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The Last Glacial and Holocene history of mountain woodlands in the southern part of the Western Carpathians, with emphasis on the spread of *Fagus sylvatica*

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ABSTRACT
The Western Carpathians have recently been examined in several palaeoecological studies. However, some of their parts remain underexplored in terms of the Holocene history of mountain woodlands. We analysed an 8000-year-old peat sequence from the southern part of the Western Carpathians (the Bykovo site) for pollen, needles and stomata, and reviewed the data on the occurrence and spread of beech since the Last Glacial times in order to put results from Bykovo into the context of the whole Western Carpathians. For pre-industrial times, we reconstructed mixed beech–fir or beech–fir–spruce woodlands in zonal habitats, noble hardwood woodlands on screes, and spruce woodlands in peaty and wet habitats. A meta-analysis of available pollen data for beech revealed that a few sites in Pannonia and on the southern Carpathian fringes reached beech pollen abundances exceeding 0.5% at the very beginning of the Holocene (12–10 cal BP). Moreover, the pattern of reaching greater pollen abundance limits showed a clear south-to-north gradient starting in the Pannonian lowland. Therefore, the direction of the spread of beech based on pollen abundances and the absence of beech macrofossil evidence during the Last Glacial Maximum do not support local glacial refugia of beech directly in the Western Carpathians. The timing of local beech occurrence (empirical pollen limit of 1.4–2%) and its expansion (rational pollen limit of up to 5%) at the Bykovo site fits well this gradual spread of beech from the south. The first period of beech spread in the Bykovo area around 6250 cal BP coincides well with the period of increased precipitation between 6100 and 6800 cal BP, as reconstructed by different proxies (e.g. stable isotopes) for the Western Carpathians.

KEYWORDS
Beech expansion; climazonal woodland; Middle Holocene; pollen analysis; Slovakia

1. Introduction

The Western Carpathians are an important interface between biogeographically contrasting European regions like the Pannonian lowland, the Hercynian Mountains and lowlands lying to the north-east (Bálint et al. 2011). They include many mountain ranges with a great proportion of typical mountain woodland vegetation such as beech, fir–beech and climazonal spruce woodlands (Korpel 1995). One way to better understand the current vegetation composition and relationship between human societies and their environment is to look at historical patterns in palaeoceological records (Tanţău et al. 2011; Feurdean et al. 2013). The Holocene history of woodlands in the mountain ranges of the Western Carpathians (with elevations greater than 800 m above sea level) has been described in several palaeoecological studies carried out over the past century (e.g. Jankovská 1984, 1988; Krupinsky 1984; Krippel 1986; Rybníčková and Rybníček 1989; Obidowicz 1996) and this research has intensified in the last two decades (e.g. Rybníčková and Rybníček 2006; Jankovská and Pokorný 2008; Rybníček and Rybníčková 2009; Pánek et al. 2010; Petr 2015; Jamrichová, Petr et al. 2017). The results have revealed great variety in the composition of climazonal mountain woodlands during the second half of the Late Holocene. Beech woodlands have been reconstructed for the mountain ranges on the southern fringes of the Western Carpathians (e.g. Rybníček and Rybníčková 2008; Petr 2015; Gálová et al. 2016), fir–beech woodlands have been reconstructed for their north-western and north-eastern parts (Rybníček and Rybníčková 2002; Wacnik et al. 2016), and spruce woodlands have been recorded strictly in the High Tatra Mountains and basins adjacent to them (Rybníčková and Rybníček 2006; Jankovská and Pokorný 2008; Hájková et al. 2015). All the mentioned palaeosequences come from the Outer Western Carpathians, which are mostly built of flysch bedrock, or from intermountain basins with a continental-like climate. Some areas that could be

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crucial for understanding the present-day distribution and diversity of Western Carpathian woodlands are only poorly represented, or have been studied using old methodologies without radiocarbon dating (Krippel 1986).

Recently, multiple palaeoecological studies have brought interesting clues about potential glacial refugia of some tree taxa. They suggest an Early Holocene expansion of spruce, which often occurred during the Last Glacial times, synchronous with the appearance or spread of noble hardwood trees in basins and adjacent uplands. These temperate tree species (e.g. oak, lime, elm or ash) might therefore have spread from northern glacial microrefugia located directly in or close to the Western Carpathians, as suggested by authors of local studies (Petr et al. 2013; Jamrichová et al. 2014; Hájek et al. 2016; Jamrichová, Petr et al. 2017; Juřičková et al. 2017). Further synthetical studies have suggested potential northern microrefugia also for beech (Magri et al. 2006; Bhagwat and Willis 2008; Willner et al. 2009; Saltré et al. 2015), albeit with a certain degree of doubt. Their results, however, stem mainly from missing evidence of beech from the Last Glacial Maximum (LGM), when the macroclimate was harshest (Jamrichová, Petr et al. 2017). Moreover, it is not clear whether the colonization process started from the south or from multiple areas, suggesting micorerefugia in suitable microhabitats scattered throughout the whole mountain chain (Magri 2008; Bradshaw et al. 2010). Moreover, palaeoenvironmental sequences from mountains close to which the occurrence of glacial microrefugia is assumed (Krippel 1971; Ložek 2006, 2009; Juřičková et al. 2014) are still missing. This is especially true for the Slovenské rudohorie Mountains, the most extensive mountain range of the Western Carpathians, for which only relatively young sequences have been published (Wiezik et al. 2019). This palaeoecologically almost unexplored part of Slovakia could be an important source of knowledge about the development of mountain woodlands, for the following reasons: (i) this area differs in numerous environmental parameters (e.g. climatic and geological) from the rest of the Western Carpathians, and (ii) the area is in close contact with mid-elevation mountains around the Carpathian/Pannonian interface, which could be important for both the postglacial expansion of deciduous woodlands from the south (Willis et al. 2000; Gardner 2002) and the survival of strictly woodland species during the LGM (Ložek 2006, 2009; Juřičková et al. 2014).

The present study fills an important gap in our knowledge about the Holocene vegetation history of the Western Carpathians using modern palaeoecological methods. We carried out a pollen analysis of an 8000-year-old peat deposit with the aim to reconstruct the development, composition and dynamics of mountain woodlands in the southern part of the Western Carpathians. Specifically, we asked whether Middle (8200–4200 cal BP) and Late Holocene (4200 cal BP–Present; Walker et al. 2012) pollen spectra differ from spectra reported from other regions of the Western Carpathians, especially in terms of the representation of spruce and beech–fir woodlands. In addition, considering the close proximity of the Bykovo profile to mountains where glacial microrefugia for temperate trees have been assumed to be located, we also asked whether there is a difference in the timing of the migration process of beech between southern and more northern areas within the Western Carpathians. To this end, we have compiled data about the timing of the appearance and expansion of beech in the Western Carpathians and southerly parts of the Carpathian mountain chain to reveal whether there is any general pattern in beech migration that might corroborate or challenge the hypothesis of northern glacial microrefugia.

2. Material and methods

2.1. Study site

The study site is a fen (3.21 ha, elevation 1053 m; co-ordinates: 48°35′9.88″N, 19°40′29.36″E) situated in the southern part of central Slovakia, in the Slovenské rudohorie Mountains within the Bykovo Massif (Figure 1). The fen is located on a plateau between two hills. To the east and south, the plateau is divided by several small valleys with abrupt slopes (with a maximum slope angle of 40°) leading to the Ipel River valley. The geological substrate is formed by granitoids and granodiorites, which are covered with eluvio-diluvial sediments. The soils of the adjacent slopes are mainly dystric cambisols; however, at the site there is a haplic histosol with a variable organic peat horizon at a depth of between 30 and 100 cm. The climate is moderately cool and humid with cold winters. The mean annual temperature is between 2 and 4 °C (average in July between 12 and 14 °C), and the annual precipitation varies from 900 to 1000 mm (Miklós 2002).

The vegetation of the study site is classified as poor fens of the *Sphagno–Caricion canescentis* Passarge (1964) 1978 alliance and alder-dominated woodlands of the *Piceo abietis–Alnetum glutinosae* Mráz 1959 association.

2.2. Field sampling and pollen analyses

The sediment was cored using a gouge auger (100 × 6 cm) and described stratigraphically in the field (Table 1). The profile was 100 cm long and was analysed for pollen at 2-cm intervals. For 1 cm^3 of peat, standard acetolysis was performed. Samples that contained some silicate material were pre-treated with concentrated hydrofluoric acid for 24 hours. At least 500 terrestrial pollen grains were counted per sample. Pollen was identified using a reference collection, a pollen key (Beug 2004) and a pollen atlas (Reille 1998).

The percentage pollen diagram was based on the total sum of arboreal and non-arboreal pollen of terrestrial herbs (AP + NAP = 100%). Percentages of local pollen taxa and spores (*Alnus*, *Salix*, Cyperaceae, *Caltha* t., *Equisetum*, *Lycopodium* undiff., Polypodiaceae, *Polypodium vulgare*, *Pteridium aquilinum*, *Bryales* and *Sphagnum*) were related to the total sum (TS) = AP + NAP + local taxa and spores = 100%. Those pollen taxa not shown in the pollen diagram because of their low abundance are listed in Supplementary material Table S1.

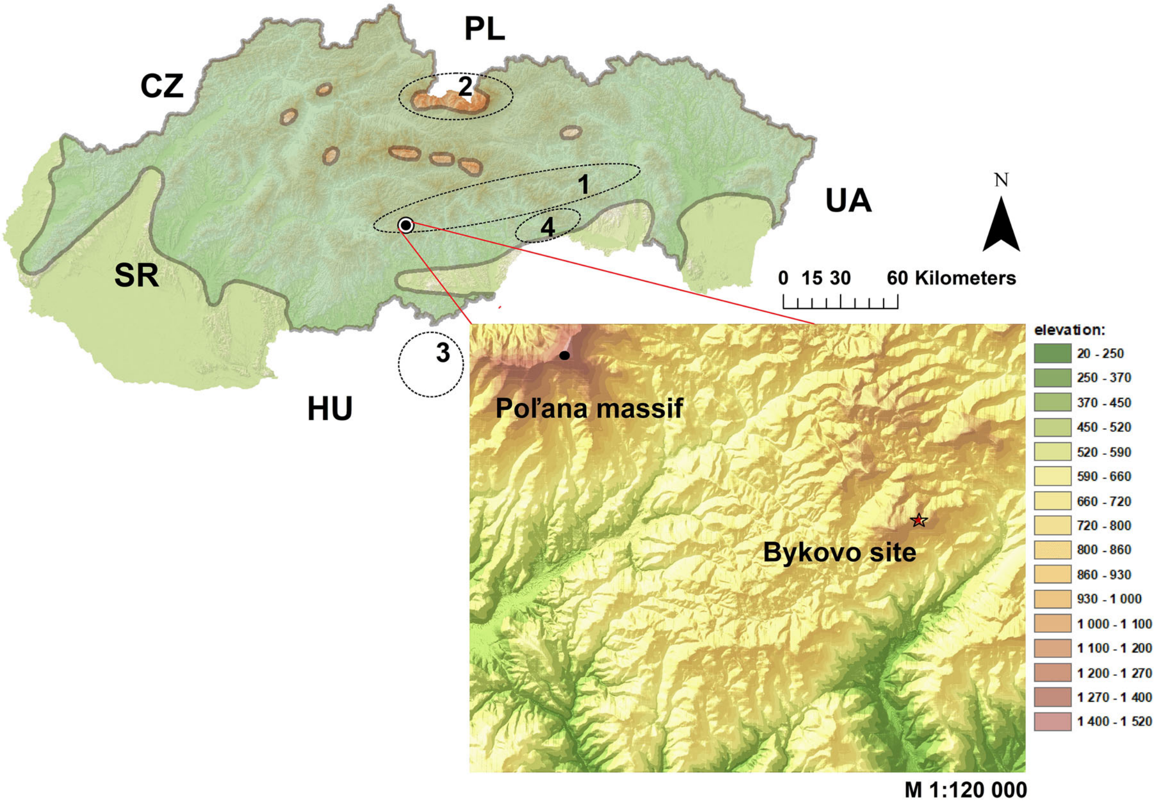

Figure 1. Map of the study locality (Bykovo: 48°35′9.88″N, 19°40′29.36″E; 1053 m above sea level) and cited sites: **1.** Slovenské rudohorie Mts, **2.** High Tatras Mts, **3.** Mátra Mts, **4.** Slovak Karst. The dark green area represents the natural distribution of *Fagus sylvatica* in Slovakia according to the Landscape Atlas of Slovakia (Miklós 2002).

Table 1. Lithological zones of the Bykovo profile.

Depth (cm)	Description	Colour
10–0	Missing part (fell out of the corer); droughty and noncoherent sediment	–
28–10	Weakly decomposed organic sediment, with admixture of wood, root zone	Light brown
48–28	Moderately decomposed organic sediment with admixture of wood, root zone	Dark brown
56–48	Moderately decomposed organic sediment with mineral admixture (10%), root zone	Dark brown
100–56	Decomposed organic sediment with mineral admixture (20%), weak root zone	Black

Besides pollen and spores, microcharcoal fragments 10–100 μm in size were counted (following Enache and Cumming 2006), fossil stomata were identified using the key of Sweeney (2004) and fossil needles were identified according to Katz et al. (1977). To calculate the concentration of microcharcoal particles, one *Lycopodium* tablet with a known concentration of spores was added to each sample, following the instructions of Stockmarr (1971). Percentage pollen diagrams were constructed using C2 v. 1.7.7 software (Juggins 2016). Local pollen assemblage zones (LPAZs) were delimited based on the outputs of the CONISS algorithm in PolPal software (Walanus and Nalepka 2004) and a visual assessment (see Supplementary material Figure S1).

2.3. Radiocarbon dating

The radiocarbon dating of the three samples was performed by the Isotoptech Laboratory in Debrecen (Hungary) using the accelerator mass spectrometry (AMS) method. Calibration of the radiocarbon data was done using Oxcal software v. 4.3.2 (Ramsey 2009) and the IntCal 13 calibration curve (Reimer et al. 2013). The dates are expressed as calendar years AD and calibrated years BP (before present, i.e. before 1950). A depth–age model was constructed with 0.25-cm resolution and based on a P_Sequence with $k_0 = 1$ and $\log_{10}(k/k_0)$ equal to 1 (see Supplementary material Figure S2). All dates in the text are expressed as calibrated years BP.

2.4. Loss on ignition analysis

To determine the magnitude of changes in the ratio of organic and mineral matter content in the peat profile, which indicates the input of mineral particles by erosion or decomposition of peat, loss on ignition (LOI; e.g. Heiri et al. 2001; Holliday 2004) was measured. Subsamples of peat (1 cm^3) were dried at room temperature for 7 days and then combusted at 550 °C for 3 hours. Values of LOI are presented as percentages of dry weight in the percentage pollen diagram (Figure 2).

2.5. Maps for absolute, empirical and rational limits

To interpret the Holocene history of beech in a broader context, we compiled data from published pollen sequences,

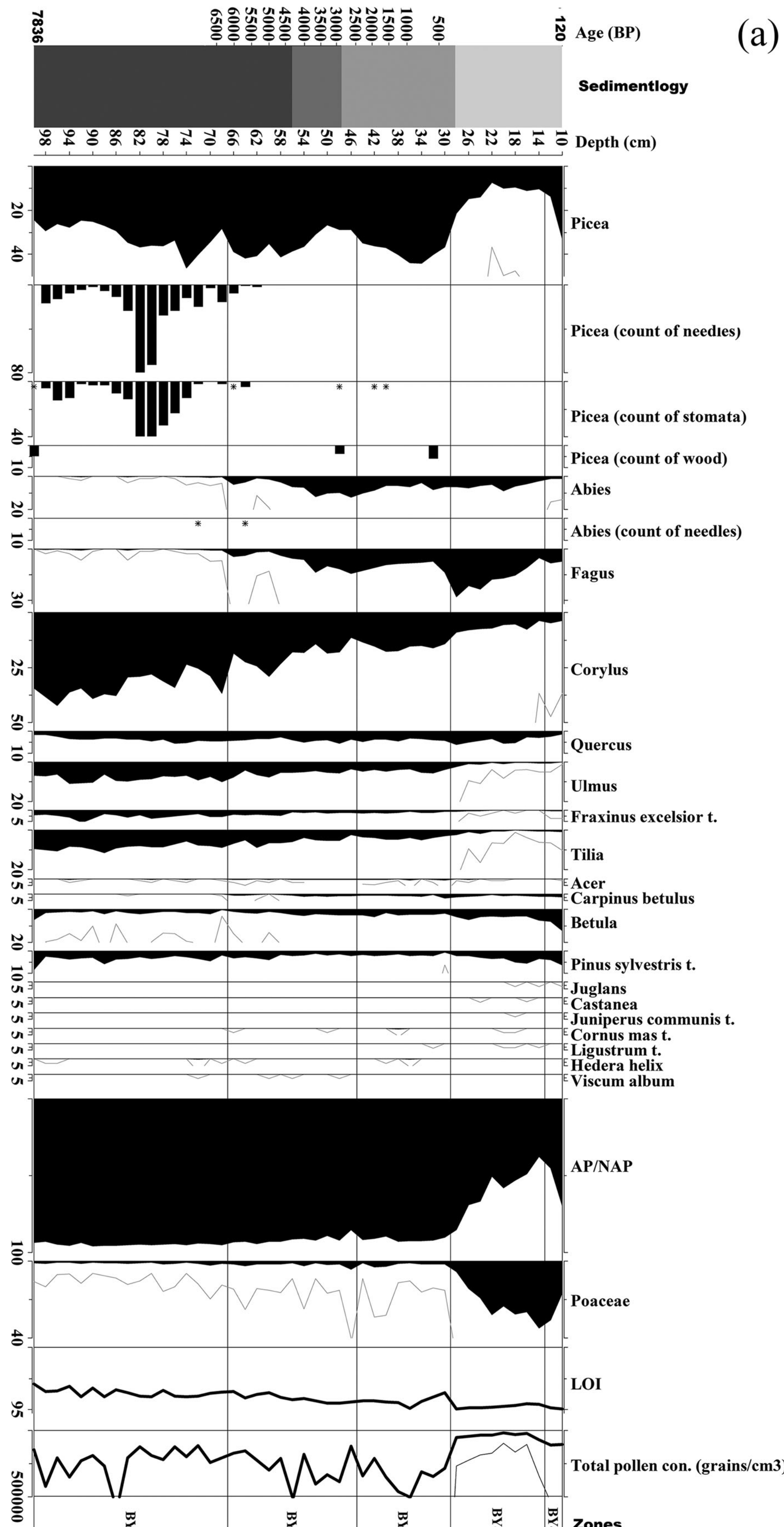

Figure 2. Percentage pollen diagram for the Bykovo profile (1053 m above sea level; Slovenské rudohorie Mts) with stomata, needles and wood of *Picea abies*. LOI: loss on ignition.

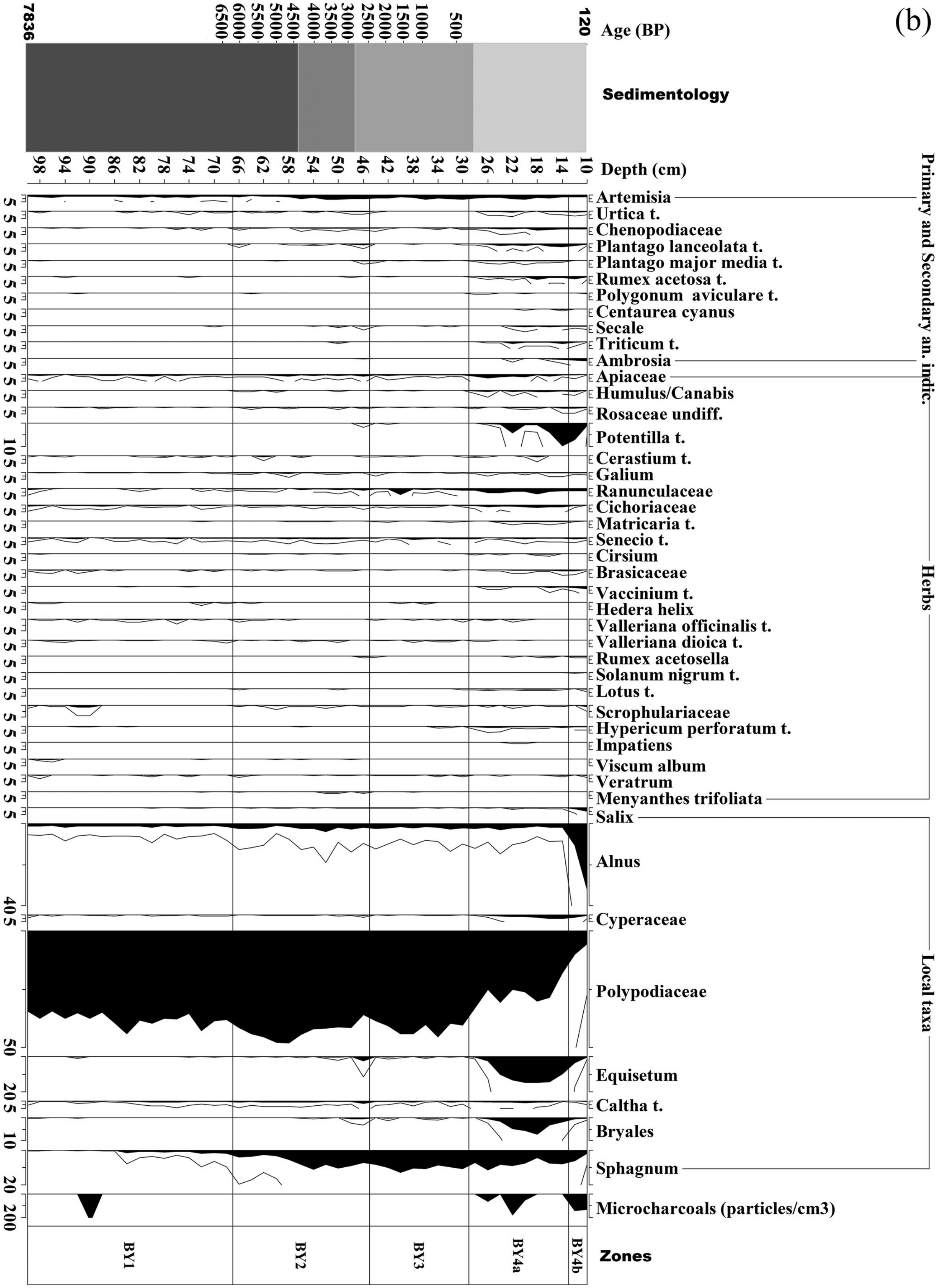

Figure 2. Continued.

unpublished pollen sequences available to us and data from the European Pollen Database (EPD) for Slovakia and adjacent areas of Hungary, Poland and the Czech Republic (Supplementary material Figure S4). We selected the areas lying outside Slovakia with regard to their proximity to the Western Carpathians and the Carpathian–Pannonian interface.

To define the beginning of the regional and local presence of beech and its expansion, we used the absolute, empirical and rational pollen limits. Taking into account the different percentage threshold values (e.g. Birks 1989; Lang 1994; Björkman and Bradshaw 1996) and results obtained from modern pollen samples (Lisitsyna et al. 2011; Wacnik et al. 2017), we used the following values of the aforesaid pollen limits: (i) the absolute pollen limit of 0.5% occurring in at least two consecutive samples spanning less than 500 years, (ii) the empirical pollen limit (a continuous pollen curve with values of 1.4–2%) indicating a high probability of the local occurrence of a taxon, and (iii) the rational pollen limit indicating the expansion of a taxon – the point at which the pollen curve begins to break towards values exceeding 5%. For interpretations of the spatial distribution of beech based on these pollen limits, we created maps using ArcGIS v. 10.2 software (ESRI 2012), employing an inverse distance weighted technique (IDW) with a variable search radius and 12 nearest input sample points.

3. Results

3.1. Stratigraphy

A simplified stratigraphy of the analysed profile (at depths between 10 and 100 cm) is presented in Table 1. The bottom half of the sequence (up to a depth of 56 cm) was formed by largely decomposed black peat with a low admixture of mineral particles. The middle part of the profile (56–26 cm) was composed of moderately decomposed woody brown peat, and its upper part (from 26 cm) was composed of dried decomposed peat. LOI analysis indicates a balanced course of changes in organic content, with a more pronounced decrease (from 93 to 69%) in the transition between zones BY4a and BY3 (see section 3.3. on the results of the pollen analysis).

3.2. Chronology

The age of the oldest layer of the profile under examination was 7836 ± 83 ^{14}C BP (Table 2). All important events in terms of the interpretation of the results were dated with a small standard deviation. The depth–age model (Supplementary material Figure S2) reached an overall agreement value of 92%, suggesting a reliable chronology. However, high errors of modelled years, with a maximum of ± 850 years, were recorded between the depths of 35 and 67 cm. Considering that more than 5000 years were represented by only 30 cm, the slow accumulation rate was probably caused by high mineralization under a local tree canopy. There was no evidence of any sedimentation hiatus in the pollen record (e.g. a distinct change in the pollen curves). Conversely, the uppermost layers (10–34 cm) exhibited low errors of modelled years (± 80 years). In the bottom section of the profile (68–100 cm), error values reached ± 150 years.

3.3. Results of pollen analysis of the Bykovo profile

The profile under study was divided into four local pollen assemblage zones (BY1–BY4), and the upper zone was divided into two subzones (BY4a and BY4b). The profile recorded a period ∼8000 years long with a gradual succession from the Middle Holocene to nearly recent climazonal woodlands and deforestation events caused by human activity (Figure 2).

Zone BY1: (100–67 cm, 7836–6250 cal BP ± 80–150)

In the oldest layer of the Bykovo profile, AP taxa prevailed over NAP taxa (ca. 95%). One conspicuous feature of this zone is the dominance of spruce (45%) with hazel (42%). Broad-leaved trees such as *Ulmus* and *Tilia* (11%) also had high and stable abundances. *Fagus, Abies* (indicated also by needles) and *Carpinus* occurred only sporadically (0.5%), but at the end of the zone their pollen abundances indicated their continuous presence (about 1%). Among NAP taxa, Poaceae, Apiaceae, *Artemisia*, *Urtica* t., Cichoriaceae and Chenopodiaceae were regularly present (all ca. 1–2%), with high values of Polypodiaceae (40%). The highest values were recorded for needles, stomata and wood of *Picea*. Microcharcoal particles produced only one peak, but their values were highest within the whole profile. Values of LOI were stable.

Zone BY2: (67–45 cm, 6250–2550 cal BP ± 49–850)

This zone was characterized by a continual decline of *Corylus* (to 11%) and *Picea* (to 29%) connected with a gradual expansion of *Fagus*, *Abies* (14% at the end of the zone) and *Carpinus* (2%). Values for other trees remained constant. In the NAP spectra, Poaceae, *Artemisia* and Apiaceae remained stable (1–2%). Other herbaceous taxa, such as *Hedera helix*, Chenopodiaceae, *Plantago lanceolata* t. and *Urtica* t. (1%), increased slightly. Primary anthropogenic indicators were represented by *Secale* (0.5%) and *Triticum* t. (one pollen

Table 2. Calibration of radiocarbon dates for the Bykovo profile. AMS: accelerator mass spectrometry.

Profile	Depth (cm)	Lab. code	Dating method	Dated material	Age in uncalibrated years BP	Calibrated years BP (interval) Range 68.2%	Range 95.4%	Calibrated years BP (median)	Agreement of model
Bykovo	34	DeA-16171	AMS	Seeds	531 ± 22	BP 547–523	BP 556–514	BP 546	
Bykovo	68	DeA-13500	AMS	Needles	5611 ± 49	BP 6375–6319	BP 6486–6301	BP 6385	A = 92
Bykovo	98	DeA-13499	AMS	Needles	7006 ± 83	BP 7934–7759	BP 7972–7677	BP 7836	

grain). The occurrence of needles and stomata of *Picea* and *Abies* was only recorded at the beginning of the zone.

Zone BY3: (45–29 cm, 2550–465 cal BP ± 850–43)

The main characteristic of this zone is a repeated increase of *Picea* (to 44%) and *Corylus* (25%), coinciding with a progressive decline of *Fagus* and *Abies* (to 7%). Other AP and NAP taxa remained relatively stable. Anthropogenic indicators, represented by *Plantago major/media* t., Chenopodiaceae, *Urtica* t. and *Secale*, exhibited a declining tendency. Stomata and wood of *Picea* were found in low quantities.

Subzone BY4a: (29–13 cm, 465–170 cal BP ± 43–85)

This zone was connected with an abrupt decline of AP taxa (to 38%). The abundances of *Picea*, *Abies*, *Corylus* and broad-leaved trees decreased to their minimum values. The curve of *Fagus* reached its maximum percentage (28%) after its previous decline and then decreased continuously (to 5%). *Pinus*, *Betula*, *Quercus* and *Juglans* increased gradually. An abrupt increase was recorded for values of Poaceae (40%), *Secale*, *Triticum* t., secondary anthropogenic indicators (*Plantago lanceolata* t., *Urtica* t., *Rumex acetosa* t.) and microcharcoal particles as well as for some local taxa, namely Bryales, *Equisetum*, Cyperaceae and *Potentilla* t. By contrast, a sharp decrease was recorded for Polypodiaceae (to 18%).

Subzone BY4b: (13–10 cm, 170–120 cal BP ± 90)

Throughout this subzone, the pollen percentages of *Picea* (33%), *Alnus* (32%), *Pinus* and *Betula* (both 10%) increased. In contrast, pollen abundances of *Fagus* and *Corylus* remained stable (8%). The increase of tree and shrub pollen was connected with a decline of Poaceae, primary and secondary anthropogenic indicators, Polypodiaceae and other local taxa. An increasing curve of microcharcoal particles was recorded.

3.4. Spatial pattern of *Fagus* appearance and spread

According to absolute pollen limits (Supplementary material Figure S3), the earliest occurrences of beech in the investigated area are located in its south-eastern (Hypkaňa 11,900 cal BP), southern (Kis Mohos 11,000 cal BP; Sarló-hát 10,500 cal BP) and south-western (Břeclav 10,900 cal BP, Šenkárka 11,250 cal BP, Šúr 10,000 cal BP) parts. Nevertheless, some sites from more northerly latitudes show an early occurrence of *Fagus* pollen as well (Kykula 9740 cal BP; Liptovský Ján 9600 cal BP; Popradské pleso 9580 cal BP). The local occurrence of beech, indicated by the empirical pollen limit (Figure 3), shows a pattern similar to that of the earliest occurrences in both the south-western (Šúr 9450; Čejčské lake 9300) and the more central parts of the Pannonian part of the area under investigation (e.g. Balaton, 9500; Mátra Mountains, 9500; Kis Mohos, 9100). The beginning of the beech expansion indicated by the rational pollen limit (Figure 4) roughly indicates an earlier spread in the south than in the north. The oldest dates refer to the Balaton region (ca 9500 cal BP) and to the Ócsa site (8800 cal BP), whereas somewhat younger dates come from the Mátra Mountains (8190 cal BP) and the former Šúr lake (7960 cal BP). Dates from more northerly positioned parts are distinctly younger, with the exception of the Stankovany site (7180 cal BP).

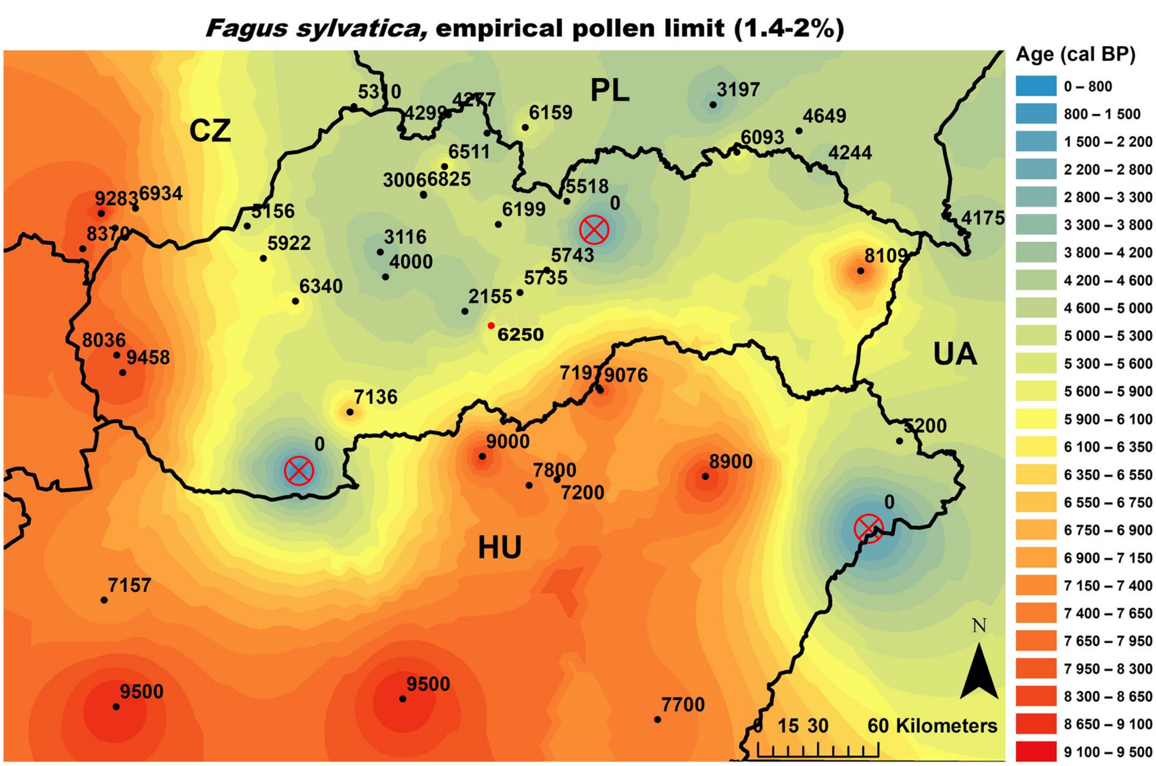

Figure 3. Interpolated ages of *Fagus sylvatica* pollen deposits based on the empirical pollen limit (1.4–2%). Localities with a red cross-hatched symbol did not exceed the threshold of 1.4%.

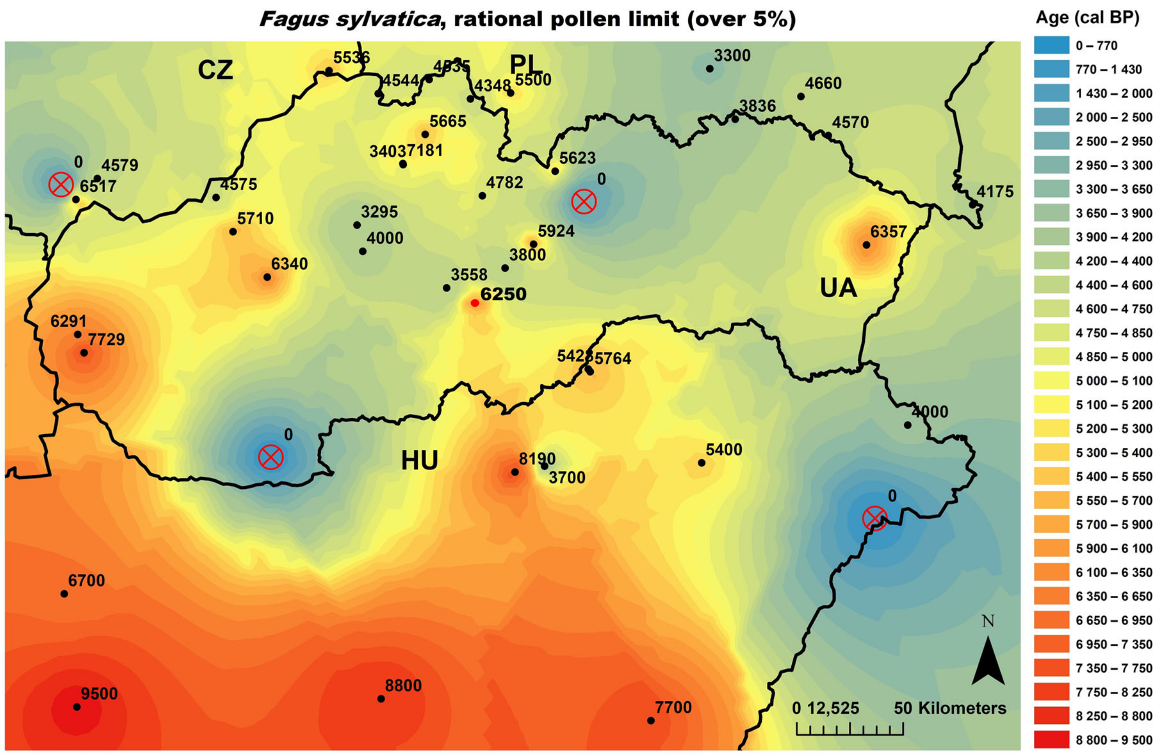

Figure 4. Interpolated ages of *Fagus sylvatica* pollen deposits based on the rational pollen limit (over 5%). Localities with a red cross-hatched symbol did not exceed the threshold of 5%.

Concerning the Last Glacial occurrence of beech and fir in the area being investigated, we found literature reports for the period between 42,900 and 12,860 uncal BP (*Abies*) and between 32,800 uncal BP and 12,260 cal BP (*Fagus*), respectively (Supplementary material Figure S3). For the LGM, macrofossil (charcoal, seed, buds and leaf scar) evidence is missing altogether. One record of *Fagus* charcoal, dated to the Late Glacial period (12,260 cal BP), comes from northeastern Hungary. Pollen evidence also comes only from the Late Glacial or a period before the LGM (26.5–19 cal BP, Clark et al. 2009). The only sequence with pollen records of beech and fir that may fall within the LGM (the Šafárka site) has a disturbed stratigraphy, and the available radiocarbon dates cannot be easily connected with individual pollen samples. The occurrence of strictly woodland snail species that indicate well-developed woodlands with late-successional temperate trees is also documented only for the period before the LGM (34,500–30,500 cal BP).

4. Discussion and conclusions

4.1. Middle and Late Holocene development of woodlands in the Slovenské Rudohorie Mountains

The characteristic feature of the oldest pollen assemblage of the Bykovo sequence is the dominance of spruce, hazel and ferns, together with quite high abundances of pollen of broad-leaved trees such as elm, lime, maple, ash and oak. We suggest that during the Middle Holocene, the vegetation in the area was a mixed deciduous–spruce woodland with ferns, forming a transitional deciduous–spruce vegetation zone between a deciduous zone at lower and a spruce zone at higher elevations. Alternatively, we suggest that the study site was located close to the boundary between these two vegetation belts, capturing pollen from both of these zones. The tree species composition found in the study sequence is similar to pollen assemblages reported from northern parts of the Western Carpathians (Rybníčková and Rybníček 2006; Pánek et al. 2010; Michczynski et al. 2013). In line with some other studies from the Western Carpathians and Eastern Sudetes (Szczepanek 1987; Rybníček and Rybníčková 2002; Dudová et al. 2010, 2013), a high abundance of hazel was found in the Middle Holocene pollen spectra (42%), along with dominant spruce pollen. Spruce woodlands with hazel in the shrub layer are known to have recently occurred in the boreo–continental parts of Europe (Gribova et al. 1980), but it seems improbable that hazel reached such high pollen abundances under a closed spruce canopy (Tallantire 2002; Ralska-Jasiewiczowa et al. 2003). Moreover, spruce very likely dominated in wet peaty places, whereas hazel occurred on better drained soils. This is supported by records of spruce needles, stomata and wood in our profile, evidencing its local occurrence that is usually associated with a high representation of spruce in pollen spectra (Rybníček and Rybníčková 2009; Pánek et al. 2010; Jamrichová, Petr et al. 2017; Juřičková et al. 2017; Dudová et al. 2018; Kołaczek et al. 2018). If spruce was indeed associated especially with wet soils (see Daněk et al. 2019 for recent patterns in mountain woodlands), the high abundance of hazel pollen challenges the assumed dominance of shady woodlands in unsettled or poorly settled Central European mountain ranges during the Middle Holocene (Fyfe et al. 2015; Hájek et al. 2016; Jamrichová, Petr et al. 2017). In our profile, the existence of a dense woodland is challenged also by continuous curves of herbs and a peak of microcharcoal particles. The landscape possibly had a mosaic structure, with hazel occupying open patches or canopy gaps created by dead trees (Tinner and Lotter 2001), large herbivores (Vera 2000) or other, sometimes larger scale, disturbances by natural fires, windthrows or insect outbreaks, which play an important role in the natural dynamics of Carpathian mountain woodlands (Bradshaw and Hannon 2004; Feurdean et al. 2017; Schurman et al. 2018).

The timing of the spread of beech at the Bykovo site closely fits the south-to-north expansion of beech, being earlier in the Pannonian Basin (Hungarian sites and sites in south Moravia and Slovakia) and later in Slovak mountain ranges. The spread appears to have taken place in two phases, one (directly AMS dated) beginning around 6250 cal BP and the second (only roughly estimated from our depth–age model) around 5100 cal BP. The same pattern of a two-phased beech expansion has been found at many sites within the Jeseníky Mountains (Dudová et al. 2018). Our review of data from the literature revealed a rather isochronal pattern of reaching the rational pollen limit of beech across similar latitudes of the area under investigation (e.g. Bielice, Hypkaňa, Mitická slatina) in this time period, but more clearly in mountains than in lowlands (Figures 4 and 5). This period of beech spread around 6250 cal BP coincides with the period of increased precipitation between 6100–6800 cal BP, as reconstructed by different proxies for the Western Carpathians by Juřičková et al. (2017), Jamrichová et al. (2018) and Dabkowski et al. (2019), for north-eastern Hungary by Magyari et al. (2008), and for the Alps by Patzelt (1977) and Haas et al. (1998). In our profile, increasing humidity is indicated also by an increase of *Hedera* pollen after 6570 cal BP. The second phase of beech expansion found in the Bykovo sequence started around 5100 cal BP and corresponds well with the beech expansion in some other regions of the Western Carpathians (Figure 5). Although the interpolated age is less certain, this phase coincides with a shift to a wetter climate on a broader geographical scale (O'Brien et al. 1995; Haas et al. 1998; Magny and Haas 2004; Jakab and Sümegi 2010). Nevertheless, the spread of fir, beech and hornbeam during the Middle and Late Holocene could have been affected not only by precipitation or temperature changes, as demonstrated by Tinner and Lotter (2006) and Giesecke et al. (2007), but also by fire or anthropogenic disturbances of already established woodlands (Küster 1997; Ralska-Jasiewiczowa et al. 2003; Feurdean et al. 2017; Jamrichová, Hédl et al. 2017; Jamrichová et al. 2018). In the Bykovo sequence, such disturbances are indicated by the appearance of anthropogenic indicators (*Plantago lanceolata*, Chenopodiaceae, *Polygonum aviculare* t., *Secale*) synchronous with the increase in beech pollen, but microscopic charcoal particles were not recorded and archaeological evidence is missing in a wider area around the site (Sokolovský 1997; Miklós 2002). One conspicuous feature of the Bykovo site is a gradual decline of beech pollen (2650–1500 BP) accompanied by an increase in pollen of spruce and hazel. The beginning of this phase perfectly fits the framework corresponding to the Bronze/Iron age transition (Novotný 1986), the Subboreal/Subatlantic transition (the Blytt–Sernander sequence) and Bray cycles (Bray 1971), all connected with abrupt climatic cooling on a wider geographical scale (e.g. Bond et al. 2001; Marcott et al. 2013; Starkel et al. 2013; Jamrichová et al. 2018; Dabkowski et al. 2019). This cold and also more humid phase likely benefited spruce, which occurred azonally around the fen (Figure 2) and probably blocked the pollen rain coming from regional woodlands. This assumption is also supported by an increase in the total pollen concentration from this phase onwards, indirectly pointing to a reduction of the sedimentation rate caused by an increase in evapotranspiration by local trees (Speranza et al. 2000). This situation, therefore, may not necessarily suggest a change in the proportion of beech and fir in regional (climazonal) woodlands, but we cannot exclude it either. Change in human impact, in addition to climate change, also possibly influenced the woodland composition, as fluctuating human activity was a relatively common feature after the Holocene climatic optimum (Kozáková et al. 2015), but the amount of anthropogenic indicators (*Cerealia*, *Pl. lanceolata* t., Chenopodiaceae, *Polygonum aviculare* t.) was generally low and did not change alongside the beech pollen decline, which suggests an influence of climatic factors rather than of humans.

In line with the previous study of Wiezik et al. (2019) and the geobotanical map of Slovakia (Michalko et al. 1986), our findings indicate that in pre-industrial times (before systematic human intervention, i.e. before the second half of the thirteenth century), mixed beech–fir or beech–fir–spruce woodlands occurred in climazonal habitats; noble hardwood woodlands with maple, elm, ash and lime occurred in azonal scree and stony habitats, but also as an admixture in beech–-fir woodlands; and spruce and spruce–alder woodlands occurred in azonal or semi-zonal habitats of peaty stands, alluvia and wet basins. The relative representation of spruce, fir and broad-leaved trees at the landscape scale is, however, difficult to reconstruct quantitatively without further research that would synthesize pollen data from different situations across a wider area and compare them with modern-day pollen spectra.

4.2. The migration history of beech in relation to the Western Carpathians

Because beech, together with spruce, represents the most frequent dominant species of Western Carpathian mountain woodlands, we synthesized existing pollen data about the history of beech to reveal the direction of its spread during the Holocene. In addition, this synthesis helped us evaluate the pollen record from the Bykovo profile in the context of the whole Western Carpathians. For Central Europe, including the Western Carpathians, it has been suggested that modern beech populations may originate from Istrian–Slovenian refugia, but northern microrefugia cannot be excluded either (Willis and van Andel 2004; Magri 2008). Present-day pollen samples indicate a poor dispersal ability of *Fagus* pollen

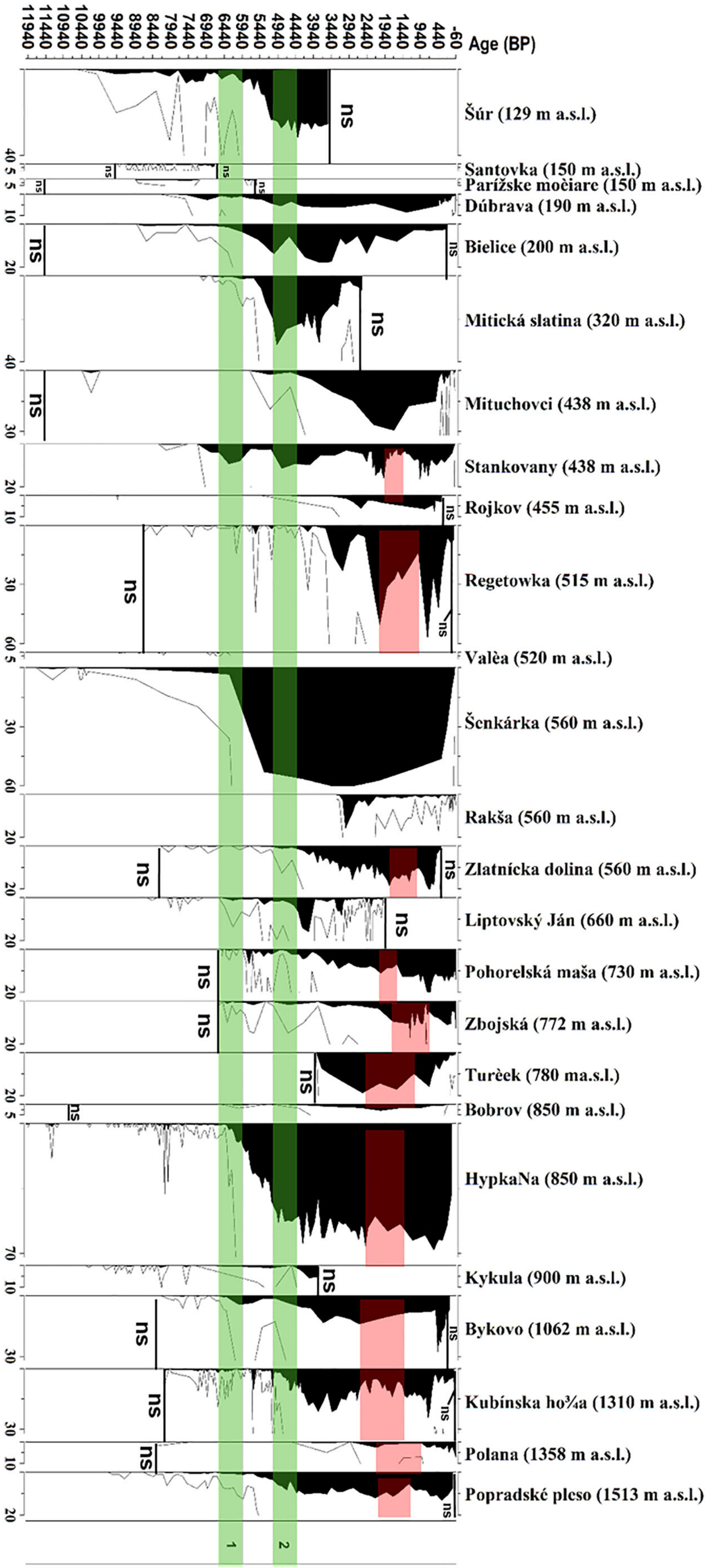

Figure 5. Summary pollen diagram for the Western Carpathians and adjacent areas of Slovakia (sorted according to elevation). The numbers 1 and 2 indicate major phases of beech population expansion at the Bykovo site (see the text for details). Lines marked 'ns' delimit periods without existing data. The red field in the diagram depicts the temporal decline of beech since the Iron Age.

(Sugita et al. 1999) and, consequently, low pollen limits needed to evidence its regional (0.5%, Lisitsyna et al. 2011) or local presence (0.3–1.3%, Wacnik et al. 2017). Low quantities of beech pollen (< 0.5%) were found in Late Glacial samples from the Western Carpathians (Supplementary material Figure S3) and may indicate small, isolated beech microrefugia bound to favourable microhabitats with enhanced soil and air humidity and less extreme frosts (Bennett 1985; Tinner and Lotter 2006). Some other studies based on fossil, genetic and phytogeographical data suppose beech survival in multiple refugia during the Last Glacial period, including northern microrefugia in or around the Western Carpathians (Magri et al. 2006; Willner et al. 2009; Saltré et al. 2015; Jiménez-Alfaro et al. 2018). On the other hand, the occasional occurrence of individual beech pollen grains in glacial samples may be a result of long-distance transport, redeposition, contamination or misidentification. Direct macrofossil evidence is still missing for the LGM and is very rare for the Late Glacial period. It is therefore possible that beech retreated southwards during the LGM, and recolonized the Western Carpathians and Pannonian Basin later (Rudner et al. 2004; Sümegi et al. 2004; Sümegi 2005). Our review indeed indicates an earlier appearance and spread of beech in the southern part of our study area. With the present state of knowledge, we cannot conclude whether it disappeared completely from the Western Carpathians during the LGM, or whether the Western Carpathians formed a transitional zone between inhospitable lands devoid of beech and southern macrorefugia – the gradient assumed by Magri (2008). Our data only show a clear south-to-north pattern of reaching higher pollen limits, suggesting that the modern-day beech and beech–fir woodlands in the study area were largely formed by northward migrations of expanding populations during the Holocene, replacing spruce and noble hardwood woodlands and hazel shrubs. Important questions have yet to be resolved, however – for example, whether northern microrefugia, if they existed, contributed to the present-day genetic and taxonomic diversity of beech and beech–fir woodlands, and whether climatic changes or fire and anthropogenic disturbances drove the expansion of beech–fir woodlands into original woodland vegetation formed of spruce and noble hardwood trees.

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No potential conflict of interest was reported by the authors.

Author Contributions

All authors provided interpretations of results and participated in the preparing of the manuscript which was led by MW. MW sampled profile, made all analyses and led writing. PH prepared samples for dating.

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