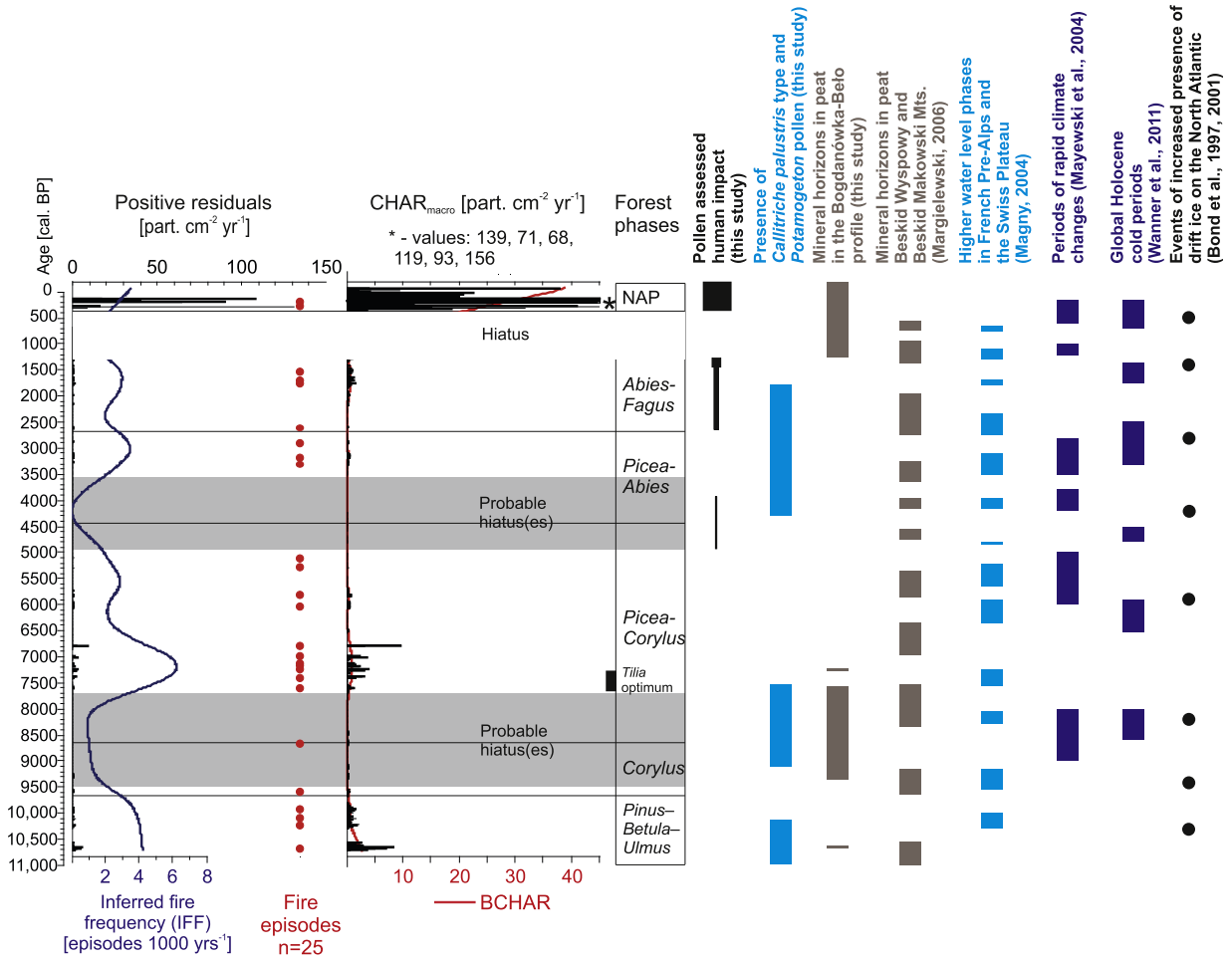


Fig. 7. Fire frequency and reconstructed significant fire events at the B-B site against regional environmental and climate change (Bond et al., 1997, 2001; Magny, 2004; Margielewski, 2006; Mayewski et al., 2004; Wanner et al., 2011). Abbreviation: part. – particles.

4.2.2. Phase II, Corylus; ca. 9680–8730 cal. BP

During this period, *C. avellana* became dominant in local woodlands, which contributed to the retreat of *P. sylvestris* and *Betula*. From ca. 9300 cal. BP, *C. avellana* significantly retreated (from 49 to 33%). During this phase, *P. abies* and *Ulmus* declined, whereas *Alnus* became more frequent. Cichoriaceae (0.6–4.8%) became more frequent, which may indicate the presence of these plants on the surface of peatland. This period was characterised by very low fire frequency (only 1 significant fire event/1000 years), but this value might have been a result of a decreased accumulation rate and/or the presence of depositional gaps in this section of the profile.

4.2.3. Phase III, Picea–Corylus; ca. 8730–4420 cal. BP

At the beginning of subphase IIIa (8730–7650 cal. BP), *P. abies* expanded contributing to *C. avellana* retreat, but this species was still important in the vicinity of the mire (24–28%). *F. excelsior* became a regular component of the local forest; however, it declined at the end of the subphase. During the period of ca. 7650–7270 cal. BP (subphase IIIb), *T. cordata* reached an optimum (type: 8–25%) becoming codominant with *F. excelsior* and *C. avellana*. *Hedera helix* and *Acer* became more frequent. All of this was linked to the fluctuations of *P. abies*, but its pollen accumulation rates (PAR) values still indicated its dominance in the forest (Fig. 6, Hicks and Sunnari, 2005). The declines of *P. abies* were related to the increases in fire activity visible in the values of $CHAR_{micro}$ and $CHAR_{macro}$, which were also seen as an increase in the fire frequency (Fig. 7). The forest gaps were entered by *P. aquilinum*. Next period (subphase IIIc, 7270–5730 cal. BP) was characterised by the dominance of *P. abies*. *T. cordata* and *Ulmus* preliminary retreated and then stabilised their presence during the subphase IIIc. This retreat was related to the first Holocene maximum of *K. deusta* simultaneous to increased fire activity and fire frequency (up to 6 events/1000 years during the period of ca. 7430–6940 cal. BP, representing the highest recorded IFF in the entire profile). *F. excelsior* remained an important forest component (Fig. 6). In the youngest subphase (IIId; ca. 5730–4420 cal. BP), *P. abies* reached an optimum (up to 40%). Simultaneously *F. sylvatica* (0.5–2.1%), and later *A. alba* (0–2.4%), probably became scattered components of the forest. Macrofossils of the latter were identified in the layer corresponding to ca. 5030 cal. BP; however, since ca. 4530 cal. BP it started to occur regularly. Together with the local appearance of *A. alba*, the fire activity was found to be slightly increased, as the values of $CHAR_{micro}$ (ca. 5330–5070 cal. BP) show. At the beginning of subphase IIId, the population of *Ulmus* and *F. excelsior* declined and remained stable during this period. *Salix* (0–16%) probably expanded in the area of the fen.

4.2.4. Phase IV Picea–Abies; ca. 4420–2690 cal. BP

A. alba expanded dynamically and formed forests with *P. abies* (Fig. 6), which retreated from some of its habitats. *Carpinus betulus* (0.6–2.7%) and *F. sylvatica* (1.7–4.6%) probably became stable forest

components (Huntley and Birks, 1983; Woods and Davis, 1989; Pidek, 2017). However, their PAR values do not provide firm evidence of their occurrence (Pidek et al., 2010). At the beginning, the population of *Ulmus* decreased and later stabilised (0.8–2.2%). A similar pattern was detected for *F. excelsior*, *C. avellana*, and *T. cordata*. Furthermore, *H. helix* probably retreated. The increasing values of herb pollen might have been a result of the spread of Cichorioideae and Apiaceae representatives on the surface of the rich fen. *Salix* was still an important component of shrub communities on the fen surface and its outskirts. The fire activity was relatively low but might have been slightly higher (increase in $CHAR_{micro}$ and $CHAR_{macro}$) in the younger part of this subphase from ca. 3560 cal. BP; however, it might be a result of the very low $AR_{deposits}$ (hiatus) in the section of ca. 4940–3550 cal. BP. This corresponds with the lowest reconstructed fire frequency values (<1 event/1000 years; Fig. 7).

4.2.5. Phase V Abies-Fagus; ca. 2690–1280 cal. BP

About 2690–2030 cal. BP (subphase Va), the population of *P. abies* gradually withdrew from the site, as evidenced by decreasing percentages (from 18 to 4.4%), but PAR values still reflected its forest dominance (120–2030 grains cm^{-2} yr^{-1}). *A. alba* reached an optimum proportion in the forest (19–35%), whereas *F. sylvatica* probably became the second important forest component (8.6–14%; Huntley and Birks, 1983; Woods and Davis, 1989). However, PAR values of *F. sylvatica* tentatively confirm this inference (Fig. 6). *Ulmus, F. excelsior*, and *Tilia* became more scattered forest elements. Similarly, *Salix* was less frequent in the fen area. *P. sylvestris* (3.2–8%) and *Betula* (5–10.6%) occurred in more open forest stands or forest gaps. The open habitats might have been temporarily adjusted by humans for agricultural and pastoral activities, which was marked by a more regular presence of Cerealia t. and *Plantago lanceolata* pollen grains. During the first stage of subphase Vb (ca. 2030–1280 cal. BP), the population of *F. sylvatica* reached an optimum in local forests (maximum 32%); however, from ca. 1710 cal. BP, it started to decline gradually. Nonetheless, PAR values revealed quite the opposite trend showing that the population of *F. sylvatica* reached an optimum in the forest during the younger part of subphase Vb. The expansion of *F. sylvatica* progressed along with the constant retreat of *A. alba* (13–28%), which was still codominant in the forest. Local fire activity probably slightly increased which was indicated by an increase in the $CHAR_{macro}$ values from ca. 1820 cal. BP. This was preceded by a distinct increase in the percentages of spores of *K. deusta* (maximum 26%; ca. 1840 cal. BP), which suggests that the local fungal outbreak initiated and/or supported an increase in fire activity. The regular presence of cereal pollen, among which *S. cereale* was detected, from ca. 1510 cal. BP shows a potential increase in local human activity, which might be the cause of the gradual decline in the population of *F. sylvatica* in the younger part of the subphase. *P. abies,* even if showed relatively low pollen percentages (2.7–7.4%), was probably an important forest component, if looking at the PAR values (170–1930 grains cm^{-2} yr^{-1}; Hicks and Sunnari, 2005). *P. sylvestris* and *Betula* probably maintained their populations at a similar level to the previous subphase. The fire frequency during this zone ranged between 1 and 3 events/1000 years with 4 significant fire events recorded.

4.2.6. Phase VI NAP; ca. 370–-64 cal. BP

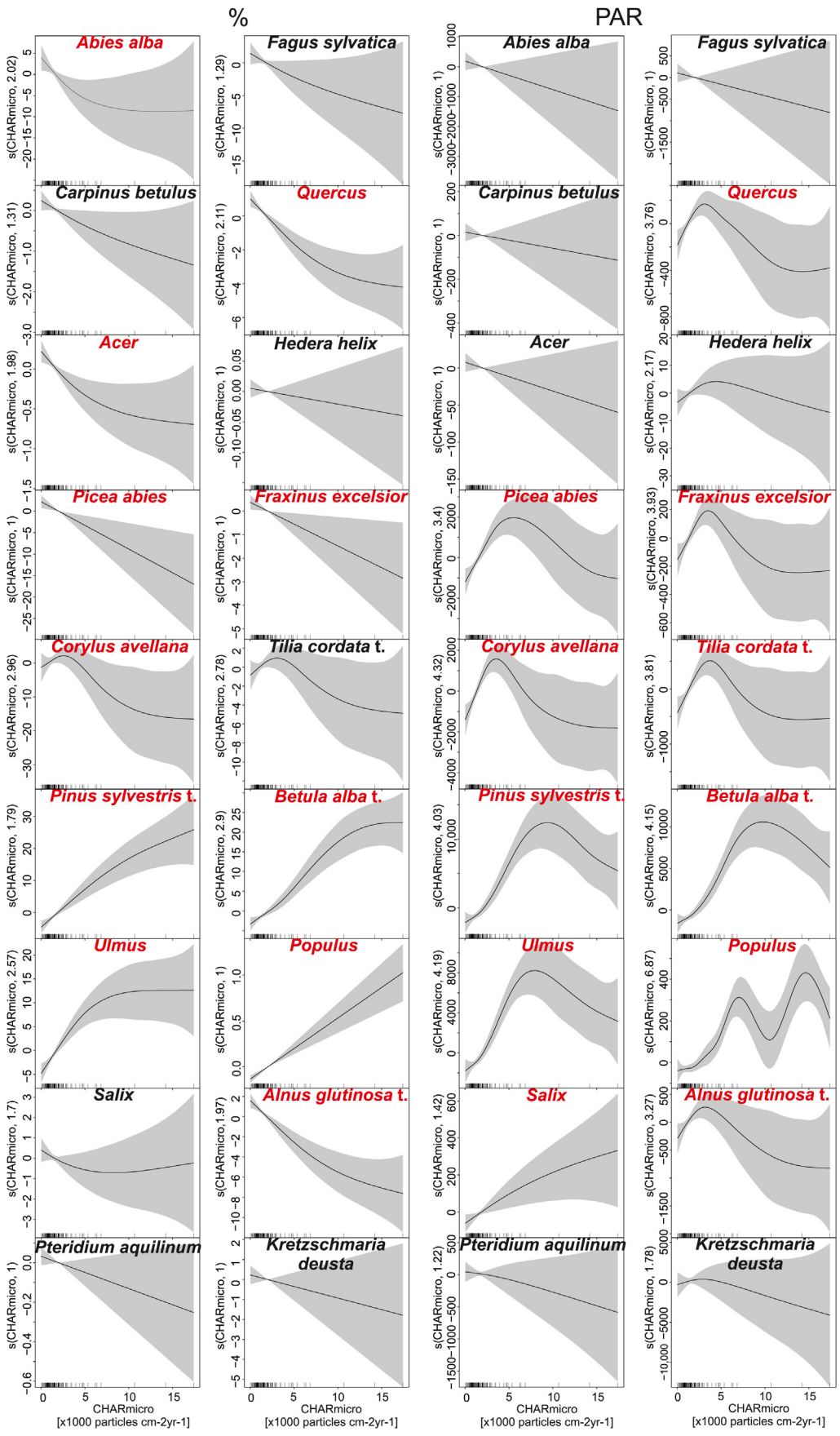
This phase represents the topmost minerogenic sediments when meadow communities developed on the surface of the fen. This is reflected in the high percentages of NAP (41–77%), among which the representatives of Poaceae (12–36%), Cichoriaceae (4.6–23%), Apiaceae (0.4–2.3%), Brassicaceae (0–1.5%), *P. lanceolata* (0.8–7%), *Ranunculus acris* t. (0.8–7.6%), and *Rumex acetosa*/*acetosella* t. (0.9–2.5%) revealed the highest values. The proximity of cultivated fields was highlighted by the optimum of Cerealia t. (0.9–7.6%), *S. cereale* (0.6–2.5%), and *C. cyanus* t. (0–1.8%). Ruderal communities were indicated by a regular presence of *Scleranthus perennis* (0–2.7%), whereas the presence of pasturelands in the fen's vicinity and/or increased pastoral activity directly on the fen's surface was indicated by the increased percentages of coprophilous fungi (0.9–7.1%). This group of fungi was represented by a broad set of taxa: *Sordaria* t. (HdV-55A), *Cercophora* t. (HdV-112), *Sporormiella* (HdV-113), *Apiosordaria* t. (HdV-169), *C. lignaria* (HdV-172), and *Podospora* t. (HdV-368) (van Geel and Aptroot, 2006; Baker et al., 2013). The phase was characterised by very high fire activity as reflected by the values of $CHAR_{micro}$ (27,640–262,720 ch. p. cm^{-2} yr^{-1}), $CHAR_{macro}$ (100–500 μm: 0–217 ch. p. cm^{-2} yr^{-1}, >500 μm: 0–7.7 ch. p. cm^{-2} yr^{-1}), and the regular presence of particles >1 mm in size. The fire frequency revealed an increasing trend from 2 to 3.5 events/1000 years.

4.3. Fire–plants–pathogens relationships

Selected GAMs, in which the strongest relationships between pollen taxa and $CHAR_{micro}$ were identified, are presented in Fig. 8, other GAMs and model parameters are included in Supplementary Data 2. GAM revealed a different pattern in the data (percentages and rate of accumulation). In general, in both cases, the models are the most reliable when the $CHAR_{micro}$ values range between 0 and 7000 ch. p. cm^{-2} yr^{-1} (Fig. 8). The relationship between pollen percentages and $CHAR_{micro}$ values revealed many responses: (i) positive quasi-linear (*Populus*), (ii) negative quasi-linear (*P. abies*, *F. excelsior*, *H. helix*, and *P. aquilinum*), (iii) logarithmic increase (*P. sylvestris* t., *B. alba* t., and *Ulmus*), (iv) exponential decrease (*A. alba*, *F. sylvatica*, *C. betulus*, *Quercus*, *Acer*, and *A. glutinosa* t.), and (v) unimodal (*C. avellana* and *T. cordata* t.). In the case of the PAR and $CHAR_{micro}$ values, GAM revealed mostly unimodal relation in most of the cases, i.e. different from the percentages versus $CHAR_{micro}$ relationships. Among taxa reflecting such type of relationship were *Quercus*, *P. abies*, *F. excelsior*, *P. sylvestris* t., *B. alba* t., *Ulmus*, *A. glutinosa* t., and *Hedera helix* (Supplementary Data 2). Other PAR to $CHAR_{micro}$ relationships were also reflected by (i) quasi-linear decline (*A. alba*, *F. sylvatica*, *C. betulus*, *Acer*, and *P. aquilinum*), (ii) quasi-linear increase (*Salix*), and (iii) bimodal (*Populus*).

Results of TITAN revealed that *Quercus*, *F. excelsior*, *P. abies*, *C. avellana*, *T. cordata* t., and *A. glutinosa* t. showed the strongest negative response (z−) to fire (expressed by $CHAR_{micro}$) (Fig. 9). The threshold values of $CHAR_{micro}$, with respect to significant changes in the patterns in taxa, were identified at the level of ca. >3500 ch. p. cm^{-2} yr^{-1}. *F. sylvatica*, *Acer*, *C. betulus*, *A. alba*, *T. baccata*, and *H. helix* also reflected a negative fire effect, and the most significant for values ca. <2000 ch. p. cm^{-2} yr^{-1}, but with a lower strength of the impact. *P. aquilinum*, which is considered the indicator species of forest clearance (Marrs and Watt, 2006), also revealed the negative feedback to fire. Among the taxa that demonstrated the positive feedback (z+) to $CHAR_{micro}$ were *Ulmus*, *P. sylvestris* t., *Betula alba* t., *Sorbus* group (the weakest effect), and *Populus*. The most unexpected constituent of this group was *Ulmus*, which is a fire-intolerant taxon (Tinner et al., 2000), but in our study, it reflected the strongest positive feedback to fire when values of $CHAR_{micro}$ were ca. 1000 ch. p. cm^{-2} yr^{-1} (i.e. the lowest within the entire group).

The results of NMDS (Fig. 10) were comparable to those of GAM and TITAN. The most significant variables were $CHAR_{micro}$ ($p = 0.001$) and *K. deusta* with cultivated land indicators ($p = 0.009$). Groups of *P. sylvestris* t., *B. alba* t., *Ulmus*, and *Populus* reflecting the Early Holocene woodlands positively correlated to


%
PAR
Abies alba
Fagus sylvatica
Carpinus betulus
Quercus
Acer
Hedera helix
Picea abies
Fraxinus excelsior
Corylus avellana
Tilia cordata t.
Pinus sylvestris t.
Betula alba t.
Ulmus
Populus
Salix
Alnus glutinosa t.
Pteridium aquilinum
Kretzschmaria deusta
s(CHARmicro, 2.02)
s(CHARmicro, 1.29)
s(CHARmicro, 1)
s(CHARmicro, 1.31)
s(CHARmicro, 2.11)
s(CHARmicro, 3.76)
s(CHARmicro, 1.98)
s(CHARmicro, 2.17)
s(CHARmicro, 3.4)
s(CHARmicro, 3.93)
s(CHARmicro, 2.96)
s(CHARmicro, 2.78)
s(CHARmicro, 4.32)
s(CHARmicro, 3.81)
s(CHARmicro, 1.79)
s(CHARmicro, 2.9)
s(CHARmicro, 4.03)
s(CHARmicro, 4.15)
s(CHARmicro, 2.57)
s(CHARmicro, 4.19)
s(CHARmicro, 6.87)
s(CHARmicro, 1.7)
s(CHARmicro, 1.97)
s(CHARmicro, 1.42)
s(CHARmicro, 3.27)
s(CHARmicro, 1.22)
s(CHARmicro, 1.78)
CHARmicro
[x1000 particles cm-2yr-1]

the values of $CHAR_{micro}$. The cultivated land taxa and coprophilous fungi were not correlated with the values of $CHAR_{micro}$ and with each other, which shows the insignificant fire–agriculture–pasture linkage during the period of ca. 10,730–1280 cal. BP. *P. abies*, *C. avellana*, *T. cordata* t., *F. excelsior*, and *Quercus* were more associated with coprophilous fungi and do not correspond to $CHAR_{micro}$. The presence of cultivated land taxa was the most correlated with the increased presence of *K. deusta* (tree pathogen, the significance of variable $p = 0.004$). *F. sylvatica*, *A. alba*, *C. betulus*, and *Sambucus nigra*/*racemosa* were linked to the presence of *K. deusta*. The results of NMDS based on the PAR were characterised by a more negative correspondence between coprophilous fungi, *K. deusta*, cultivated land plants, and $CHAR_{micro}$. Most of the taxa did not change or changed their position only slightly. The most significant variables were $CHAR_{micro}$ ($p = 0.001$) and cultivated land indicators ($p = 0.002$).

5. Discussion

5.1. Problematic palaeoecological archive

5.1.1. Pollen accumulation rates versus percentages – two different views on the same story

Percentage and PAR data, if combined together, reveal some inconsistencies related to the interpretation of population density of particular taxa (Fig. 6). This is especially seen at (i) ca. 10,730–9680 cal. BP when *Betula* was codominant and PAR reflects the more prominent population in comparison with the percentages, (ii) ca. 10,730–1280 cal. BP when $PAR_{P.\ abies}$ indicated the presence of dense forests in contrast to percentages showing mostly the local presence of *P. abies*, (iii) ca. 5730–2690 cal. BP when percentages show the local presence of *F. sylvatica*, whereas $PAR_{F.\ sylvatica}$ points to the lack of *F. sylvatica* in the forest within the radius of 2 km, and (iv) ca. 4940–3550 cal. BP when *T. cordata* was present *in situ* according to the percentages, whereas PAR failed to indicate it. *A. alba* showed similar results as *F. sylvatica,* whose percentages indicated its higher frequency in comparison with PAR. The first two examples might have been caused by the differences in the climate of places from where the B-B palaeorecord and PAR calibration dataset (Hicks and Sunnari, 2005) were retrieved, i.e. southern Poland and northern Finland. Among the factors that may positively influence the pollen productivity are as follows: (i) weather during the former year and a year of pollen production (van der Knaap et al., 2010), (ii) nutrient availability (Phoenix et al., 2012), (iii) forest age (Matthias et al., 2012), and (iv) light penetration through the canopy (Baker et al., 2016). Hence, in the case of Central Europe, PAR thresholds retrieved from northern Finland seems to be better suited for colder periods, stands characterised by poor development of soil and poor availability of the nutrients, when pollen productivity was lower, as Late Weichselian (e.g. Kołaczek et al., 2015). In the B-B profile, the discrepancies between PAR and percentage data of *T. cordata* t., *F. sylvatica* (cases iii and iv) and, to a lesser degree, of *A. alba* are seen in the sections with sedimentary gaps (with strong declines in the accumulation rate; Fig. 6). Even though the age-depth modelling based on densely dated deposits enabled the detection of hiatuses, it cannot provide full information about the exact loss of deposit and specific time interval that is not represented in such section. Therefore, any inferences from accumulation rates calculated for such sections are encumbered by high uncertainties. The strong declines in accumulation rates of proxy data related to declines in deposits' accumulation rate were also distinct in other studies (e.g. Lamentowicz et al., 2015; Kołaczek et al., 2018). Nonetheless, the data regarding the accumulation rates, if calculated independently from each other, may minimise the bias toward the strong increases of single pollen taxa (e.g. due to the presence of anthers in the investigated deposit samples) as it may appear in case of percentage data. So then juxtaposing both type of data may improve the inferences drawn from palaeoecological research.

5.1.2. Climate changes and anthropogenic disturbances "recorded" in hiatuses

Both sections of the peat core with sediment gaps, which influenced PAR data, (i) ca. 9500–7690 cal. BP and (ii) ca. 4940–3550 cal. BP, seem to be connected with global climate changes. The first one overlaps two events of the increased presence of drifted ice in the North Atlantic at ca.9.4 and 8.2 ka. BP (Bond et al., 1997, 2001) and global cold period 8.6–8.0 ka. BP (Wanner et al., 2011) or a global period of rapid climate changes (RCC) ca. 9000–8000 cal. BP (Mayewski et al., 2004). In general, in the Beskid Makowski Mountains and adjacent Beskid Wyspowy Mountains, mineral layers of similar age to the gap(s) at B-B site were also identified (Margielewski, 2006, 2018). This suggests that increased erosion was not only a site-specific event. The presence of representatives of *Callitriche* sp. and *Potamogeton* sp. (ca. 9070–7520 cal. BP) indicates wetter conditions on the B-B fen and at least temporal stagnation of water during the most of the silt deposition period (Fig. 7). The climate-environmental changes related to the 8.2 ka. BP event might have been driving forces for erosion. This event is regarded as the largest abrupt climate change event of the Holocene (e.g. Alley et al., 1997). In Central-Western Europe, higher water level, as a result of wetter conditions, was parallel to this event and/or in a broader context to the 8.6–8.0 ka. BP cold period (Magny, 2004). Moreover, cooler spring and increased availability of moisture were detected during that period (Tinner and Lotter, 2001). In the Eastern Carpathians, dry summers with cold winters characterised this event (Schnitchen et al., 2006; Feurdean et al., 2008a,b), whereas in the Southern Carpathians, decreased temperatures in the growing season, frequent summer droughts, and associated recurrent fire events were recorded (Pál et al., 2016, 2018). Tóth et al. (2015) recognised a decline in mean July temperatures during ca. 8700–8500 cal. BP. Hájková et al. (2016) showed that this decline had a longer duration that spanned the period of ca. 8700–8000 cal. BP in the western part of the Eastern Carpathians. In the White Carpathian Mountains (southwestern part of the Western Carpathians), a steep increase in the rainfall at ca. 8500 cal. BP was preceded by cold and dry events, which was evidenced in the form of calcareous tufa deposits (Dabkowski et al., 2019).

The probable depositional gap(s) at ca. 4940–3550 cal. BP in the B-B deposits overlap (i) 4.2 ka. BP event, (ii) 4.8–4.5 ka. BP (Wanner et al., 2011), and (iii) 4200–3800 cal. BP (Mayewski et al., 2004) (Fig. 7). This layer is not distinctly marked by the presence of the mineral horizon in peat; however, from ca. 4300 cal. BP until 1790 cal. BP the constant presence of *C. palustris* t. pollen was identified indicating wetter conditions at least temporarily on the B-B fen. During the period of ca. 4940–3550 cal. BP (hiatus(es) in B-B) several mineral or illuvial horizons in peat were found in the Beskid Makowski and Beskid Wyspowy Mountains (Margielewski, 2006, 2018), which may confirm some increases in humidity

Fig. 8. Taxa response curves illustrating the relationships between percentages and accumulation rates of selected pollen and spore taxa and $CHAR_{micro}$ – General Additive Models (GAM). The taxa which model of response have significance at the level $p < 0.05$ were marked in red. The grey area shows 95% confidence intervals. For detailed GAM parameters see Supplementary Data 2. Abbreviation: t. – type. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

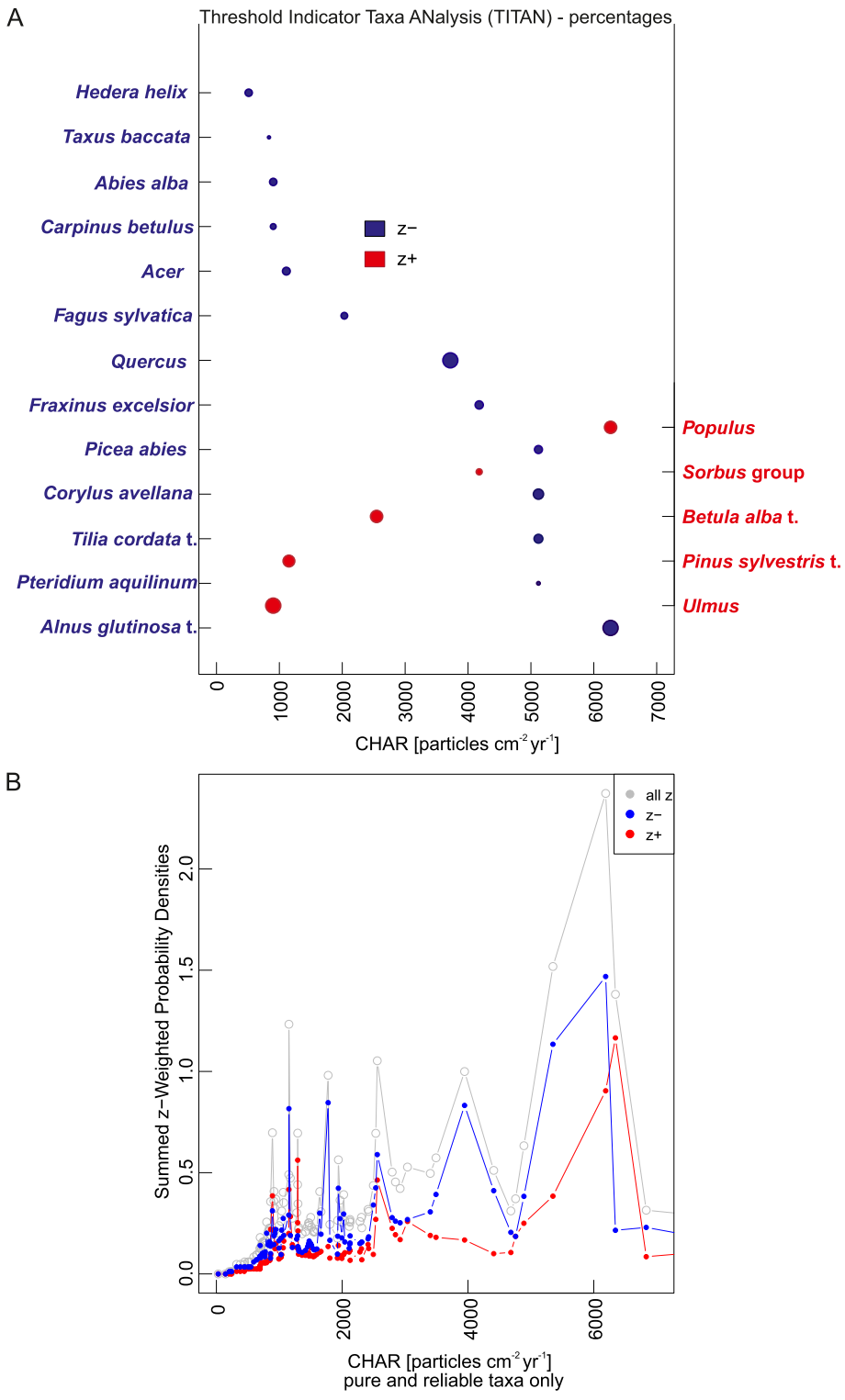
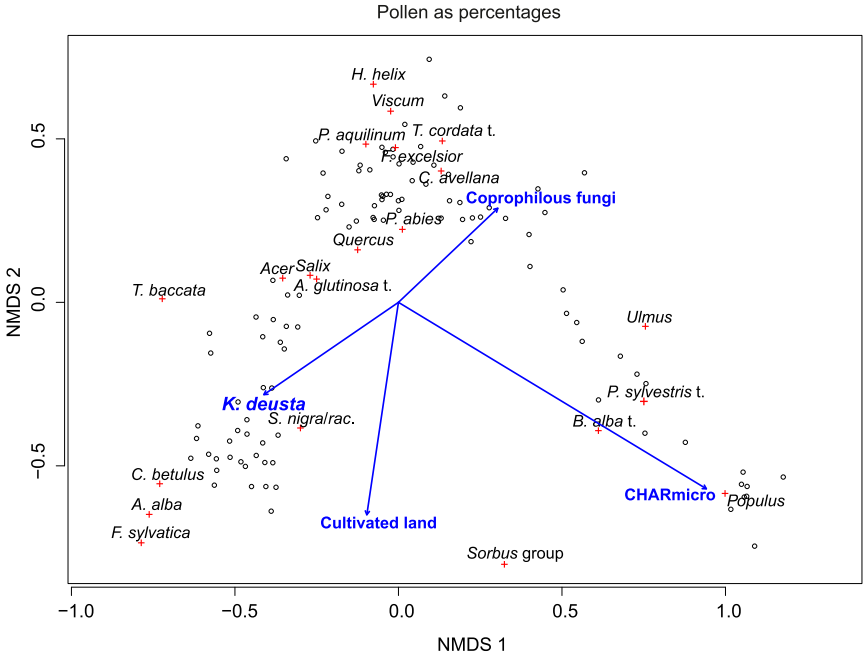


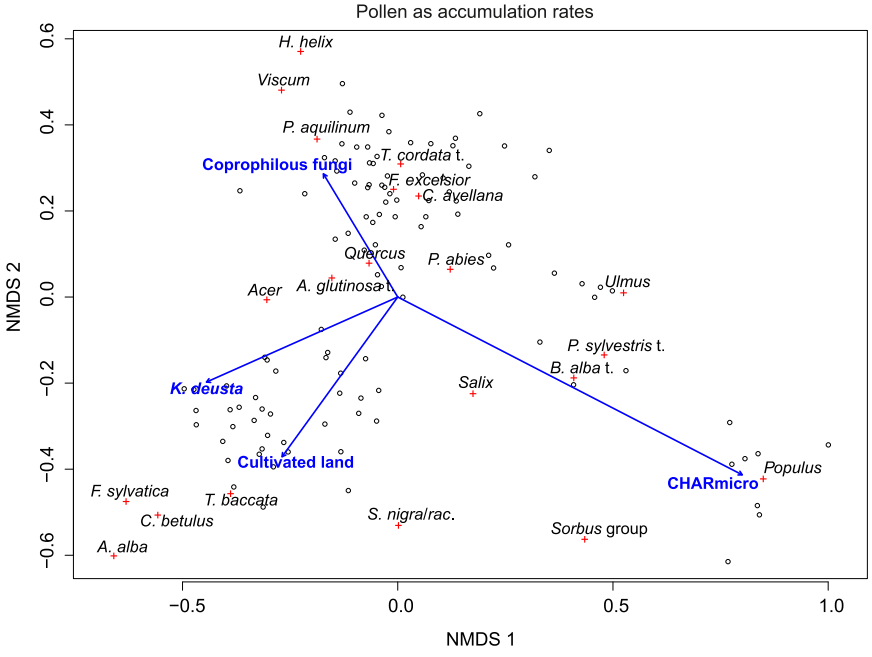
Fig. 9. Critical transition in pollen taxa composition in relation to microcharcoal accumulation rate ($CHAR_{micro}$) – TITAN analysis. A – Pollen taxa composition change along $CHAR_{micro}$ gradient (purity >99%, $p < 0.05$ in >99% bootstraps) showing 5% and 95% bootstrap percentiles; dot colours show the species that either increase (z+) or decrease (z-) in abundance along the $CHAR_{micro}$ gradient. B – TITAN sum(z−) and sum(z+) values along the gradient. Abbreviation: t. – type. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

during this period. These, in consequence, may have contributed to intensive slope processes, like surface outwash, and furtherly to the loss of deposits accumulated in the B-B landslide. This layer in the B-B profile represents the period simultaneous to the one characterised by lower temperatures in summer and high water table (maximum ca. 4200 cal. BP) at ca. 4500–3150 cal. BP in the Rodna



	NMDS 1	NMDS 2	r2	Pr(>r)
CHARmicro	0.88862	-0.45864	0.3965	0.001 ***
K. deusta	-0.91380	-0.40616	0.1156	0.004 **
Copr. fungi	-0.51673	0.85615	0.0546	0.041 *
Cultiv. land	-0.58662	-0.80986	0.1026	0.009 **

Significance levels:
*** - p ≤ 0.001
** - p (0.001-0.01>
* - p (0.01-0.05>



	NMDS 1	NMDS 2	r2	Pr(>r)
CHARmicro	0.85537	-0.51801	0.3972	0.001 ***
K. deusta	0.72595	0.68775	0.0574	0.038 *
Copr. fungi	-0.82471	-0.56556	0.0816	0.015 *
Cultiv. land	-0.14728	-0.98910	0.1414	0.002 **

Significance levels:
*** - p ≤ 0.001
** - p (0.001-0.01>
* - p (0.01-0.05>

Mountains (1360 m a.s.l., Eastern Carpathians; Gałka et al., 2016; Diaconu et al., 2017; Panait et al., 2017). Wet conditions between 4000 and 3550 cal BP were documented in the Valea Morii spring-fed fen ecosystem (NW Romania, 640 m a.s.l., Gałka et al., 2018). Furthermore, in the Eastern Carpathians, in the Dniester River valley, traces of increased fluvial activity were detected at ca. 4000–3900 cal. BP (Kołaczek et al., 2017), whereas higher water level in the lakes was reconstructed for the period of ca. 4150–3950 cal. BP in Central-Western Europe (Magny, 2004).

Hiatus at ca. 1280–370 cal. BP, marked by a distinct boundary between peat and sandy clayey silt in the B-B profile, was probably induced by enhanced human activity and reinforced by climate changes, as this gap covers Little Ice Age (LIA). LIA was characterised generally by colder and wetter climatic conditions in Central and Western Europe (Büntgen et al., 2011; Wanner et al., 2011). The topmost mineral layer revealed the biggest concentration of micro- and macrocharcoal particles and coprophilous fungi, which indicates an important role of fire and pastoral activity as a factor responsible for the deposition of this layer. A rapid retreat of forest communities with increasing frequency of pollen indicators of cultivated land and ruderal habitats suggest human activity as the main factor of fire-induced deforestations. It is not possible to assess the beginning of these catastrophic deforestations because the thickness of peat, which probably was eroded or disrupted during the intensification of slope processes, is unknown. However, these human-induced fire deforestations might be ascribed, with high probability, to the waves of the Wallachian migrations. These shepherd groups came from Balkan Peninsula and colonised the area of the Beskid Makowski Mountains during the 16th century AD (450–350 cal. BP) in search for pastures for their goat, sheep, and cattle flocks. Even though there are no written sources confirming their presence directly at the B-B site, it is highly probable that they were present in that area (Sadowski, 2003; Jawor, 2016b). The Wallachians massively destroyed primaeval forest also by the use of fire (http://www.beskidmaly.pl, Access: December 12, 2019). The rich fens that developed in the Polish Western Carpathians are frequently characterised by a strong decline of accumulation rate of deposits or hiatus(es) in the topmost sections of deposits, at the contact between peat and mineral deposits (Margielewski, 2006, 2018; Margielewski et al., 2010a, 2011; Michczyński et al., 2013; Bucała et al., 2014; Czerwiński et al., in press). The activity of Wallachians was also recorded as an increase in the concentration of microcharcoal particles in peatland from AD 1550 (400 cal. BP) in the Slovenské Rudohorie Mountains (southern Slovakia) but without traces of a decline in the accumulation rate of deposits (Wiezik et al., 2019). Kapustová et al. (2018) claimed that the geomorphological impact of the Wallachian-induced deforestations, land use policy, and climatic deterioration of LIA, caused increased runoff, accelerated sheet erosion, and the delivery of minerogenic deposits to sedimentary sinks such as peat bogs and floodplains. Using the example of the Moravskoslezské Beskydy Mountains (Western Carpathians), Wistuba et al. (2018) showed that Wallachians may have significantly affected land relief and peat deposition. On the basis of our results, it would be far-fetched to draw conclusions about the impact of Wallachians and their settlement on the land relief. Nonetheless, it is noteworthy that the topmost mineral cover is the thickest among mineral insertions in peat from the beginning of the fen functioning, and that the fen still cannot return to the baseline conditions for the accumulation of peat.

5.2. Fire activity and the retreat of the Early Holocene boreal forests (*Pinus–Picea—Betula–Ulmus*)

The woodland communities dominated by *P. sylvestris*, *Betula* sp., *P. abies*, and *Ulmus* sp., with an admixture of *Populus*, were present during the Early Holocene and were characterised by high fire activity. In the nearest sites, in the Beskid Makowski Mountains (650–740 m a.s.l.), a major retreat of woodlands dominated by *Pinus* sp. and *Betula* sp. occurred between 10,500 and 9000 cal. BP (Margielewski, 2006). Unfortunately, there is no data about the effect of fire on the long-term functioning of this type of forests in the Polish Western Carpathians. In the Vihorlat Mountains (Eastern Carpathians, eastern Slovakia; 820 m a.s.l.), a distinct decline of *Pinus* occurred together with the expansion of *Ulmus* (11,650 cal. BP), and then the gradual decline in *Pinus* progressed until ca. 9700 cal. BP along with the expansion of *C. avellana* (Hájková et al., 2016). Similar to B-B site, the period before the expansion of *C avellana* was characterised by high fire activity ($CHAR_{micro}$). The falling of leaves and the accumulation of humus aided *C. avellana* in its competition with *P. sylvestris*, whose seedlings do not thrive when they are covered by leaves (Tallantire, 2002). In the Transylvanian Plain (239 m a.s.l., north-western Romania), the decline of *P. sylvestris* progressed along with the increase in fire activity from ca. 11,000 cal. BP. Similarly, in Šumava National Park (north-western Czech Republic; 1079 m a.s.l.), the retreat of *Pinus sylvestris/mugo* progressed along with the increasing fire frequency; however, the highest value of $CHAR_{micro}$ was detected during the *Pinus sylvestris/mugo* optimum (Carter et al., 2018). In summary, it seems that the expansion of *C. avellana* was a detrimental factor for pine–birch forests in the lower montane zone at the B-B site, which in consequence led to decline in fire activity.

The B-B site revealed positive correspondence between *Ulmus* and high fire activity (Figs. 8–10). *U. glabra* was the most probable species present on this site, because nowadays it is the most widespread elm species seen in the Polish Western Carpathians (Mirek, 2013). Based on the palaeobotanical data, Tinner et al. (2000) qualified *Ulmus glabra* to the group of taxa sensitive to medium and high fire activity. As the study on the oldest part of the B-B profile revealed, the expansion of *Ulmus* was possible despite the constant presence of *P. abies* and *P. sylvestris* at the B-B site (Kołaczek et al., 2017). *Ulmus* probably was only slightly affected by fire because it occurred in wetter habitats, whereas *P. sylvestris* occupied drier ones, which were more affected by fire. Despite the fragility of the young specimens, the thicker bark of older *U. glabra* trees can offer more protection against fire (Thomas et al., 2018 after Stipes and Campana, 1981), so the age structure of elm population might have supported its maintenance under high fire activity. Similar Early Holocene relationship between elm and fire activity was identified in the following cases: (i) Transylvanian Plains ca. 11,500–9000 cal. BP (239 m a.s.l., Feurdean et al., 2013), (ii) the Vihorlat Mountains (Eastern Carpathians) ca. 11,500–9700 cal. BP (820 m a.s.l.; Hájková et al., 2016), and in (iii) the Dniester River valley in western Ukraine ca. 11,160–10,340 cal. BP (ca. 226 m a.s.l.; Kołaczek et al., 2018). Feurdean et al. (2013) suggested that *Ulmus* expanded at the time of increasing fire activity but reached dominance when fire activity was low. Unfortunately, the lack of macrocharcoal data from the beginning of the expansion of *Ulmus* at the B-B site (Kołaczek et al., 2017) and other reference sites from the north-western Carpathians limited our interpretation of this relationship at this moment.

Fig. 10. Non-metric Multidimensional Scaling (NMDS) scattered plot reflecting relationships between fire, human impact, parasitic fungi and selected forest arboreal plants and ferns. Abbreviations: Copr. fungi – coprophilous fungi, Cultiv. land – cultivated land taxa, *S.nigra/rac.* – *Sambucus nigra/racemosa*, t. – type.

5.3. C. avellana and T. cordata versus P. abies

The pollen data revealed that a period between 7650 and 7270 cal. BP was characterised by the most prominent occurrence of *T. cordata* at the B-B site. It was concurrent to a substantial decline in the population of *P. abies* (but not seen in $PAR_{P.\ abies}$ values). Moreover, this optimum occurred simultaneously to the increasing local fire frequency (from 3 to 6 events/1000 years), whereas regional fire activity (inferred from $CHAR_{micro}$) fluctuated at that time. Such short-term expansions of *T. cordata* in the lower montane forest were asynchronous and stimulated by different factors. For instance, Czerwiński et al. (in press) identified it at ca. 4100 cal. BP and the expansion of *T. cordata* was linked to the low fire activity ($CHAR_{micro}$). Tinner et al. (2000) listed *T. cordata* among taxa negatively reacting to medium and high fire activity. On the other hand, *C. avellana* was classified as a species whose abundance is favoured by fire activity and the seeds of which sprouts well after the fire (Tinner et al., 2000; Finsinger et al., 2006). Our study revealed that *C. avellana* reacted positively to fire, up to a certain limit (Figs. 8 and 9). At the B-B site, regular but not severe fires might have played an important role in providing forest gaps resulting in better recruitment of lime seedlings. The seedlings, even if shade-tolerant, require more light in the early years of their life for a successful regeneration (Pigott, 1991). At the northern border of *T. cordata* range, which might be considered an analogue for an altitudinal limit in the mountainous areas for this species, *T. cordata* is considered shade-intolerant due to the difficulty in surviving under the dense canopy of *P. abies* (Seppä et al., 2009). The light requirement of *T. cordata* increases with age, and when the stands are well established, it reacts positively to a gradual opening in the canopy (Kulagin and Shayakhmetov, 2007; De Jaegere et al., 2016). Therefore, fires of low severity may support the competitiveness of *T. cordata*.

Another factor that may contribute to the local dominance of *T. cordata* is fungal infections. Latałowa et al. (2013) suggested that infection by *K. deusta* stimulated the vigorous vegetative development of *T. cordata*. There is also an example of a correspondence between *K. deusta* and *T. cordata* from the White Carpathians (Western Carpathians, Hájek et al., 2016). Nonetheless, the B-B palaeorecord revealed a negative correlation between *T. cordata* and *K. deusta* (Fig. 10). The production and germination of *K. deusta* ascospores require warm climatic conditions between October and March (minimum 10 °C; Wilkins, 1938). Hence, the optimum of this fungus at ca. 6970–6820 cal. BP at the B-B site, may not only reflect the level of pathogenic infection but also indicates milder autumn–winter temperatures. Nonetheless, this interpretation of the presence of *K. deusta* is weakly applicable in this case because mild winters stay in contradiction to the demands of *P. abies*, a dominant forest constituent. Colder winters with increasing snowfall have been suggested as the predominant climatic factor that influenced the expansion of *P. abies* (Bradshaw et al., 2000; Seppä et al., 2005).

5.4. A. alba –F. sylvatica forest expansion

The expansion of *A. alba* at ca. 4420 cal. BP was related to the temporal inundations of the B-B fen, and this species dominated with *P. abies* in the local forest until 2690 cal. BP. In the North-Western Carpathians, both species prefer fresh-to-wet soils with a distinct content of organic matter (Jaworski and Zarzycki, 1983). The expansion of silver fir was simultaneous with an increase in the water table on the fen and tentatively connected with global climatic changes (subchapter 5.1; Fig. 7). The penetration of a well-established spruce forest by *A. alba* might have been stimulated by a slight increase in human activity, as reflected by the presence of single cereal pollen. Margielewski et al. (2010b, 2011) suggested that during periods of disadvantageous environmental conditions, people occupying mountain valleys might have migrated upward and flattened the areas of landslides to support agricultural activity. Kozáková et al. (2011) revealed that the expansion of *A. alba* in the area of Czech Republic took place after some heavier human impact. This species is known as fire-intolerant (Tinner et al., 2000, Tinner et al., 2013), which is also seen in the summary results of our study (Figs. 8 and 9). The fire frequency during the expansion of *A. alba* was identified as 3–4 events/1000 years (excluding the section with hiatus) with a slightly increasing trend in (palaeo-) fire activity over time (Figs. 3 and 7). Similar fire regime parameters have been reconstructed before ca. 4900 cal. BP (below the hiatus(es) section) when *A. alba* probably appeared in the B-B site vicinity, so probably fire frequency did not influence its expansion. Martin and Marks (2006) demonstrated, using the example of *Acer pseudoplatanum*, that shade-tolerant tree species, such as *A. alba* (Ellenberg and Leuschner, 2010), can easily colonise dense, intact resident forests; however, the rate of such invasion is suppressed. The presence of *P. abies* stands may have facilitated the expansion of *A. alba*. A positive effect of Norway spruce on the regeneration of silver fir in fir–spruce–beech stands in southern Poland was observed (Paluch and Jastrzębski, 2013; Dobrowolska et al., 2017). *A. alba* seeds germinate better and seedling survival is higher on moder (mor) humus (Dobrowolska et al., 2017), whose establishment was an effect of a long-term dominance of *P. abies*. Climatic changes might also have influenced the expansion of *A. alba*. Even if it is not a rule, numerous sites in the Polish Western Carpathians and in other Carpathian regions showed the expansion of silver fir simultaneous to the 4.2 ka. BP event (Feurdean and Willis, 2008; Czerwiński et al., in press), reported mostly as cool and wet period (Magny, 2004; Diaconu et al., 2017). At that time, the B-B fen revealed the presence of wetter conditions which lasted until ca. 1790 cal. BP (Fig. 7). *A. alba* is relatively resistant to wind, snow, and ice storms if compared to other dominant tree species such as *P. abies* (Dobrowolska et al., 2017). Hence, the increased frequency and/or severity of catastrophic events related to global climatic changes might have contributed to the selective *P. abies* tree fells. Small-scale disturbances are essential for the regeneration of silver fir stands in Central Europe (Dobrowolska and Veblen, 2008; Kucbel et al., 2010). Concurrently, *A. alba* is less drought-sensitive and more competitive than *F. sylvatica* and *P. abies* (van der Maaten-Theunissen et al., 2013; Tinner et al., 2013). Silver fir, being a very palatable food source in winter, is particularly sensitive to ungulate grazing, which leads to recruitment failure (Tinner et al., 2013; Orman et al., 2018). This might be visible in the results of NMDS that revealed a clear negative correlation between *A. alba* and coprophilous fungi (Fig. 10); however, it is not clearly pointed out by the raw data itself (Fig. 3). Finally, the appearance of forest gaps, also these of fire origin, probably stimulated the expansion of *A. alba* and the simultaneous decreases in ungulate browsing might have supported this process. Because the ecological niche of *A. alba* is not fully recognised (Tinner et al., 2013), it is safer to assume that other factors might have also been responsible for this expansion.

A challenging issue seems to be an explanation of the expansion of *F. sylvatica* that remained a scattered forest component for three millennia until ca. 2690 cal. BP and then it probably limited the occurrence of *P. abies* (Figs. 3, 5 and 6). The expansion of *F. sylvatica* was delayed in comparison with *A. alba* by ca. 1700 years. Both species expanded together in the Polish Western Carpathians, but some time-lags in their appearance were also identified in other palaeorecords (Czerwiński et al., in press). The competition with co-occurring *F. sylvatica* is among the most selective factors for *P. abies* growth (Modrzyński, 2007 and references therein). However, fir, spruce, and beech may coexist without having a significant

competitive advantage over others in mixed stands (Romania; Stancioiu and O'Hara, 2006). A higher proportion of beech trees in forest stands can lessen the silver fir regeneration ability in the Western Carpathians (Janík et al., 2014). This might be seen from ca. 2030 cal. BP when *F. sylvatica* probably contributed to a decline in the population of *A. alba* (Fig. 3). The chronological agreement of *F. sylvatica* expansion with climatic event 2.8 ka. BP or in a broader context with the global cold event 3.3–2.5 ka. BP (Wanner et al., 2011) is a striking finding. One of the driving forces of the 2.8 ka. BP event was the Homeric Solar Minimum that occurred between ca. 2750 and 2550 cal. BP (van Geel et al., 1999). The minimum was characterised by cooling and an increase in wind strength and climate humidity in Western Europe (Martin-Puertas et al., 2012; Engels et al., 2016). As mentioned before, on the B-B fen, rather wet conditions prevailed until ca. 1790 cal. BP (Fig. 7). In the Polish Western Carpathians, mineral horizons in peat suggest stronger runoff at that time (Margielewski, 2006). Cold and wet conditions were identified in the White Carpathians (southern part of the Western Carpathians) at ca. 2800 cal. BP (Dabkowski et al., 2019). In the Eastern Carpathians, the short phase between ca. 3390 and 3030 cal. BP was terminated by a major increase in water tables, culminating at 2725 cal. BP in the Maramureş Mountains (north-western Romania; Schnitchen et al., 2006). The wet stage was identified in the period of ca. 3550–2450 cal. BP in the Feleac Hills (Transylvanian Depression) in north-western Romania (Gałka et al., 2018). However, a dry stage during ca. 2750–1300 cal. BP and warmer July temperatures during ca. 3150–1550 cal. BP were identified in the Rodna Mountains (northern Romania; Diaconu et al., 2017). Palaeorecords from Central and Western European lakes revealed higher water levels (Magny, 2004, Fig. 7). At the B-B site, the expansion of *F. sylvatica* is related to more regular, but not intensive, agricultural activity and a slight increase in fire activity ($CHAR_{micro}$) but without changes in the fire frequency (Fig. 7). Similar to previous studies (e.g. Carter et al., 2018; Rey et al., 2018), our study revealed a clear negative correlation between *F. sylvatica* and the increase in fire activity (Figs. 8–10). As mentioned before, periods of high humidity during the Bronze/Iron age may have forced people to penetrate higher elevations, which in consequence contributed to the appearance of forest gaps. These gaps were later colonised by pioneer trees such as *Betula* (an increase in pollen values) and probably re-colonised by *F. sylvatica* (Fig. 3). The studies on modern autecology suggest that *F. sylvatica* starts to regenerate soon after fire disturbance (Ascoli et al. 2013, 2015; Maringer et al., 2016). European beech life-history traits seem to be compatible with low-frequency fire regimes (e.g., FRI >50 years) and fire events of low to moderate intensity. Single fire event preceding mast year may support beech regeneration in old-growth forests, inducing canopy mortality and partially litter removing, which in turn enhances seed-bed receptivity (Ascoli et al., 2013). Ascoli et al. (2015) revealed that under intermediate and low severity fires, the production of seeds is similar to unburnt sites, whereas the germination of seeds and the emergence of seedlings is higher. The tendency of *F. sylvatica* to expand on abandoned farmlands and/or on postfire areas have been recorded in different places across Europe (Ralska-Jasiewiczowa et al., 2003; Bradshaw and Lindbladh, 2005; Bradshaw et al., 2010; Feurdean et al., 2017b). Nonetheless, it must be stressed that increasing fire activity, above certain levels, is a detrimental factor for the expansion of *F. sylvatica*, which was revealed in this study as well (Figs. 8 and 9).

During the maximum of *F. sylvatica* percentages in the B-B profile, the second maximum of *K. deusta* percentages was recorded. *K. deusta* is strongly invasive and favours beech wood, especially after wounding (Deflorio et al., 2008). A temporal decline in the population of beech during this fungus maximum was detected; however, there were no dramatic changes in the beech population (Fig. 3). An increased human activity, especially coppicing, might have been one of the agents contributing to the expansion of *K. deusta*, as it has been suggested by other studies from Central Europe (Karpińska-Kołaczek et al., 2014; Szal et al., 2015). Nonetheless, *F. sylvatica* is more tolerant to grazing than other broadleaved species of trees and conifers (Packham et al., 2012). The optimum occurrence of *K. deusta*, simultaneous to the expansion of *F. sylvatica*, was also identified in the Western Carpathians (Hájková et al., 2018; Czerwiński et al., in press) and in the Novohradské Mountains (Bobek et al., 2018b). However, there are palaeoecological sites within the Carpathian region, where there is no clear association between *K. deusta* and beech-fir forest expansion (Margielewski et al., 2011; Hájek et al., 2016). Nonetheless, deciphering the interactions between fungal infections, human activity, climate, fires, and forest functioning in the Western Carpathian remains an open issue that requires further investigation.

6. Conclusions

The first complex fire–vegetation reconstruction from the northern part of the Polish Western Carpathians, conducted on the profile from the Bogdanówka-Beło (B-B) site in the Beskid Makowski Mountains, revealed characteristic patterns in the forest development and recognised mechanisms responsible for these processes:

—*Ulmus,* despite the low fire resistance, seems to take advantage of the climate-driven high fire activity during the Early Holocene, which is consistent with the patterns identified in the Eastern and Southern Carpathian regions. At the B-B site, high fire activity at that time was probably induced by the prominent presence of *P. sylvestris* occupying probably drier habitats, different than *Ulmus*, which probably occurred in wetter ones.
—The retreat of *P. sylvestris–Betula* woodlands occurred along with declining fire activity but stable palaeofire frequency (ca. 4 events/1000 years). The rapid expansion of *C. avellana* probably contributed to the final disruption of these woodlands.
—The low magnitude of fire disturbances with the increasing frequency from 4 to 6 fire events/1000 years (high in the scale of the B-B site), supported the competitiveness of *T. cordata* and *C. avellana* in comparison with *P. abies.* It is noteworthy that *T. cordata* is a taxon characterised by low fire resistibility.
—Cooler and wetter conditions probably forced humans to migrate to higher elevations (within lower montane zone). In consequence, it contributed to, at least partly, fire-induced deforestations of small extension which together with appropriate climate conditions stimulated the expansion of *A. alba* from ca. 4420 cal. BP and the expansion of *F. sylvatica* from ca. 2690 cal. BP. The latter phenomenon seems to be linked to the climate changes induced by the Homeric Solar Minimum. However, this mechanism is not a rule for the expansion of *F. sylvatica* in the Polish Western Carpathians. It must be highlighted that an analysis of the entire B-B pollen profile (results of GAM, NMDS, and TITAN), revealed a negative response both of *A. alba* and *F. sylvatica* to fire activity. Nonetheless, minor fire disturbances may be a factor positively influencing the maintenance of forests dominated by *F. sylvatica* and *A. alba* in the lower montane zone.

Our study revealed that absolute chronologies based on high-resolution age-depth modelling enable identification of depositional gaps, which significantly affect the reconstruction of data regarding accumulation rates and disrupt the perception of past environmental processes. These gaps substantially diminished the signal of fire activity, fire frequency and, at least partly, contributed

to discrepancies between timing and plant population structure reconstructed from pollen percentages and pollen accumulation rates. In studied profile, probable hiatuses spanned the following time intervals: (i) ca. 9500–7690 cal. BP, (ii) ca. 4940–3550 cal. BP, and (iii) ca. 1280–370 cal. BP. The first two might have been direct or indirect consequences of global climatic changes at ca. 8.2 and 4.2 ka. BP. Human destructive activity that started along with the Wallachian colonisation (from ca. 450 to 350 cal. BP) changed the accumulation capability of the mire, which failed to regain it.

Authors contribution

PK – an author of pollen and microcharcoal analysis, an age-depth modelling prepared full draft of the manuscript and most of the figures, coordinated study as the grant leader from which the study was financed; WM – discovered the site, an author of lithological analyses, description of the site setting considering geology, geomorphology and hydrology, organised and participated in the core retrieval, MG – carried out plant macrofossil analysis (profile fragment: 400–100 cm) and selected material for ^{14}C AMS dates, MK-K – analysed NPP data, KB – an author of the subfigure 1b, participated in the core retrieval, ML – was responsible for most of the statistical analyses: NMDS, GAM and TITAN, AB – analysed plant macrofossil (profile fragment: 100–0 cm), VZ – an author of preliminary pollen analysis (data published by Margielewski, 2006), which inspired further study, KM – analysed macrocharcoal from contiguous sampling and prepared fire regime statistics. All authors supplemented, commented and corrected draft version and figures provided by PK.

Acknowledgements

Scientific work financed from the budget sources for science activity in 2016–2019, project number 0342/IP1/2016/74. We thank anonymous reviewers who took the effort of reading and commenting on this manuscript, which helped us to improve it. We are grateful to PhD. Eng. Jan Urban (Institute of Nature Conservation PAS in Kraków) for his help with drilling and Małgorzata Suchorska for the preparation of samples to palynological analysis. The LIDAR-derived topographical map of the Bogdanówka site was made under license DIO.DFT.7211.1018.2015_PL_N given to the Institute of Nature Conservation PAS in Kraków. We thank the Palaeoecology Section, Institute of Plant Sciences, University of Bern for providing lab facilities for the macroscopic charcoal analyses.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2019.106137.

References

Alley, R.B., Mayewski, P.A., Sowers, T., Stuiver, M., Taylor, K.C., Clark, P.U., 1997. Holocene climatic instability: a prominent, widespread event 8200 yr ago. Geology 25, 483–486.
Archibald, S., Lehmann, C.E.R., Gómez-Dans, J.L., Bradstock, R.A., 2013. Defining pyromes and global syndromes of fire regimes. In: Proceedings of the National Academy of Sciences of the United States of America, vol. 110, pp. 6442–6447.
Ascoli, D., Castagneri, D., Valsecchi, C., Conedera, M., Bovio, G., 2013. Postfire restoration of beech stands in the Southern Alps by natural regeneration. Ecol. Eng. 54, 210–217.
Ascoli, D., Vacchiano, G., Maringer, J., Bovio, G., Conedera, M., 2015. The synchronicity of masting and intermediate severity fire effects favour beech recruitment. For. Ecol. Manag. 353, 126–135.
Baker, A.G., Bhagwat, S.A., Willis, K.J., 2013. Do dung fungal spores make a good proxy for past distribution of large herbivores? Quat. Sci. Rev. 62, 21–31.
Baker, A.G., Zimny, M., Keczyński, A., Bhagwat, S.A., Willis, K.J., Latałowa, M., 2016. Pollen productivity estimates from old-growth forest strongly differ from those obtained in cultural landscapes: evidence from the Białowieża National Park, Poland. Holocene 26, 80–92.
Berglund, B.E., Ralska-Jasiewiczowa, M., 1986. Pollen analysis and pollen diagrams. In: Berglund, B.E. (Ed.), Handbook of Holocene Palaeoecology and Palaeohydrology. Chichester–New York–Brisbane–Toronto–Singapore. John Wiley & Sons, pp. 455–484.
Baker, M.S., King, R., 2010. A new method for detecting and interpreting biodiversity and ecological community thresholds. Methods Ecol. Evol. 1, 25–37.
Beug, H.-J., 2004. Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Verlag Dr. Friedrich Pfeil, München.
Björkman, L., 1996. Lundqua Thesis. The Late Holocene History of Beech Fagus Sylvatica and Norway Spruce Picea Abies at Stand-Scale in Southern Sweden, vol. 39. Lund University, Department of Quaternary Geology, Lund.
Bobek, P., Šamonil, P., Jamrichová, E., 2018a. Biotic controls on Holocene fire frequency in a temperate mountain forest, Czech Republic. J. Quat. Sci. 33, 892–904.
Bobek, P., Svobodová, H.S., Werchan, B., Švarcová, M.G., Kuneš, P., 2018b. Human-induced changes in fire regime and subsequent alteration of the sandstone landscape of Northern Bohemia (Czech Republic). Holocene 28, 427–443.
Bobek, P., Svobodová-Svitavská, H., Pokorný, P., Šamonil, P., Kuneš, P., Kozáková, R., Abraham, V., Klinerová, T., Švarcová, M.G., Jamrichová, E., Krauseová, E., Wild, J., 2019. Divergent fire history trajectories in Central European temperate forests revealed a pronounced influence of broadleaved trees on fire dynamics. Quat. Sci. Rev. 222, 105865.
Bond, G., Showers, W., Cheseby, M., Lotti, R., Almasi, P., de Menocal, P., Priore, P., Cullen, H., Hajdas, I., Bonani, G., 1997. A pervasive millennial-scale cycle in north Atlantic Holocene and glacial climates. Science 278, 1257–1266.
Bond, G., Kromer, B., Beer, J., Muscheler, R., Evans, M.N., Showers, W., Hoffmann, S., Lotti-Bond, R., Hajdas, I., Bonani, G., 2001. Persistent solar influence on North Atlantic climate during the Holocene. Science 294, 2130–2136.
Bowman, D.M.J.S., Balch, J., Artaxo, P., Bond, W.J., Cochrane, M.A., D'Antonio, C.M., DeFries, R., Johnston, F.H., Keeley, J.E., Krawchuk, M.A., Kull, C.A., Mack, M., Moritz, M.A., Pyne, S., Roos, C.I., Scott, A.C., Sodhi, N.S., Swetnam, T.W., 2011. The human dimension of fire regimes on Earth. J. Biogeogr. 38, 2223–2236.
Bradshaw, R.H.W., Lindbladh, M., 2005. Regional spread and stand-scale establishment of *Fagus sylvatica* and *Picea abies* in Scandinavia. Ecology 86, 1679–1686.
Bradshaw, R.H.W., Holmqvist, B.H., Cowling, S.A., Sykes, M.T., 2000. The effects of climate change on the distribution and management of *Picea abies* in southern Finland. Can. J. For. Res. 30, 1992–1998.
Bradshaw, R., Kito, N., Giesecke, T., 2010. Factors influencing the Holocene history of Fagus. For. Ecol. Manag. 259, 2204–2212.
Bronk Ramsey, C., 1995. Radiocarbon calibration and analysis of stratigraphy: the OxCal program. Radiocarbon 37, 425–430.
Bronk Ramsey, C., 2008. Deposition models for chronological records. Quat. Sci. Rev. 27, 42–60.
Bronk Ramsey, C., Lee, S., 2013. Recent and planned developments of the program OxCal. Radiocarbon 55, 720–730.
Bucała, A., Margielewski, W., Starkel, L., Buczek, K., Zernitskaya, V., 2014. The reflection of human activity in the sediments of Iwankowskie lake from subatlantic phase (polish outer Carpathians). Geochronometria 41 (4), 377–391.
Büntgen, U., Tegel, W., Nicolussi, K., McCormick, M., Frank, D., Trouet, V., Kaplan, J.O., Herzig, F., Heussner, K.-U., Wanner, H., Luterbacher, J., Esper, J., 2011. 2500 Years of European climate variability and human susceptibility. Science 331, 578–582.
Carter, V., 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.
Conedera, M., Tinner, W., Neff, C., Meurer, M., Dickens, A.F., Krebs, P., 2009. Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. Quat. Sci. Rev. 28, 555–576.
Czerwiński, S., Margielewski, W., Gałka, M., Kołaczek, P., 2019. The late Holocene transformations of lower montane forest in the Beskid Wyspowy mountains (western Carpathians, central Europe): a case study from mount Mogielica. in press Palynology. https://doi.org/10.1080/01916122.2019.1617207.
Dabkowski, J., Frodlová, J., Hájek, M., Hájková, P., Petr, L., Fiorillo, D., Dudová, L., Horsák, M., 2019. A complete Holocene climate and environment record for the Western Carpathians (Slovakia) derived from a tufa deposit. Holocene 29, 493–504.
Daniau, A.L., Bartlein, P.J., Harrison, S.P., Prentice, I.C., Brewer, S., Friedlingstein, P., Harrison-Prentice, T.I., Inoue, J., Izumi, K., Marlon, J.R., Mooney, S., Power, M.J., Stevenson, J., Tinner, W., Andrič, M., Atanassova, J., Behling, H., Black, M., Blarquez, O., Brown, K.J., Carcaillet, C., Colhoun, E.A., Colombaroli, D., Davis, B.A.S., D'Costa, D., Dodson, J., Dupont, L., Eshetu, Z., Gavin, D.G., Genries, A., Haberle, S., Hallett, D.J., Hope, G., Horn, S.P., Kassa, T.G., Katamura, F., Kennedy, L.M., Kershaw, P., Krivonogov, S., Long, C., Magri, D., Marinova, E., McKenzie, G.M., Moreno, P.I., Moss, P., Neumann, F.H., Norström, E., Paitre, C., Rius, D., Roberts, N., Robinson, G.S., Sasaki, N., Scott, L., Takahara, H., Terwilliger, V., Thevenon, F., Turner, R., Valsecchi, V.G., Vannière, B., Walsh, M., Williams, N., Zhang, Y., 2012. Predictability of biomass burning in response to climate changes. Glob. Biogeochem. Cycles 26, GB4007.
Davis, M.B., Deevey, E., 1964. Pollen accumulation rates: estimates from late-glacial sediment of Rogers Lake. Science 145, 1293–1295.
Dietze, E., Theuerkauf, M., Bloom, K., Brauer, A., Dörfler, W., Feeser, I., Feurdean, A., Gedminienė, L., Giesecke, T., Jahns, S., Karpińska-Kołaczek, M., Kołaczek, P., Lamentowicz, M., Latałowa, M., Marcisz, K., Obremska, M., Pędziszewska, A., Poska, A., Rehfeld, K., Stančikaitė, M., Stivrins, N., Święta-Musznicka, J., Szal, M.,

Vassiljev, J., Veski, S., Wacnik, A., Weisbrodt, D., Wiethold, J., Vannière, B., Słowiński, M., 2018. Holocene fire activity during low-natural flammability periods reveals scale-dependent cultural human-fire relationships in Europe. Quat. Sci. Rev. 201, 44–56.
Deflorio, G., Johnson, C., Fink, S., Schwarze, F.W.M.R., 2008. Decay development in living sapwood of coniferous and deciduous trees inoculated with six wood decay fungi. For. Ecol. Manag. 255, 2373–2383.
De Jaegere, T., Hein, S., Claessens, H., 2016. A review of the characteristics of small-leaved lime (*Tilia cordata* Mill.) and their implications for silviculture in a changing climate. Forests 7 (3), 56.
Denisiuk, Z., 1995. Ochrona przyrody i krajobrazu. In: Warszyńska, J. (Ed.), Karpaty Polskie. Przyroda, Człowiek I Jego Działalność. Jagiellonian University publ, p. 367.
Denisiuk, Z., Pilipowicz, W., Bieniek, M., Kalemba, A., Mielnicka, B., 1993. Program rezerwatowej ochrony przyrody i krajobrazu polskich Karpat na tle aktualnej sieci obszarów chronionych. Studia Naturae 39, 1–102.
Diaconu, A.-C., Tóth, M., Lamentowicz, M., Heiri, O., Kuske, E., Tanţău, I., Panait, A.-M., Braun, M., Feurdean, A., 2017. How warm? How wet? Hydroclimate reconstruction of the past 7500 years in northern Carpathians, Romania. Palaeogeogr. Palaeoclimatol. Palaeoecol. 482, 1–12.
Dobrowolska, D., Veblen, T.T., 2008. Treefall-gap structure and regeneration in mixed *Abies alba* stands in central Poland. For. Ecol. Manag. 255, 34–69.
Dobrowolska, D., Bončina, A., Klumpp, R., 2017. Ecology and silviculture of silver fir (*Abies alba* Mill.): a review. J. For. Res. 22, 326–335.
Eide, W., Birks, H.H., Bigelow, N.H., Peglar, S.M., Birks, H.J.B., 2006. Holocene forest development along the Setesdal valley, southern Norway, reconstructed from macrofossil and pollen evidence. Veg. Hist. Archaeobotany 15, 65–85.
Ellenberg, H., Leuschner, C., 2010. Vegetation Mitteleuropas mit den Alpen. Ulmer, Stuttgart, Germany.
Engels, S., Bakker, M.A.J., Bohncke, S.J.P., Cerli, C., Hoek, W.Z., Jansen, B., Peters, T., Renssen, H., Sachse, D., van Aken, J.M., van den Bos, V., van Geel, B., van Oostrom, R., Winkels, T., Wolma, M., 2016. Centennial-scale lake-level lowstand at Lake Uddelermeer (The Netherlands) indicates changes in moisture source region prior to the 2.8-kyr event. Holocene 26, 1075–1091.
Feurdean, A., Willis, K.J., 2008. Long-term variability of *Abies alba* in NW Romania: implications for its conservation management. Divers. Distrib. 14, 1004–1017.
Feurdean, A., Klotz, S., Mosbrugger, V., Wohlfarth, B., 2008a. Pollen-based quantitative reconstructions of Holocene climate variability in NW Romania. Palaeogeogr. Palaeoclimatol. Palaeoecol. 260, 494–504.
Feurdean, A., Klotz, S., Brewer, S., Mosbrugger, V., Támas, T., Wohlfarth, B., 2008b. Lateglacial climate development in NW Romania e Comparative results from three quantitative pollen-based methods. Palaeogeogr. Palaeoclimatol. Palaeoecol. 265, 121–133.
Feurdean, A., Spessa, A., Magyari, E.K., Veres, D., Hickler, T., 2012. Trends in biomass burning in the Carpathian region over the last 15,000 years. Quat. Sci. Rev. 45, 111–125.
Feurdean, A., Liakka, J., Vannière, B., Marinova, E., Hutchinson, S.M., Mosburgger, V., Hickler, T., 2013. 12,000-Years of fire regime drivers in the lowlands of Transylvania (Central-Eastern Europe): a data-model approach. Quat. Sci. Rev. 81, 48–61.
Feurdean, A., Veski, S., Florescu, G., Vannière, B., Pfeiffer, M., O'Hara, R.B., Stivrins, N., Amon, L., Heinsalu, A., Vassiljev, J., Hickler, T., 2017a. Broadleaf deciduous forest counterbalanced the direct effect of climate on Holocene fire regime in hemiboreal/boreal region (NE Europe). Quat. Sci. Rev. 169, 378–390.
Feurdean, A., Florescu, G., Vannière, B., Tanţău, I., O'Hara, R.B., Pfeiffer, M., Hutchinson, S.M., Gałka, M., Moskal-del Hoyo, M., Hickler, T., 2017b. Fire has been an important driver of forest dynamics in the Carpathian Mountains during the Holocene. For. Ecol. Manag. 389, 15–26.
Feurdean, A., Vannière, B., Finsinger, W., Warren, D., Connor, S.C., Forrest, M., Liakka, J., Panait, A., Werner, C., Andrič, M., Bobek, P., Carter, V.A., Davis, B., Diaconu, A.-C., Dietze, E., Feeser, I., Florescu, G., Gałka, M., Giesecke, T., Jahns, S., Jamrichová, E., Kajukało, K., Kaplan, J., Karpińska-Kołaczek, M., Kołaczek, P., Kuneš, P., Kupriyanov, D., Lamentowicz, M., Lemmen, C., Magyari, E.K., Marcisz, K., Marinova, E., Niamir, A., Novenko, E., Obremska, M., Pędziszewska, A., Pfeiffer, M., Poska, A., Rösch, M., Słowiński, M., Stančikaitė, M., Szal, M., Święta-Musznicka, J., Tanţău, I., Theuerkauf, M., Tonkov, S., Valkó, O., Vassiljev, J., Veski, S., Vincze, I., Wacnik, A., Wiethold, J., Hickler, T., 2019. Fire risk modulation by long-term dynamics in land cover and dominant forest type in Eastern and Central Europe. Biogeosci. Discuss. https://doi.org/10.5194/bg-2019-260, 2019.
Finsinger, W., Tinner, W., van der Knaap, W.O., Ammann, B., 2006. The expansion of hazel (*Corylus avellana* L.) in the southern Alps: a key for understanding its early Holocene history in Europe? Quat. Sci. Rev. 25, 612–631.
Finsinger, W., Morales-Molino, C., Gałka, M., Valsecchi, V., Bojovic, S., Tinner, W., 2017. Holocene vegetation and fire dynamics at Crveni Potok, a small mire in the Dinaric Alps (Tara National Park, Serbia). Quat. Sci. Rev. 167, 63–77.
Finsinger, W., Fevre, J., Orbán, I., Pál, I., Vincze, I., Hubay, K., Birks, H.H., Braun, M., Tóth, M., Magyari, E.K., 2018. Holocene fire-regime changes near the treeline in the Retezat Mts. (southern Carpathians, Romania). Quat. Int. 477, 94–105.
Florescu, G., Brown, K.J., Carter, V., Kuneš, P., Veski, S., Feurdean, A., 2019. Holocene rapid climate changes and ice-rafting debris events reflected in high-resolution European charcoal records. Quat. Sci. Rev. 222, 105877.
Gałka, M., Tanţău, I., Ersek, V., Feurdean, A., 2016. A 9000 year record of cyclic vegetation changes identified in a montane peatland deposit located in the Eastern Carpathians (Central-Eastern Europe): autogenic succession or regional climatic influences? Palaeogeogr. Palaeoclimatol. Palaeoecol. 449, 52–61.
Gałka, M., Feurdean, A., Hutchinson, S., Milecka, K., Tanţău, I., Apolinarska, K., 2018. Response of a spring-fed fen ecosystem in Central Eastern Europe (NW Romania) to climate changes during the last 4000 years: a high resolution multi-proxy reconstruction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 504, 170–185.
Grimm, E.C., 1992. TILIA/TILIA GRAPH Computer Program. Illinois State Museum.
Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Comput. Geosci. 13, 13–35.
Grosse-Brauckmann, G., 1974. Über pflanzliche Makrofossilien mitteleuropäscher Torfe, II. Weitere Reste (Frühte und Samen, Moose u.a.) und ihre Bestimmungsmölichkeiten. Telma 4, 51–117.
Hájek, M., Dudová, L., Hájková, P., Roleček, J., Moutelíková, J., Jamrichová, E., Horsák, M., 2016. Contrasting Holocene environmental histories may explain patterns of species richness and rarity in a Central European landscape. Quat. Sci. Rev. 133, 48–61.
Hájková, P., Pařil, P., Petr, L., Chattová, B., Matys Grygar, T., Heiri, O., 2016. A first chironomid-based summer temperature reconstruction (13–5 ka BP) around 49°N in inland Europe compared with local lake development. Quat. Sci. Rev. 141, 94–111.
Hájková, P., Jamrichová, E., Petr, L., Dudová, L., Roleček, J., Gálová, A., Dresler, P., Novák, J., Hájek, M., 2018. Persistence of a vegetation mosaic in a peripheral region: could turbulent medieval history disrupt Holocene continuity of extremely species-rich grasslands? Veg. Hist. Archaeobotany 27, 591–610.
Hastie, T.J., Tibshirani, R.J., 1986. Generalized additive models. Stat. Sci. 1, 297–318.
Hicks, S., Sunnari, A., 2005. Adding precision to the spatial factor of vegetation reconstructed from pollen assemblages. Plant Biosyst. 139, 127–134.
Higuera, P.E., Brubaker, L.B., Anderson, P.M., Hu, F.S., Brown, T.A., 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. Ecol. Monogr. 79, 201–219.
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.
Huntley, B., Birks, H.J.B., 1983. An Atlas of Past and Present Pollen Maps for Europe: 0–13000 Years Ago. Cambridge University Press, Cambridge.
Jamrichová, E., Petr, L., Jiménez-Alfaro, B., Jankovská, V., Dudová, L., Pokorný, P., Kołaczek, P., Zernitskaya, V., Čierniková, M., Břízová, E., Syrovátka, V., Hájková, P., Hájek, M., 2017. Pollen-inferred millennial changes in landscape patterns at a major biogeographical interface within Europe. J. Biogeogr. 44, 2386–2397.
Janík, D., Adam, D., Hort, L., Král, K., Šamonil, P., Unar, P., Vrška, T., 2014. Tree spatial patterns of *Abies alba* and *Fagus sylvatica* in the Western Carpathians over 30 years. Eur. J. For. Res. 133, 1015–1028.
Jawor, G., 2016a. Northern extent of settlement on the Wallachian law in medieval Poland. Res Historica 41, 35–49.
Jawor, G., 2016b. Seasonal pastoral exploitation of forests in the area of Subcarpathia in the 15th and 16th century. Balcanica Posnaniensia 23, 175–185.
Jaworski, A., Zarzycki, K., 1983. Ekologia. In: Białobok, S. (Ed.), Jodła Pospolita *Abies alba* MILL. Nasze Drzewa Leśne 4. PWN, Warszawa–Poznań, pp. 317–430.
Kapustová, V., Pánek, T., Hradecký, J., Zernitskaya, V., Hutchinson, S.M., Mulková, M., Bajer, V., 2018. Peat bog and alluvial deposits reveal land degradation during 16th and 17th century colonisation of the Western Carpathians (Czech Republic). Land Degrad. Dev. 29, 894–906.
Karpińska-Kołaczek, M., Kołaczek, P., Stachowicz-Rybka, R., 2014. Pathways of woodland succession under low human impact during the last 13,000 years in northeastern Poland. Quat. Int. 328, 196–212.
Kołaczek, P., Gałka, M., Karpińska-Kołaczek, M., 2015. Succession of arboreal taxa during the Late Glacial in south-eastern Poland: climatic implications. Palaeogeogr. Palaeoclimatol. Palaeoecol. 421, 1–14.
Kołaczek, P., Margielewski, W., Gałka, M., Apolinarska, K., Płóciennik, M., Gąsiorowski, M., Buczek, K., Karpińska-Kołaczek, M., 2017. Five centuries of the Early Holocene forest development and its interactions with palaeoecosystem of small landslide lake in the Beskid Makowski Mountains (Western Carpathians, Poland) — high resolution multi-proxy study. Rev. Palaeobot. Palynol. 244, 113–127.
Kołaczek, P., Gałka, M., Apolinarska, K., Płóciennik, M., Gąsiorowski, M., Brooks, S.J., Hutchinson, S.M., Karpińska-Kołaczek, M., 2018b. A multi-proxy view of exceptionally early postglacial development of riparian woodlands with *Ulmus* in the Dniester River valley, western Ukraine. Rev. Palaeobot. Palynol. 250, 27–43.
Korpel, Š., 1995. Die Urwälder der Westkarpaten. Gustav Fischer Verlag, Stuttgart.
Kozáková, R., Šamonil, P., Kuneš, P., Novák, J., Kočár, P., Kočárová, R., 2011. Contrasting local and regional Holocene histories of *Abies alba* in the Czech Republic in relations to human impact: evidence from forestry, pollen and anthracological data. Holocene 21 (3), 431–444.
Krukar, W., 2004. Wołoskie nazwy topograficzne w Bieszczadach Zachodnich i Beskidzie Niskim. Wierchy 69, 103–113 (in Polish).
Kucbel, S., Jaloviar, P., Saniga, M., Vencurik, J., Klimaš, V., 2010. Canopy gaps in an old-growth fir-beechforest remnant of Western Carpathians. Eur. J. For. Res. 129, 249–259.
Kulagin, A.Y., Shayakhmetov, I.F., 2007. Natural under-canopy regeneration and height-age structure of small-leaved linden (*Tilia cordata* Mill.) undergrowth in water-conservation forests around Pavlovskoe Reservoir, Ufa River. Russ. J. Ecol. 38, 247–252.
Lamentowicz, M., Słowiński, M., Marcisz, K., Zielińska, M., Kaliszan, K., Lapshina, E.,

Gilbert, D., Buttler, A., Fiałkiewicz-Kozieł, B., Jassey, V.E.J., Laggoun-Defarge, F., Kołaczek, P., 2015. Hydrological dynamics and fire history of the last 1300 years in Western Siberia reconstructed from a high-resolution, ombrotrophic peat archive. Quat. Res. 84, 312–325.
Latałowa, M., Pedziszewska, A., Maciejewska, E., Świeta-Musznicka, J., 2013. *Tilia* forest dynamics, *Kretzschmaria deusta* attack, and mire hydrology as palaeoecological proxies for mid-Holocene climate reconstruction in the Kashubian Lake District (N Poland). Holocene 23, 667–677.
Lis, T., Stańczuk, P., 2008. Gminny Program Ochrony Środowiska Na Lata 2008–2011 Z Perspektywą Do 2016. In: Małopolska Agencja Energii I Środowiska Sp. z o.o, Kraków.
Magny, M., 2004. Holocene climate variability as reflected by mid-European lake level fluctuations and its probable impact on prehistoric human settlements. Quat. Int. 113, 65–79.
Marcisz, K., Vanniere, B., Blarquez, O., 2018. Taking fire science and practice to the next level: report from the PAGES global paleofire working group Workshop 2017 in Montreal, Canada – paleofire knowledge for current and future ecosystem management. Open Quat. 4 (1), 1–7. https://doi.org/10.5334/oq.44.
Marcisz, K., Lamentowicz, M., Gałka, M., Colombaroli, D., Adolf, C., Tinner, W., 2019. Responses of vegetation and testate amoeba trait composition to fire disturbances in and around a bog in central European lowlands (northern Poland). Quat. Sci. Rev. 208, 129–139.
Margielewski, W., 2006. Records of the late glacial–Holocene palaeoenvironmental changes in landslide forms and deposits of the Beskid Makowski and Beskid Wyspowy Mts. Area (polish outer Carpathians). Folia Quat. 76, 1–149.
Margielewski, W., 2018. Landslide fens as a sensitive indicator of paleoenvironmental changes since the late glacial: a case study of the Polish Western Carpathians. Radiocarbon 60, 1199–1213.
Margielewski, W., Michczyński, A., Obidowicz, A., 2010a. Records of the Middle- and late Holocene palaeoenvironmental changes in the Pcim-Sucha landslide peat bogs (Beskid Makowski Mts., polish outer Carpathians). Geochronometria 35, 11–23.
Margielewski, W., Krąpiec, M., Valde-Nowak, P., Zernitskaya, V., 2010b. A Neolithic yew bow in the Polish Carpathians. Evidence of the impact of human activity on mountainous palaeoenvironment from the Kamiennik landslide peat bog. Catena 80, 141–153.
Margielewski, W., Kołaczek, P., Michczyński, A., Obidowicz, A., Pazdur, A., 2011. Record of the Meso- and Neoholocene palaeoenvironmental changes in the Jesionowa landslide peat bog (Beskid Sądecki Mts. Polish outer Carpathians). Geochronometria 38, 138–154.
Maringer, J., Conedera, M., Ascoli, D., Schmatz, D.R., Wohlgemuth, T., 2016. Resilience of European beech forests (*Fagus sylvatica* L.) after fire in a global change context. Int. J. Wildland Fire 25 (6), 699–710.
Marlon, J.R., Bartlein, P.J., Daniau, A.L., Harrison, S.P., Maezumi, S.Y., Power, M.J., Tinner, W., Vannière, B., 2013. Global biomass burning: a synthesis and review of Holocene paleofire records and their controls. Quat. Sci. Rev. 65, 5–25.
Marrs, R.H., Watt, A.S., 2006. Biological flora of the British Isles: *Pteridium aquilinum* (L.) Kuhn. J. Ecol. 94, 1272–1321.
Martin, P.H., Marks, P.L., 2006. Intact forests provide only weak resistance to a shade-tolerant invasive Norway maple (*Acer platanoides* L.). J. Ecol. 94, 1070–1079.
Martin-Puertas, C., Matthes, K., Brauer, A., Muscheler, R., Hansen, F., Petrick, C., Aldahan, A., Possnert, G., van Geel, B., 2012. Regional atmospheric circulation shifts induced by a grand solar minimum. Nat. Geosci. 5, 397–401.
Matthias, I., Nielsen, A.B., Giesecke, T., 2012. Evaluating the effect of flowering age and forest structure on pollen productivity estimates. Veg. Hist. Archaeobotany 21, 471–484.
Mayewski, P.A., Rohling, E.E., Stager, C.J., Karlén, W., Maasch, K.A., Meeker, D.L., Meyerson, E.A., Gasse, F., van Kreveld, S., Holmgren, K., Lee-Thorp, J., Rosqvist, G., Rack, F., Staubwasser, M., Schneider, R.R., Steig, E.J., 2004. Holocene climate variability. Quat. Res. 62, 243–255.
Michczyński, A., Kołaczek, P., Margielewski, W., Michczyńska, D.J., Obidowicz, A., 2013. Radiocarbon age-depth modeling prevents misinterpretation of past vegetation dynamics: case study of Wierchomla mire (Polish Outer Carpathians). Radiocarbon 55, 1724–1734.
Mirek, Z., 2013. Altitudinal vegetation belts of the western Carpathians. In: Obidowicz, A., Madeyska, E., Turner, C. (Eds.), Postglacial History of Vegetation in the Polish Part of Western Carpathians Based on Isopollen Maps. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, pp. 15–21.
Modrzyński, 2007. Ecology. In: Tjoelker, M.G., Boratyński, A., Bugała, W. (Eds.), Biology and Ecology of Norway Spruce. Springer, pp. 195–220.
Moore, P.D., Webb, J.A., Collinson, M.E., 1991. Pollen Analysis. Blackwell Scientific Publications, Oxford.
Mráz, P., Ronikier, M., 2016. Biogeography of the Carpathians: evolutionary and spatial facets of biodiversity. Biol. J. Linn. Soc. 119, 528–559.
Obidowicz, A., 2013a. History of palynological studies in the polish part of Western Carpathians. Remarks on pollen analysis at montane sites and the importance of research of modern pollen rain. In: Obidowicz, A., Madeyska, E., Turner, C. (Eds.), Postglacial History of Vegetation in the Polish Part of Western Carpathians Based on Isopollen Maps. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, pp. 23–29.
Obidowicz, A., 2013b. Holocene history of development of zonal forest communities in the Western Carpathians. In: Obidowicz, A., Madeyska, E., Turner, C. (Eds.), Postglacial History of Vegetation in the Polish Part of Western Carpathians Based on Isopollen Maps, W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, pp. 161–163.
Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. Vegan: Community Ecology Package. R Package Version 2.4-2.
Orman, O., Dobrowolska, D., Szwagrzyk, J., 2018. Gap regeneration patterns in Carpathian old-growth mixed beech forests – interactive effects of spruce bark beetle canopy disturbance and deer herbivory. For. Ecol. Manag. 430, 451–459.
Packham, J.R., Thomas, P.A., Atkinson, M.D., Degen, T., 2012. Biological flora of the British Isles: *Fagus sylvatica*. J. Ecol. 100, 1557–1608.
Pál, I., Buczkó, K., Braun, M., Vincze, I., Pálfy, J., Molnár, M., Finsinger, W., Magyari, E.K., 2016. Small-scale moisture availability increase during the 8.2 ka climatic event inferred from biotic proxy records in the South Carpathians (SE Romania). Holocene 26, 1382–1396.
Pál, I., Buczkó, c, Vincze, I., Finsinger, W., Braun, M., Biró, T., Magyari, E.K., 2018. Terrestrial and aquatic ecosystem responses to early Holocene rapid climate change (RCC) events in the South Carpathian Mountains, Romania. Quat. Int. 477, 79–93.
Paluch, J.G., Jastrzębski, R., 2013. Natural regeneration of shade-tolerant *Abies alba* Mill. in gradients of stand species compositions: limitation by seed availability or safe microsites? For. Ecol. Manag. 307, 322–332.
Panait, A., Diaconu, A., Gałka, M., Grindean, R., Hutchinson, S.M., Hickler, T., Lamentowicz, M., Mulch, A., Tanţău, I., Werner, C., Feurdean, A., 2017. Hydrological conditions and carbon accumulation rates reconstructed from a mountain raised bog in the Carpathians: a multi-proxy approach. Catena 152, 57–68.
Pausas, J.G., Ribeiro, E., 2017. Fire and plant diversity at the global scale. Glob. Ecol. Biogeogr. 26, 889–897.
Phoenix, G.K., Emmett, B.A., Britton, A.J., Caporn, S.J.M., Dise, N.B., Helliwell, R., Jones, L., Leake, J.R., Leith, I.D., Sheppard, L.J., Sowerby, A., Pilkington, M.G., Rowe, E.C., Ashmore, M.R., Power, S.A., 2012. Impacts of atmospheric nitrogen deposition: responses of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments. Glob. Chang. Biol. 18 (4), 1197–1215.
Pidek, I.A., 2017. *Carpinus betulus* pollen accumulation rates in Roztocze (SE Poland) in relation to presence of *Carpinus* in Ferdynandovian pollen diagrams. Ecol. Quest. 26, 95–101.
Pidek, I.A., Svitavská-Svobodová, H., van der Knaap, W.O., Noryśkiewicz, A.M., Filbrandt-Czaja, A., Noryśkiewicz, B., Latałowa, M., Zimny, M., Świeta-Musznicka, J., Bozilova, E., Tonkov, S., Filipova-Marinova, M., Poska, A., Giesecke, T., Gikov, A.I., 2010. Variation in annual pollen accumulation rates of *Fagus* along a N-S transect in Europe based on pollen traps. Veg. Hist. Archaeobotany 19, 259–270.
Pidek, I.A., Svitavská-Svobodová, H., Van der Knaap, W.O., Magyari, E., 2013. Pollen percentage thresholds of *Abies alba* based on 13-year annual records of pollen deposition in modified Tauber traps: perspectives of application to fossil situations. Rev. Palaeobot. Palynol. 195, 26–36.
Pigott, C.D., 1991. *Tilia cordata* miller biological flora of the British Isles. J. Ecol. 79, 1147–1207.
R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
Ralska-Jasiewiczowa, M., Nalepka, D., Goslar, T., 2003. Some problems of forest transformation at the transition to the oligocratic/Homo sapiens phase of the Holocene interglacial in northern lowlands of central Europe. Veg. Hist. Archaeobotany 12, 233–247.
Randerson, J.T., Liu, H., Flanner, M.G., Chambers, S.D., Jin, Y., Hess, P.G., Pfister, G., Mack, M.C., Treseder, K.K., Welp, L.R., Chapin, F.S., Harden, J.W., Goulden, M.L., Lyons, E., Neff, J.C., Schuur, E.A.G., Zender, C.S., 2006. The impact of boreal forest fire on climate warming. Science 314, 1130–1132.
Reimer, P., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, F.K., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, M.E., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. IntCal13 and Marine 13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55, 1869–1887.
Rey, F., Gobet, E., Schwörer, C., Wey, O., Hafner, A., Tinner, W., 2018. Causes and mechanisms of synchronous succession trajectories in primeval Central European mixed *Fagus sylvatica* forests. J. Ecol. 107, 1392–1408.
Sadowski, P., 2003. Gmina Pcim. Monografia Geograficzno-Historyczna. Pcim.
Schnitchen, C., Charman, D.J., Magyari, E., Braun, M., Grigorszky, I., Tóthmérész, B., Molnár, M., Szántó, Z., 2006. Reconstructing hydrological variability from testate amoebae analysis in Carpathian peatlands. J. Paleolimnol. 36, 1–17.
Seppä, H., Hammarlund, D., Antonsson, K., 2005. Low-frequency and high-frequency changes in temperature and effective humidity during the Holocene in south-central Sweden: implications for atmospheric and oceanic forcings of climate. Clim. Dyn. 25, 285–297.
Seppä, H., Alenius, T., Bradshaw, R.H.W., Giesecke, T., Heikkilä, M., Muukkonen, P., 2009. Invasion of Norway spruce (*Picea abies*) and the rise of the boreal ecosystem in Fennoscandia. J. Ecol. 97, 629–640.
Skrzydłowski, T., 2019. Lasy Pierwotne Regla Dolnego. http://www.poznajtatry.pl/?strona,doc,pol,glowna,1386,0,161,1,1386,ant.html. (Accessed 11 June 2019).
Stancioiu, P.T., O'Hara, K.L., 2006. Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania. Eur. J. For. Res. 125, 151–162.
Stipes, R., Campana, R.J., 1981. Compendium of Elm Diseases. The American Phytopathological Society, St. Paul, MN.
Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. Pollen

Spores 13, 615–621.
Słowiński, M., Lamentowicz, M., Łuców, D., Barabach, J., Brykała, D., Tyszkowski, S., Pieńczewska, A., Śnieszko, Z., Dietze, E., Jażdżewski, K., Obremska, M., Ott, F., Brauer, A., Marcisz, K., 2019. Paleoecological and historical data as an important tool in ecosystem management. J. Environ. Manag. 236, 755–768.
Szal, M., Kupryjanowicz, M., Wyczółkowski, M., 2015. Anthropogenic transformation of the vegetation in the immediate vicinity of the settlement complex at Poganowo (Mrągowo Lakeland, NE Poland). Stud. Quat. 32 (1), 19–29.
Szwagrzyk, J., Holeksa, J., 2004. Żyzne buczyny górskie. In: Herbich, J. (Ed.), Lasy I Bory. Poradniki Ochrony Siedlisk I Gatunków Natura 2000 – Podręcznik Metodyczny. Ministerstwo Środowiska, Warszawa, pp. 62–70. T. 5.
Tallantire, P.A., 2002. The early-Holocene spread of hazel (*Corylus avellana* L.) in Europe north and west of the Alps: an ecological hypothesis. Holocene 12, 81–96.
Thomas, P.A., Stone, D., La Porta, N., 2018. Biological flora of the British Isles: *Ulmus glabra*. J. Ecol. 106, 1724–1766.
Tinner, W., Hu, F.S., 2003. Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. Holocene 13, 499–505.
Tinner, W., Colombaroli, D., Heiri, O., Henne, P.D., Steinacher, M., Untenecker, J., Vescovi, E., Allen, J.R.M., Carraro, G., Conedera, M., Joos, F., Lotter, A.F., Luterbacher, J., Samartin, S., Valsecchi, V., 2013. The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. Ecol. Monogr. 83, 419–439.
Tinner, W., Conedera, M., Gobet, E., Hubschmid, P., Wehrli, M., Ammann, B., 2000. A palaeoecological attempt to classify fire sensitivity of trees in the southern Alps. Holocene 10, 565–574.
Tinner, W., Lotter, A.F., 2001. Central European vegetation response to abrupt climate change at 8.2 ka. Geology 29, 551–554.
Tobolski, K., 2000. Przewodnik Do Oznaczania Torfów I Osadów Jeziornych. Vademecum Geobotanicum. Wydawnictwo Naukowe PWN, Warszawa.
Tóth, M., Magyari, E.K., Buczkó, K., Braun, M., Panagiotopoulos, K., Heiri, O., 2015. Chironomid-inferred Holocene temperature changes in the south Carpathians (Romania). Holocene 25, 569–582.
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 complexity of climatic control on pollen productivity in Europe and the Caucasus. Veg. Hist. Archaeobotany 19, 285–307.
van der Maaten-Theunissen, M., Kahle, H.-P., van der Maaten, E., 2013. Drought sensitivity of Norway spruce is higher than that of silver fir along an altitudinal gradient in southwestern Germany. Ann. For. Sci. 70, 185–193.
van Geel, B., Aptroot, A., 2006. Fossil ascomycetes in Quaternary deposits. Nova Hedwig. 82, 313–329.
van Geel, B., Raspopov, O.M., Renssen, H., van der Plicht, J., Dergachev, V.A., Meijer, H.A.J., 1999. The role of solar forcing upon climate change. Quat. Sci. Rev. 18, 331–338.
Vannière, B., Blarquez, O., Rius, D., Doyen, E., Brücher, T., Colombaroli, D., Connor, S., Feurdean, A., Hickler, T., Kaltenrieder, P., Lemmen, C., Leys, B., Massa, C., Olofsson, J., 2016. 7000-year human legacy of elevation-dependent European fire regimes. Quat. Sci. Rev. 132, 206–212.
Wanner, H., Solomina, O., Grosjean, M., Ritz, S.P., Jetel, M., 2011. Structure and origin of Holocene cold events. Quat. Sci. Rev. 30, 3109–3123.
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, Volume 3: Terrestrial, Algal, and Siliceous Indicators. Kluwer, Dordrecht, pp. 75–97.
Wiezik, M., Hájková, P., Jamrichová, E., Hrivnák, R., Hájek, M., 2019. Pre-industrial composition of woodlands and modern deforestation events in the southern part of the Western Carpathians. Rev. Palaeoebot. Palynol. 260, 1–16.
Wilkins, W.H., 1938. Studies in the genus *Ustulina*. III. Spores – germination and infection. Trans. Br. Mycol. Soc. 22, 47–93.
Wistuba, M., Sady, A., Poręba, G., 2018. The impact of Wallachian settlement on relief and alluvia composition in small valleys of the Carpathian Mts. (Czech Republic). Catena 160, 10–23.
Wood, S.N., 2006. Generalized Additive Models: an Introduction with R. CRC/Chapman & Hall, Boca Raton.
Woods, K.D., Davis, M.B., 1989. Palaeoecology of range limits: beech in Upper Peninsula of Michigan. Ecology 70, 681–696.