Exposure matters: forest dynamics reveal an early Holocene conifer refugium on a north facing slope in CE Europe

Pató, Zsuzsanna Anna[1, 2]; Standovár, Tibor[1], Gałka, Mariusz[3]; Jakab, Gusztáv[4, 5]; Molnár, Mihály.[2], Szmorad, Ferenc[6], Magyari Enikő[2,6,7]

[1]Eötvös Loránd University, Department of Plant Systematics, Ecology and Theoretical Biology, H-1117, Budapest, Pázmány Péter stny. 1/c., Hungary; patozsu@caesar.elte.hu

[2]Isotope Climatology and Environmental Research Centre (ICER), Institute for Nuclear Research, Hungarian Academy of Science, H-4026, Debrecen, Bem tér 18/c, Hungary;

[3]University of Lodz, Faculty of Biology and Environmental Protection, Department of Geobotany and Plant Ecology, 90-237 Lodz, Poland;

[4]Szent István University, Faculty of Agricultural and Economics Science, Szarvas, Hungary;

[5]Hungarian Academy of Science, Research Centre for the Humanities, Institute of Archaeology, Budapest, Hungary;

[6]Eötvös Loránd University, Department of Environmental and Landscape Geography, H-1117, Budapest, Pázmány Péter stny. 1/c., Hungary;

[7]MTA-MTM-ELTE Research Group for Palaeontology, H-1083 Budapest Ludovika tér 2, Hungary

Abstract

Although several studies provide a broad overview of vegetation changes in the Carpathian Basin during the Holocene, stand-scale vegetation changes are lesser known because of the rarity of suitable sampling sites. In this study we investigated the sediment of a small closed-canopy site (Nagy-forrás forest hollow, 685 m a.s.l., 0.1 ha), located in the Mátra Mountains, on the north facing slope of Kékes (1014 m a.s.l.). We carried out detailed pollen, conifer stomata and plant macrofossil analyses, as well as radiocarbon dating to examine Late Glacial and Holocene dynamics of vegetation development. The site dates back to ca. 15 500 cal yr BP, when open boreal forests and wet tundra-like habitats occurred around the hollow. Closed forest cover developed around 14 600 cal yr BP, when a boreal European larch-Swiss stone pine (*Larix decidua-Pinus cembra*) forest surrounded the hollow. This vegetation type remained stable up to 7700 cal yr BP. We observed a hiatus between 7700 and 2710 cal yr BP, followed by a beech (*Fagus sylvatica*) dominated mixed temperate deciduous forest. Our results confirmed that the area was covered by a primary forest, as human influence was visible only from 175 cal yr BP. The relatively long lasting persistence of *Pinus cembra* in the Holocene at relatively low altitude was documented, which has never been found in Holocene sediments in the Pre-Carpathians before. We hypothesize that the north facing slope acted as a cold-stage refugium in the Early Holocene and could play the same role for the present-day beech forest that is threatened by recent climate change.

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Introduction

The last major climatic shift, the Pleistocene/Holocene transition that took place around 11 700 years ago is an intensively studied time period, partially because it gives us a better understanding of the ongoing climate change and its potential consequences. The effects of warming climate on ecosystem functioning, and particularly on vegetation dynamics are important fields of paleoenvironmental studies, because they directly influence our economy and civilization to a great extent (Elias, 2007; Willis et al., 2007, 2010). Information about past rapid ecosystem reorganizations and their effects on human societies provide us useful lessons as to what mitigation measures should be done regarding ongoing climate change (Petit et al., 2008; Willis et al., 2007). They also help us designating the potential directions of habitat-targeted nature conservation (Birks, 1996; Jackson and Hobbs, 2009; Lindbladh et al., 2007).

If we turn our attention to past vegetation changes and look at paleoecological studies, most of them describe vegetation dynamics on a regional scale due to the routinely used main proxy method pollen analysis (Birks and Birks, 2000, 2006) and basin size (> 5 ha, see in Bradshaw, 2007; Elias, 2007) that will result in regional vegetation reconstructions. Even though such studies are unquestionably important, the detection of local, i.e. population-level changes is also necessary to understand how climate change affects different microhabitats. Such knowledge about the stand-scale vegetation is particularly instructive for conservation planning (Birks, 1996; Jackson and Hobbs, 2009; Lindbladh et al., 2007) and forest management (Jasinski and Angelstam, 2002). Local information not only helps us to assess what factors threaten populations and what could be the potential vegetation response in general (Jackson and Sax, 2010), but it may also help us identifying places where a species can survive the otherwise unfavourable climatic conditions (Dobrowski, 2011; Gavin et al., 2014; Suggitt et al., 2011, 2018). These places serve as refugia (Birks and Willis, 2008); they can either be relatively large and continuous, or smaller, hosting isolated populations (Gavin et al., 2014; Stewart et al., 2010). Such areas are immensely important, as they provide sources for recolonization (Väliranta et al., 2011) . For example, the spread of deciduous trees after the Last Glacial Maximum (LGM) was suggested to be facilitated by cryptic refugial populations (Birks and Willis, 2008; Provan and Bennett, 2008). Refugia also have a key role in preserving the genetic diversity of a species (Höhn et al., 2009; Stewart et al., 2010; Svenning et al., 2008).

Local scale (2-10 km^2) vegetation history data can be obtained, among others, by studying macrofossils from lake and peatland sediments (Birks, 1996, 2003), and also by studying the pollen composition of small sites under closed canopy, so-called ‘forest hollows’ (Bradshaw, 1988, 2007;

Overballe-Petersen and Bradshaw, 2011). Local-scale pollen studies (stand-scale palynology) require closed-canopy sites with accumulated dry sediments (e.g. mor humus) or special natural water bodies ('forest hollows') of 10-100 m diameter without in- and outflow (Bradshaw, 1988, 2007; Overballe-Petersen and Bradshaw, 2011). Under these circumstances the plant remains (including macrofossils and pollen) are mostly transported into the sediment under the canopy from 20-150 m distance (Calcote, 1995; Parshall and Calcote, 2001). In the last few decades, stand-scale studies were successfully used to investigate the forest development and long-term forest dynamics in Western and Northern Europe (Clear et al., 2015; Overballe-Petersen et al., 2013, 2014; Parshall, 1999) and in Central Europe (Hájková et al., 2015; Jamrichová et al., 2013; Novák et al., 2019).

Macrofossil analysis has been long used to complement pollen analysis by tracking local vegetation changes (Birks and Birks, 1975). Furthermore, plant macrofossils (e.g. fruits, seeds, bud scales, leaves) can be identified with a better taxonomic resolution than pollen grains, and many of them also represent species that produce low amount of pollen and would otherwise go unnoticed in the pollen record (Birks, 2007; Birks and Birks, 1975, 2000). Detailed macrofossil analyses were successfully used to track, among others, the paleohydrological and temperature changes during the postglacial period and geochemical conditions of wetland ecosystems (Gałka et al., 2017; Jakab and Sümegi, 2005; Magyari et al., 2001), forest development and dynamics (Birks, 2003; Jankovská, 1988; Kołaczek et al., 2017) and tree- and timberline changes (Birks and Willis, 2008; Feurdean et al., 2016; Magyari et al., 2018; Orbán et al., 2018)

In the neighbouring area of our study site, local vegetation development was studied mostly in higher mountainous areas, like the Precarpathian Hills and the Carpathian Mountains (Feurdean et al., 2013; Gałka et al., 2017, 2018). At lower altitudes (< 750 m a.s.l.) of the Carpathian Basin, only few stand-scale studies were carried out so far (Hájková et al., 2015; Jamrichová et al., 2017). The main reason for this is the rarity of suitable sites due the arid, continental summers and recently the high density of wild game (biodisturbance) that disfavour mor humus accumulation and the long-term persistence of undisturbed forest hollows.

Regional vegetation historical studies (Buczkó et al., 2009; Feurdean et al., 2014; Magyari, 2015) suggest that the Carpathian Region served as refugium for many species in different areas. Several deciduous tree species had small populations (cryptic refugia) during the LGM (Provan and Bennett, 2008), which became important sources of recolonization (Birks and Willis, 2008; Magri, 2008; Willis et al., 2000). The vegetation of the Pannonian Basin reflects this historically large diversity in different floristic elements: several glacial relict species, Atlantic, Montane, Mediterranean and Steppe elements are present today (Fekete et al., 2014).

In this study, we present the results of a stand-scale paleoecological study that we undertook on the deposits taken at a small forest hollow (a spring-fed fen next to Nagy-Forrás) in the Mátra Mountains. These mountains are part of the North Hungarian Mountains, a separate geomorphological unit of the Western Carpathians. Since the site is located in close proximity of the Kékes Forest

Reserve, our study has a high nature conservation relevance as it sheds light on the vegetation history of one of the last primary forests in Hungary (Czájlik, 2009) and also in Europe (Sabatini et al., 2018). To our knowledge, our research is the first stand-scale paleoecological study in Hungary.

The aims of this study are: i) to reconstruct stand-scale vegetation changes and succession over the Late Glacial and Holocene period; ii)_to compare the local vegetation changes with regional trends, and to identify potential Late Glacial refugia for cold tolerant vegetation iii) to specify when the present-day beech dominated forest was formed and iv) to identify the first signs of human impact.

Materials and Methods

The locations of the potential forest hollows in the North Hungarian Mountains were collected using the geomorphological literature, the maps of the area and information given by the rangers of the Bükk National Park Directorate. Altogether 61 potential forest hollows were identified, from these 41 were visited and evaluated as a potential coring site. The vast majority of these places were disturbed by game and/or did not accumulate enough sediment. Altogether five sites were identified with undisturbed thick sediment layer and therefore suitable for multi-proxy paleoecological analyses. All of them are located in the Mátra Mountains and are landslide basins (Szabó, 1992, 1993; Szabó and Félegyházi, 1997)._This study focuses on the paleoecological study of the site called Nagy-forrás forest hollow.

Regional setting

The Mátra Mountains (Figure 1) is one of the highest mountain ranges in Hungary, with the highest peak of the country (Kékes, 1014 m a.s.l.). The climate of the region is continental temperate (Standovár et al., 2017) with a mean annual temperature of 5.7 °C, while the mean monthly temperature is 15.5 ºC in July and -4.4 ºC in January (Ódor, 2000). The annual precipitation is 784 mm at the Kékes meteorological station, the number of snow covered days is 112 (Ódor, 2000). The area of the Mátra Mountains is mostly covered by deciduous forests and partly (12 178 ha) protected since 1985 (Mátra Landscape Protection Area).

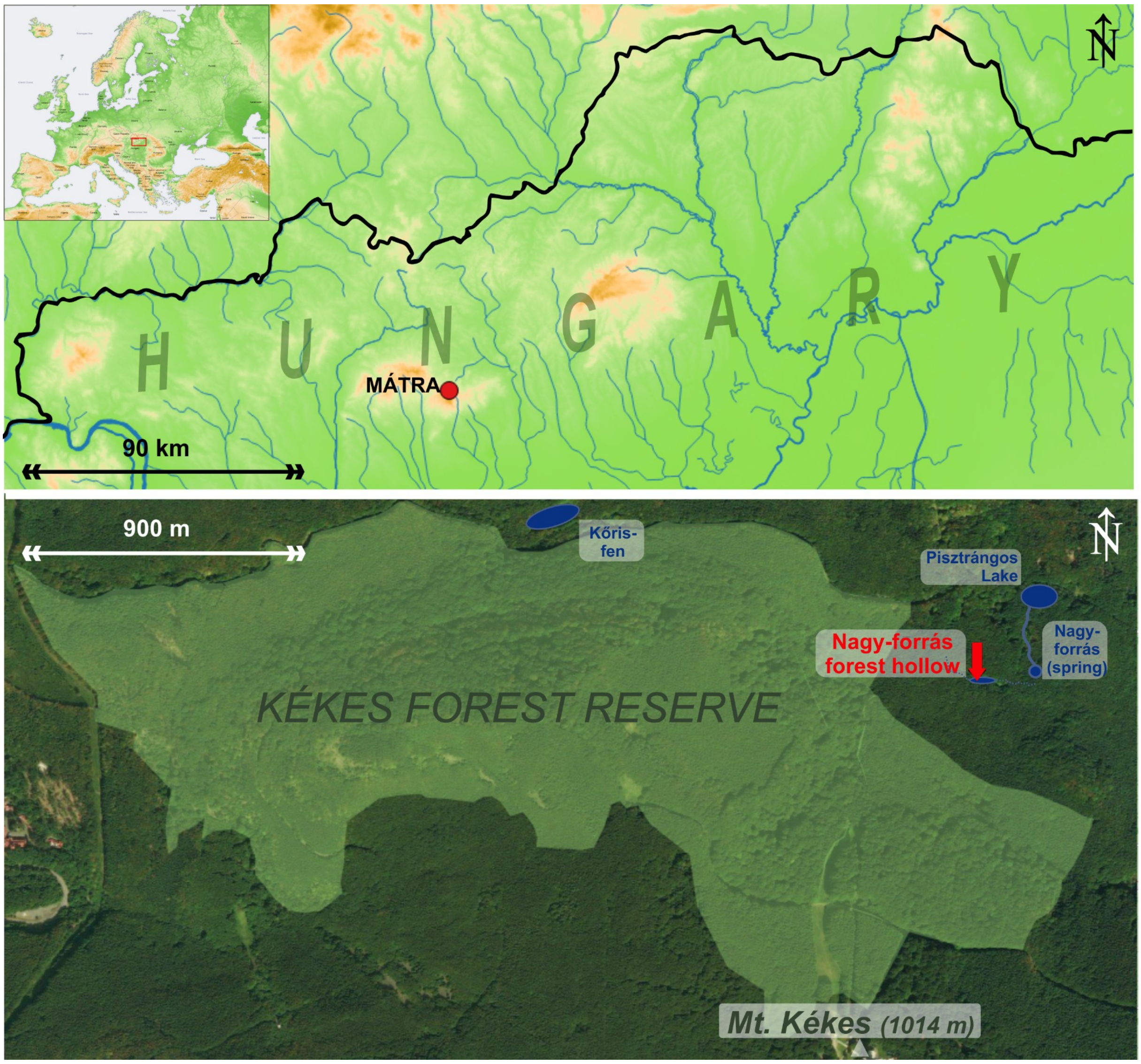


Fig. 1. Location of Nagy-forrás forest hollow in the Carpathian Basin and in the Mátra Mountains.

The Mátra Mountains have been populated for several millennia: the first signs of human presence date back to the Upper Paleolithic (*Blattshaber-Blattspitzen complex, unknown dates*, see in Bíró, 1984; Gutay, 2016). Permanent settlements were found on the lower slopes from the Late Neolithic (*Linear Pottery Culture* 5600-4500 cal yr BC, see in Domboróczki et al., 2016), while hillforts (Supplementary Figure 1) were built on several peaks during the Bronze Age (*Füzesabony Culture* 1700-1300 cal yr BC in Hungary, *Kyjatice Culture* 1100-700 cal yr BC in Hungary, see in Dénes and Nováki, 2010; Metzner-Nebelsick, 2012). Several towns and villages were established in the foothills during the Middle Ages (Fodor, 2010). The intensive use of the forests started only after AD 1708, when glasswork and potash production manufactures were established in the villages of the northern foothills. Despite the long history of human occupation in the region, the inner part of Mátra Mountains remained relatively undisturbed throughout prehistoric times and also during historical times due the relatively long distance from the foothills and the steep slopes (Czájlik, 2009).

Our study site lies on the northern slope of Kékes Peak that is dominated by submontane beech forests (*Melittio-Fagetum,* Soó 1964) and montane beech forests (*Aconito-Fagetum*) with patches of scree forests (*Mercuriali-Tilietum*) and mixed maple-ash-lime forests (*Parietario-Aceretum*). In the much lower (northern) parts of the slope, Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) plantations occur (Vojtkó et al., 2010). The bedrock is andesite that is covered by shallow lessivated brown forest soils (Dávid, 1992; Láng et al., 2013). The slope above our coring site is covered by the last primary forests of Hungary, and therefore it is a well-studied and strictly protected area (Kékes Forest Reserve, see in Czájlik, 2009; Standovár et al., 2017). The area below our site has been heavily impacted by human activities: the first evidence of clearings dates back to AD 1856 (see Supplementary Figure 1), when a *ca*. 2 ha meadow appeared around Lake Pisztrángos (Biszak et al., 2014; Tímár et al., 2010). More extended deforestation started only after 1945, while an asphalt road was built in 1949 (Czájlik, 2009). Nowadays this part is covered by middle-aged (94 years old) beech forest mixed with silver birch (*Betula pendula)* and planted Norway spruce trees. These forests are managed for timber production by forestry; the last intervention was 25 years ago.

The studied site, Nagy-forrás forest hollow (Figure 1) is located between Lake Pisztrángos and the Kékes Forest Reserve (47°52'48.8"N 20°00'44.3"E, 685 m a.s.l.). It is located in a small depression which was most probably formed by a landslide (Szabó, 1992; Szabó and Félegyházi, 1997), and filled up slowly with sediment. Its extent according to our measurements is 25 x 50 m (ca. 980 m^2) and today it is covered by the forest community of *Carici remotae-Fraxinetum* (Vojtkó et al., 2010). The canopy is characterized by common ash (*Fraxinus excelsior*), European aspen (*Populus tremula*), European beech (*Fagus sylvatica*) and black alder (*Alnus glutinosa*); canopy closure is around 50%. The herb layer covers the entire surface; the dominant species are *Carex remota* and *Athyrium filix-femina* (70-70%). Abundant species are *Solanum dulcamara* (20%), *Chrysosplenium alternifolium* (15%), *Circaea lutetiana* (10%) and *Impatiens noli-tangere* (10%). *Lycopus europaeus* (5%), *Eupatorium cannabinum* (3%), *Ranunculus repens* (3%), *Lysimachia nummularia* (3%), *Galium palustre* (2%), *Oxalis acetosella* (2%), *Dryopteris carthusiana* (1%), *Stachys sylvatica* (1%) and *Urtica dioica* (1%) also have a considerable cover.

Methods

Two overlapping sediment cores were taken from the forest hollow (PM-1 and PM-2) in the fall of 2016 with a modified Russian peat corer equipped with a 40 cm long sampling chamber. The core segments were wrapped in cling film and aluminum foil in the field, and stored at 4 °C in the laboratory. Sediment lithology was recorded following the Troels-Smith scheme (Troels-Smith, 1955). The two cores (PM-1, PM-2) were aligned according to the lithology, and were used for further analyses. Subsequently, the cores were sliced up into 1 cm thick slices, from which 1 cm^3 subsamples were taken for pollen and 1 cm^3 for loss on ignition (LOI) analyses; the remaining sediment(5–16 cm^3, median: 8 cm^3) was used for macrofossil analysis. The resolution of the pollen and plant macrofossil records is 4 cm, while loss-on-ignition was measured at 2 cm intervals.

For AMS ^{14}C dating terrestrial plant macrofossils (seeds, needles, leaf- and twig fragments, see Table 1.) were collected from 11 sediment layers. All samples were taken from the same core (PM-1). The measurements were done at the Laboratory of Climatology and Environmental Physics (ICER), Institute of Nuclear Research of the Hungarian Academy of Sciences. Outliers were identified with OxCal (v4.3) outlier analysis. We used the IntCal13 calibration curve (Reimer et al., 2013) in OxCal (Ramsey, 2009) for calibrating the ^{14}C dates. Bayesian age-depth models were made without the outliers using the rbacon (v2.2) package in R v3.5.5 (Blaauw and Christen, 2011). The maximum possible age was defined as 20 000 cal yr BP based on previous publications about these landslide basins (Szabó, 1992, 1993; Szabó and Félegyházi, 1997).

For determining the organic content of the sediment, subsamples were dried, weighed and subsequently heated in a muffle furnace to 550 °C for 4 hours (Heiri et al., 2001). Organic carbon percentages were calculated from the loss of weight upon ignition, the results were plotted using program R (3.5.0) with the rioja package (Juggins, 2017).

Pollen grains were extracted following the method of Willis and Bennett (Bennett and Willis, 2001). Acetolysis was followed by 1% sodium hypochlorite treatment in order to dissolve resistant ligneous matter. *Lycopodium* tablets (Lund University, Batch: 1031 and 3862) were used to calculate pollen concentrations and accumulation rates. At least 500 terrestrial pollen grains were counted in most samples (Beug, 2004; Moore et al., 1991). However, eight samples from the bottom part of the sediment had very poor pollen preservation; here the terrestrial pollen sum was between 300-400 grains. Pollen taxon nomenclature follows Moore et al. (1991). Microcharcoals (10-125 μm), microspores, non-pollen palynomorphs (Van Geel, 2006; Van Geel et al., 1980, 1983) and conifer stomata (Magyari et al., 2012; Sweeney, 2004; Zhang et al., 2011) were also counted on the pollen slides. Pollen percentages, charcoal and stomata concentrations were calculated, and Tilia 2.1.0 (Grimm, 2011), and CorelDraw X8 were used to plot the diagrams. Pollen assemblage zones were defined based on terrestrial pollen data using the binary splitting function in Psimpoll v4.26 (Bennett, 2008). Principal Component Analysis (PCA) was done using the most abundant 23 pollen types (attaining 5% at least in one sample) using a covariance matrix and square-root transformation in Psimpoll v4.26. Results were plotted in Microsoft Excel.

For plant macrofossil analysis 1 cm thick sediment slices (mean volume: 7.5 cm^3) were used at 4 cm intervals, as described above. Their volume was measured by water displacement. Samples were disaggregated and wet sieved through a 250 μm mesh. Plant macrofossil analysis was done according the modified "semi-quantitative quadrate and leaf-count macrofossil analysis technique" (Jakab and Sümegi, 2012). Plant remains were identified using identification keys (Berggren, 1981; Bojnanský and Fargašová, 2007; Cappers et al., 2012; Jakab and Sümegi, 2004, 2012; Katz et al., 1965) and reference materials stored at the Department of Environmental and Landscape Geography (ELTE) and at the Seed Collection of Hungarian Natural History Museum. In the case of the conifer needle fragments, minimum number of needles were calculated following the equation MN=WN+NH+NF/2 (MN: minimum number of needles, WN: whole needles, NH: number of the needle tips or the needle bases-depends on which one is highest, NF: needle fragments), as described in detail in Vincze et al. (2017). All plant macrofossil concentrations were calculated to the minimum volume (5 cm^3). Results were plotted using Tilia 2.1.0 (Grimm, 2011) and CorelDraw X8.

Results and interpretation

Sediment stratigraphy and chronology

The full length of the sediment was 240 cm with 5 main lithostratigraphic units visible (Figure 2). The bedrock was andesite gravel (grain size: 5-25 mm). Results of the radiocarbon dating are presented in Table 1.

Table 1. Results of the AMS ^{14}C measurements from Nagy-forrás forest hollow (core PM-1)

Laboratory code	**Dated material**	**Depth (cm)**	**^{14}C age years BP**	**Calibrated age years BP**	**Remarks**
DeA-15374	Deciduous leaf fragments	16	1 ± 27	-27 ±15	
DeA-15375	Deciduous leaf fragments	36	174 ± 27	148 ± 122	
DeA-13965	*Fagus sylvatica* budscales and twigs, *Rubus* seed	64	2826 ± 25	2928 ± 33	
DeA-16685	*Fagus sylvatica* twigs	72	2503 ± 20	2612 ±81	
DeA-15378	*Larix* and *Pinus cembra* needles	76	6918 ± 39	7753 ± 44	
DeA-13966	Woods, twigs, *Quercus* and *Pinus* budscales	84	4821 ± 30	5547 ± 48	outlier
DeA-15379	Conifer needles	100	11211 ± 52	13111 ± 107	
DeA-16686	*Fagus sylvatica* budscales	107-109	2640 ± 21	2762 ± 7	outlier
DeA-15376	Conifer needles	116	11480 ± 46	13389 ± 121	
DeA-15377	Conifer needles	174	12013 ± 48	13991 ± 202	
DeA-13967	*Larix* needle, conifer budscales, moss remains, *Juncus* seeds	229	5445 ± 36	6254 ± 32	outlier

Three dates (229 cm, 109 cm and 84 cm) were identified as outliers. The bottom part of the sediment was poor in macrofossils and organic matter, and the small amount of datable organic material could account for the young obtained age at 229 cm. The other two outliers (109 cm and 84 cm) can be explained by the downward movements of small (2-3 mm) fragments of deciduous macrofossil either washed down during the sedimentation process or relocated during the coring. The fact that the sample from 107-109 cm composed only of deciduous material gave a very young age (107-109 cm, only Fagus budscales, 2762 ± 7 cal yr BP), whereas the sample composed of mixed coniferous and deciduous material gave an intermediate age (84 cm, Quercus and Pinus budscales, 5547 ± 48 cal yr BP) confirms the relocation of small deciduous macrofossils. However, the ages obtained from coniferous remains and the succession reflected by the changes of dominant species in the macrofossil and pollen records let us conclude that the sediment shows a consistent stratigraphy with minor down-core movement of deciduous macrofossils.

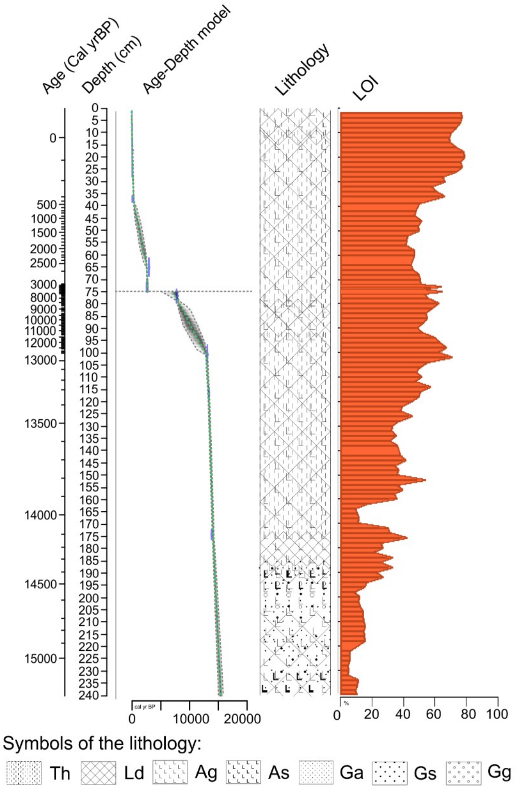
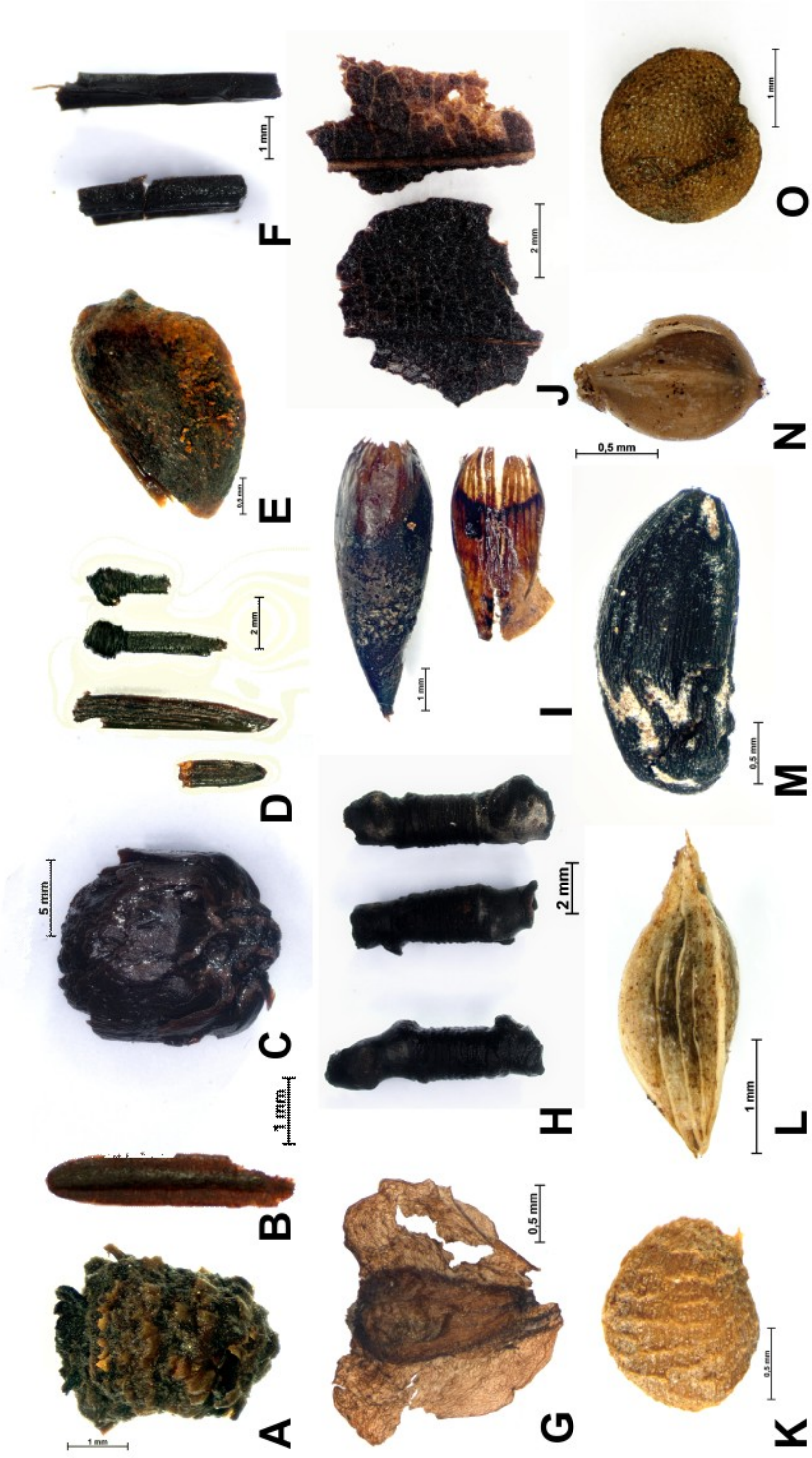


Fig.2. The results of age-depth modelling, lithostratigraphical description and loss on ignition measurements of the Nagy-forrás forest hollow, core PM-1. The symbols of the lithography follow the Troels-Smith nomenclature: Th-*Turfa herbacea*, Ld-*Limus humosus*, Ag-*Argilla granosa*, As-*Argilla steatodes*, Ga-*Grana arenosa*, Gs-*Grana saburralia*, Gg-*Grana glaerosa* (min)

Age-depth models were constructed without the outliers for the entire length of the core, extrapolation was made between 174 cm and 240 cm (see Figure 2). The radiocarbon ages in association with the abrupt change in the plant macrofossil types and the high abundance of fungal remains (sclerotia) between 72 and 76 cm altogether pointed to a presumable time gap in the sediment, therefore a hiatus was introduced at 74 cm.

Pollen, stomata and plant macrofossil results and inferred vegetation changes

The sediment was relatively rich in plant remains: 88 pollen, 7 spore, 8 NPP (non-pollen palynomorph), 4 stomata and 113 plant macrofossil types were observed along the entire length of the core. Plant macrofossil abundance of trees and shrubs was exceptionally high in the top 175 cm of the core. The pollen zonation resulted in 5 significant assemblage zones (PH-1 to 5). For the zones and detailed vegetation changes see Supplementary Table 1. The main plant macrofossil types are presented in Figure 3., pollen and plant macrofossil diagrams are presented in Figures 4 & 5.



Plant macrofossil remains from Nagy-forrás forest hollow. A. *Larix* sp. dwarf shoot **B.** *Larix* sp. needle tip **C.** *Larix decidua* cone **D.** *Pinus sylvestris* needles **E.** *Pinus sylvestris* seed **F.** *Pinus cembra* needle **G.** *Betula pubescens* seed **H.** *Fagus sylvatica* twigs **I.** *Popolus* sp. budscales **J.** deciduous leaf fragments **K.** *Batrachium* sp. seed **L.** *Carex* sp. perigynium **M.** *Caltha palustris* seed **N.** *Scirpus sylvaticus* fruit **O.** *Solanum* sp. seed

Fig. 3. **Plant macrofossil remains from Nagy-forrás forest hollow**. The pictures were taken with a Zeiss SteREO Discovery.V12 microscope in the Institute of Archaeology of the Research Centre for the Humanities (Hungarian Academy of Sciences)

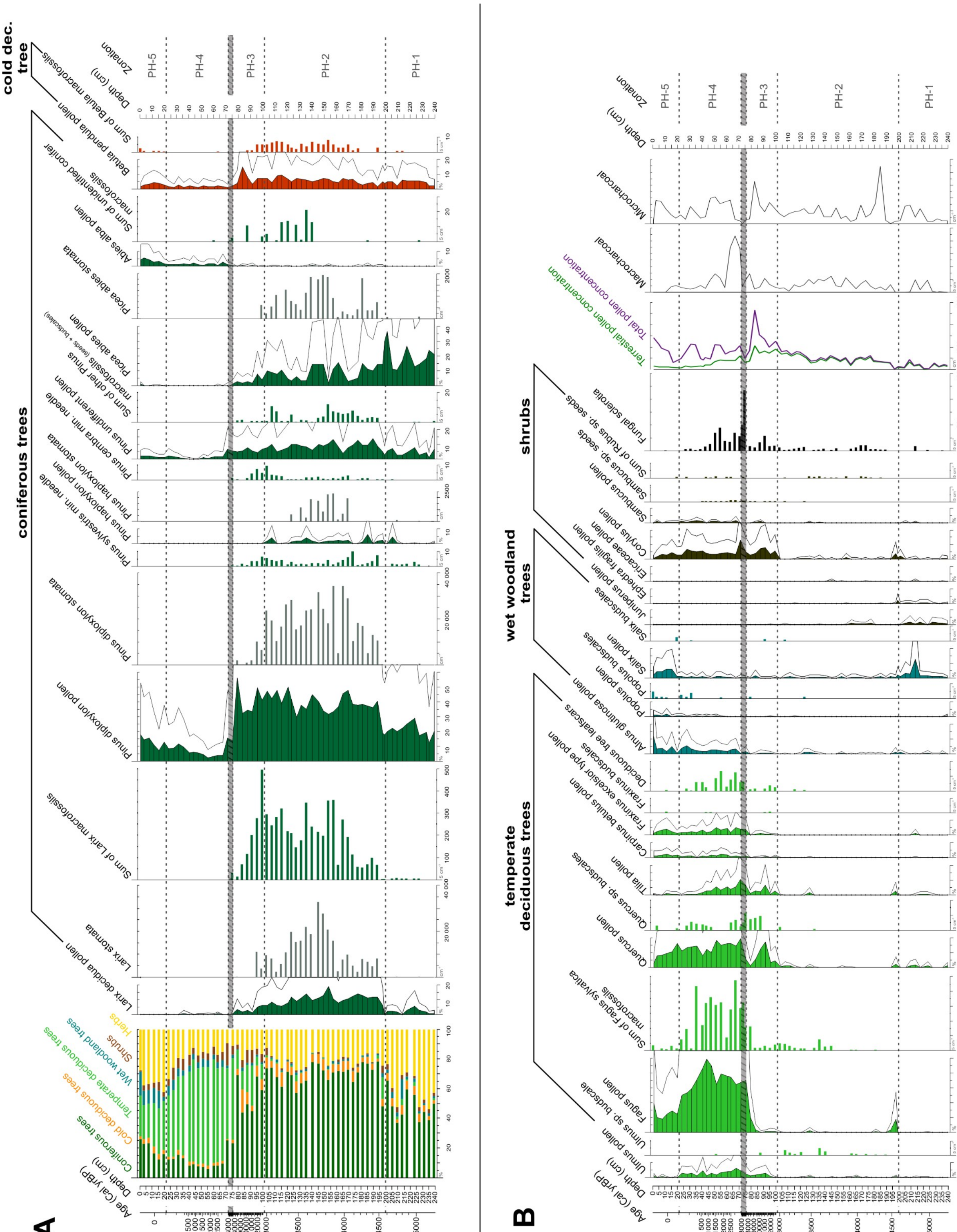


Fig. 4. **Pollen percentage diagrams of selected tree and shrub pollen types and concentration diagrams of the selected plant macrofossils.**

A. Coniferous trees and cold-tolerant deciduous trees.

B. Temperate deciduous trees, wet woodland trees and shrubs.

The stacked bar chart shows the relative proportion of the different vegetation types (based on pollen record). Filled line charts represent the pollen proportions in percentage, where 100% is the sum of all terrestrial taxa (see total terrestrial pollen), the exaggeration factor (black line) was 3. Grey bar charts: stomata concentrations (pieces in 1 cm^3). Bar charts: macrofossil concentrations (pieces in 5 cm^3). Line charts: the total pollen concentration (in 1 cm3) and charcoal records

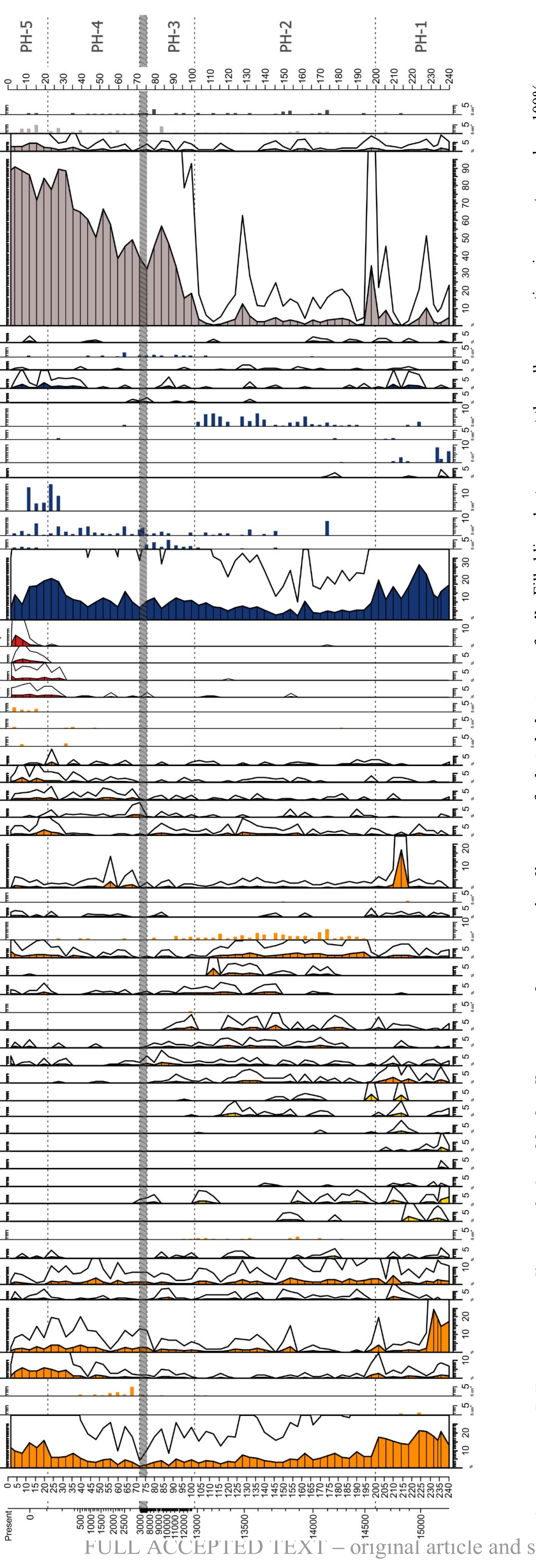


Fig. 5. **Pollen percentage diagram of selected herb pollen types and concentration diagrams of selected plant macrofossils.** Filled line charts represent the pollen proportions in percentage, where 100% is the sum of all terrestrial taxa (see total terrestrial pollen), the exaggeration factor (black line) was 3. Bar charts: macrofossil remains concentrations (pieces in 5 cm^3)

PH-1, 240-200 cm, 15 425-14 615 cal yr BP

The bottom zone is composed of sandy sediment with mineral particles and clay and has low organic matter content (LOI < 20%). The equal proportion of terrestrial herb pollen (mainly Poaceae, *Artemisia* and *Ranunculus* type) and coniferous tree pollen (*Pinus* diploxylon *type* and *Picea*) suggested open boreal forest vegetation (Figures 4 & 5). The occurrence of cold-tolerant herbs (*Selaginella selaginoides*, *S. denticulata*, *Oxyria dygina*, *Saxifraga oppositifolia*, *S. granulata* and *S. stellaria*) is notable (Figure 5) and their presence indicates alpine snow beds, wet rock surfaces, grasslands and nearby springs or seep-water. Overall, they are indicative of boreal and wet tundra-like habitats around the hollow. Submerged aquatic species (*Batrachium* sp.), hydro- and helophytes (*Comarum palustre, Caltha palustris, Typha* sp., Cyperaceae) and NPP types from this zone indicate shallow, oligo-mesotrophic pond environment. According to the plant macrofossil record the open boreal forest around the lake was dominated by *Picea* sp., *Larix* sp. and *Pinus sylvestris*. The lakeshore was covered by *Betula pendula/pubescens* trees and *Salix* sp. shrubs.

PH-2, 200-102 cm, 14 615-12 980 cal yr BP

In zone PH-2, the brown sandy sediment is turning to dark brown (almost black) decomposed sediment with turfa (peat); the amount of organic matter increases through the zone (Figure 2). This zone is the most diverse both in pollen and macrofossil types and is characterized by very well preserved plant and moss remains (Figures 3 & 5). The relatively high proportion of conifer pollen (*Picea, Larix decidua*, *Pinus* haploxylon *type* and diploxylon *type*) and the abundant finds of *L. decidua*, *Pinus cembra* and *Pinus sylvestris* needles and stomata suggest the presence of a local European larch-swiss stone pine dominated boreal forest. According to the macrofossils, *Betula pendula* and *B. pubescens* grew on the site, too. The presence of *Ephedra, Juniperus*, Ericaceae, *Spiraea, Sambucus* and *Rubus* may point to a relatively rich shrub layer and light-demanding shrubs likely indicate poorly vegetated scree surfaces. The significant proportion of *Picea* pollen and stomata suggests Norway spruce populations close to the hollow. The diverse moss community (11 species, e.g. *Drepanocladus aduncus*, *Calliergon cordifolium*, Supplementary Figure 4) and the presence of *Comarum palustre, Caltha palustris*, *Urtica* sp., *Carex appropinquata* and other *Carex* species indicate mesotrophic fen habitats in the mire.

PH-3, 102-74 cm, 12 980-7050 cal yr BP

This zone has uniform lithostratigraphy (dark brown, almost black decomposed lake sediment with turfa) and constantly high organic matter content (50-60%). Based on changes in the macrofossil and pollen types (Figure 4), the importance of conifers decreases, while deciduous trees (mostly *Quercus, Ulmus* and *Tilia*, see Supplementary Table 1) become more abundant. *Larix decidua*, *Pinus cembra* and *P. sylvestris* macrofossils are still abundant suggesting the persistence of boreal forest elements. *L.*

decidua and *P. cembra* needles were dated directly to 7753 ± 44 cal yr BP (76 cm) suggesting their local persistence in the Holocene. The proportion and the diversity of taxa associated with the herb layer decreased mainly because of the strong increase in the elements of the shrub layer (*Corylus*, *Frangula* and *Sambucus*). This zone is likely a transition between the previous coniferous and subsequent deciduous forest, however the surprisingly young and most likely mixed age at 84 cm (5547 ± 48 cal yr BP; Table 1) suggests that the deciduous tree remains come from a younger layer. The brown-mosses, *Caltha palustris, Comarum palustre, Carex appropinquata* disappeared from the wetland vegetation, while the presence of *Epilobium, Filipendula ulmaria* and *Scirpus sylvaticus* seeds (Figure 5) point to a tall-herb marsh in the vicinity of the core location. These data suggest that *Larix decidua, Pinus cembra* and *Pinus sylvestris* survived until *ca*. 7050 cal yr BP on the northern slope of Kékes Mount. The presence of macroscopic remains of several temperate deciduous trees like *Ulmus* sp., *Quercus sp*. and *Fagus sylvatica* bud scales, accompanied by 5-15 % *Tilia sp.* and *Corylus sp.* pollen suggest that deciduous trees might have been present locally and were certainly present regionally in the late glacial and early Holocene. However, the absence of directly dated early Holocene or late glacial deciduous plant macrofossils in addition to the different behaviour of the pollen curves warrant that at least some of the macrofossils are contaminations by later animal disturbances. *Ulmus sp.* was however likely present locally since at least the Late Glacial period, as its macrofossils were more abundant in the late glacial sediment layers than in the Holocene, particularly from 13 600 cal yr BP. The pollen and plant macrofossil data on the whole suggest that the transition from boreal to temperate deciduous forest lagged behind.

Hiatus, 74 cm, 7050 – 2710 cal yr BP

The vegetation showed a rapid transition between 76 and 72 cm, where the conifers were replaced by deciduous trees. One additional sample (74 cm) was analysed to define the length of transition. It indicated an abrupt change that occurred between the 74 cm and 72 cm. The relatively big difference in ages (7050 cal yr BP at 74 cm and 2680 cal yr BP at 72 cm), the sharp transition in the macrofossil composition and the high amount of fungal remains (*Cenococcum geophylum* sclerotia) at 74 cm altogether suggest a hiatus at this point (the possible reasons for the hiatus are discussed in the supplementary material).

PH-4, 72-22 cm, 2710-110 cal yr BP

This zone has similar uniform lithostratigraphy to the previous one (PH-3). The organic matter content, after a short decrease between 72 and 55 cm, increased to 80%. At 74 cm (7050 cal yr BP) coniferous tree remains still dominated, while above 72 cm (2710 cal yr BP) *Fagus sylvatica* remains dominated pointing to the presence of a mixed deciduous forest with *F. sylvatica*, *Quercus*, *Fraxinus*, *Carpinus betulus* and light-demanding shrubs *(Corylus, Sambucus)* around the hollow. The high abundance of temperate deciduous tree pollen at this time indicates that these forests developed long before 2700 cal yr BP. The increased relative frequencies of *Campanula* and *Galium* pollen also support the presence of deciduous forest. According to the macrofossils and pollen, *Alnus* and *Salix* trees replaced *Betula* trees in the hollow. The presence of *Triticum/Avena* pollen from 28 cm (175 cal yr BP) and the increase in *Plantago major* type and Chenopodiaceae pollen indicate human presence in this time period. According to the historical maps (Biszak et al., 2014) this time period coincides with the time when the people of the foothill villages began to cut the forest in the higher and more distant parts of the mountain too. While on the map of Second Military Survey (1819-1869), only deforestations near to the settlements are marked, the Cadastral Map (from 1887) shows many new clearings and meadows within the 2 km radius of the Nagy-Forrás forest hollow (see Supplementary Figure 2).

PH-5, 22-0 cm, 110 cal yr BP to present

The uppermost zone has a uniform lithostratigraphy and high organic matter content similar to the previous one (PH-4, see Figure 2). The pollen and plant macrofossil composition and thus the inferred vegetation are also similar to the previous zone, but it shows more signs of human disturbance. The increase in the relative proportion of herbs, and the presence of *Triticum/Avena, Secale, Ambrosia artemisiifolia, Juglans regia, Abies alba, Pinus* diploxylon *type* pollen and *Betula pubescens* macrofossils indicate additional deforestation and artificial plantations. *Populus*, *Salix* and *Alnus* macrofossils together with *Carex paniculata, Hypericum maculatum*, *Solanum dulcamara* and a large amount of Filicales spores show a community very similar to the present-day vegetation on the site.

Statistical analysis and vegetation trajectory

Altogether 23 pollen types passed the abundance criteria and were used for the principal component (PC) analysis (see Supplementary Table 2). Only the first two axes were statistically significant. The first axis represented 64% of the total variance and showed the difference between the coniferous and deciduous tree dominated vegetation phases (high species scores are attained by coniferous taxa and low scores by deciduous taxa). The second axis represented 11% of the total variance and reflected the openness of the vegetation (high positive taxon scores are attained by Poaceae, Chenopodiaceae, *Senecio* and *Salix*). The samples were separated well along the first two axes, grouped according to the pollen zones and followed the succession from open boreal forest to *Larix-Pinus* forest, and from coniferous to deciduous forest (Figure 6). All other axes were below 5%. Overall, the PC biplot shows that the vegetation trajectory in the investigated sediment profile is unidirectional, i.e., it represents a secular successional series It is notable, too that zones PH-4-5 have distinct different pollen compositions, from that of the transitional PH-3 zone, which is more similar to the Late Glacial and Early Holocene pollen assemblages. Overall, the PC biplot shows that the vegetation trajectory in the investigated sediment profile is unidirectional, i.e., it represents a secular successional series.

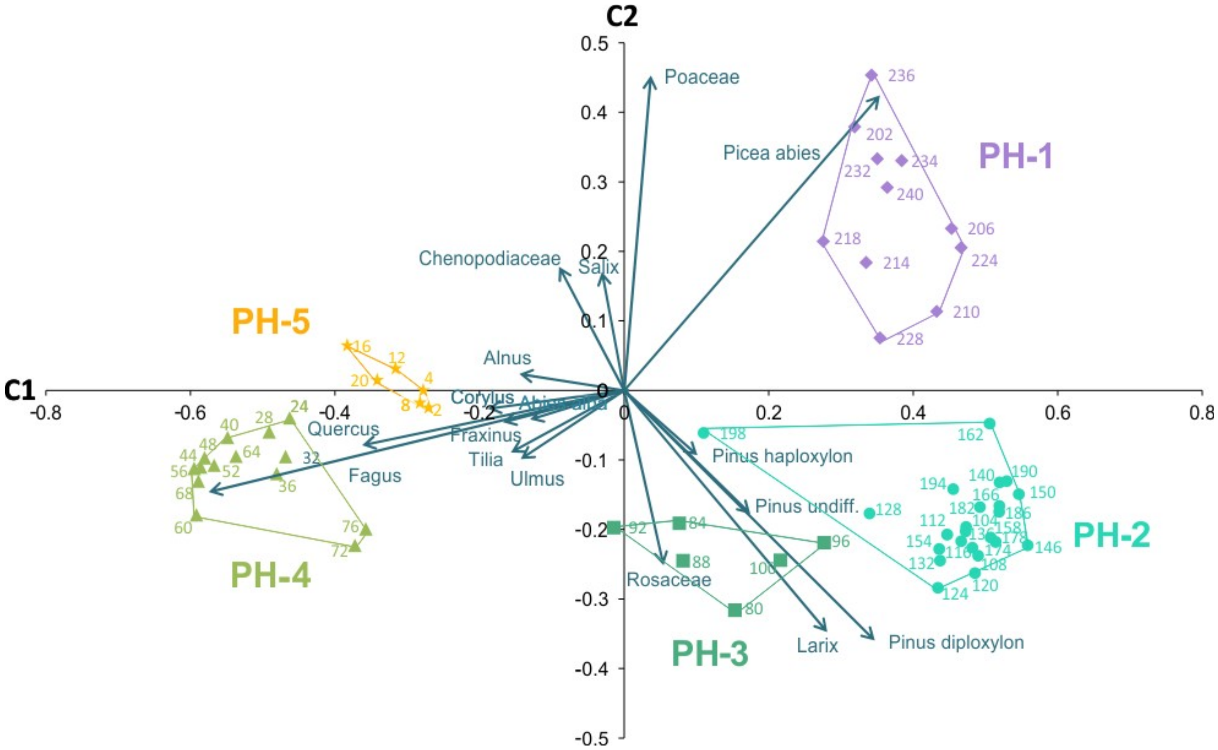


Fig. 6. Principal component analysis (PCA) biplot of main terrestrial taxa. Only the taxa with loadings higher than 0.1 for both axes were plotted. PH 1-5 represents the local pollen zones.

Discussion

On the basis of paleobotanical results, the vegetation history of the area is clearly different from other parts of the North Hungarian Mountains, and also from the Carpathian Basin in general (Feurdean et al., 2014; Magyari, 2015; Magyari et al., 2014; Sümegi et al., 2012). In the Carpathian Basin the transition from boreo-nemoral taiga to temperate deciduous forest started roughly around 11 700-10 100 cal yr BP with the persistence of mixed Scots pine-deciduous (*Ulmus*, *Quercus*, *Corylus*) forests in Transdanubia until *ca*. 8000 cal yr BP (Magyari, 2015). The long-term existence of a conifer population at relatively low altitude (685 m a.s.l.) is unprecedented in the region during the Holocene (Feurdean et al., 2014; Gardner, 2002; Jakab and Sümegi, 2010; Magyari et al., 1999, 2001, 2008; Sümegi and Náfrádi, 2015; Willis et al., 1995, 1997; Willis and van Andel, 2004), and suggests that the northern slope of Kékes could have served as a refugium for coniferous species.

Regional to local distribution patterns of coniferous species – a Holocene conifer refugium

On the northern slope of Kékes, at least four coniferous species were present during the Late Glacial period: *Pinus sylvestris*, *Pinus cembra*, *Picea abies* and *Larix decidua*. Two of them (*Picea abies* and *Pinus sylvestris*) still have some sporadic native populations in Western Hungary, while *P. cembra* and *L. decidua* are not part of the native flora of present-day Hungary (Fekete et al., 2014). *P. abies* is one of the main tree species in Europe and covers large areas between 800-1800 m a.s.l. in the Carpathians and in the Alps (Caudullo and de Rigo, 2016; Leuschner and Ellenberg, 2017). *Larix decidua* and *P. cembra* are less common, their closest mixed stands are located in the upper alpine and subalpine belts in the Alps (between 1100 and 2500 m), and occur as population fragments in the Southern and Eastern Carpathians (1300-1900 m) and in the High Tatra Mountains (Casalegno et al., 2010; Caudullo and de Rigo, 2016; Leuschner and Ellenberg, 2017). It is well known that all of these conifer species survived the LGM in the Great Hungarian Plain (Magyari et al., 2014; Rudner and Sümegi, 2001; Willis et al., 2000; Willis and van Andel, 2004) and also occurred constantly in the North Hungarian Mountains during the late Pleistocene (see Supplementary Table 3). Although all of these taxa disappeared from the North Hungarian Mountains during the Holocene, their withdrawal dynamics were slightly different.

The recession of *Picea abies* started between 12 000 and 11 000 cal yr BP and was completed by around 10 000-9 000 cal yr BP in the North Hungarian Mountains (Jakab and Sümegi, 2005; Latałowa and van der Knaap, 2006; Willis et al., 1997). Some isolated *P. abies* stands possibly remained until 8 000 cal yr BP in the North Hungarian Mountains (Jakab and Sümegi, 2005) and there are signs of *P. abies* presence in the study region after 3750 cal yr BP too (Szabó and Félegyházi, 1997). In parallel, it expanded its range to north- and westwards and to higher altitudes in the Alps and the Carpathians (Birks and Willis, 2008; Latałowa and van der Knaap, 2006). Nowadays some extrazonal spruce stands still occur at the lower altitudes, usually in the cool microclimate of deep valley bottoms or at the margins of bogs (Leuschner and Ellenberg, 2017)

In contrast, *Pinus sylvestris* was an important element of the vegetation in the Carpathian Basin even after the beginning of the Holocene, as it formed extended mixed stands with deciduous trees (Juhász, 2007; Magyari, 2015; Moskal-del Hoyo et al., 2018). Later in the Mid-Holocene its population size dramatically decreased due to competition by deciduous tree species (Jakab and Sümegi, 2005, 2010; Willis et al., 1997) and only small populations survived mostly at edaphically specialized habitats throughout the whole Carpathian Basin (Tóth et al., 2019).

Larix decidua was also restricted to mid- and high-altitude places in the Early Holocene (10 500-9500 cal yr BP), but some stands survived until 5000 cal yr BP at low altitudes (Wagner et al., 2015) and until around 4000 cal yr BP in the Southern-Carpathians (Magyari et al., 2018). According to pollen and macrofossil evidences, some small population of *Larix* survived even until historical times in the Polish Carpathians at mid (640-680 m a.s.l) altitudes (Krąpiec et al., 2016), in the Czech Republic (Kuneš and Abraham, 2017) and were later eliminated by human deforestation. Overall, this species has small refugial populations in the Carpathian Mountains today (Mihai and Teodosiu, 2009; Fărcaş et al., 2013).

While *P. abies* and *P. sylvestris* have broad distributions, the present-day area of *P. cembra* and *Larix decidua* are smaller compared to the period before the Holocene. Based on charcoals preserved in cave sediments and loess deposits, we can say that *P. cembra* was already present in the North Hungarian Mountains 140 000 years ago (Greguss, 1940; Sárkány, 1937) and its stands also occurred in the

Hungarian Plain at lower altitudes (Hermann, et al., 1956; Jánossy, 1961; Magyari, 2015; Magyari et al., 1999; Stieber, 1967, 1969). With the warming after the LGM, it also appeared at higher altitudes: it colonized the mid-altitudes (450-750 m a.s.l.) in the West Beskids and Poprad basin at ~15 500 cal yr BP (Krapiec and Margielewski, 2003; Kuneš et al., 2008; Margielewski et al., 2003, 2010), and the subalpine region earliest at 16 000 cal yr BP in the Alps (Hofstetter et al., 2006). It reached the subalpine regions of the Southern Carpathians around 14 500-12 850 cal yr BP in the Retezat (Magyari et al., 2012; Orbán et al., 2018; Vincze et al., 2017) and was documented in the Rodna Mts. between *ca*. 11 250 and 9800 cal. yr BP (Feurdean et al., 2016). In parallel with these events, the conifer-to-deciduous forest change occurred at lower altitudes. Most of the *P. cembra* populations disappeared from the lowlands and from the mid-mountain regions around 11 500 cal yr BP (Jankovská, 1988; Kołaczek et al., 2017; Kuneš et al., 2008; Willis et al., 1995), or shortly after the beginning of the Holocene at the latest (Jankovská, 1984; Krapiec and Margielewski, 2003; Kuneš and Abraham, 2017; Margielewski et al., 2010; Pokorný et al., 2017). Based on these data, the Holocene *P. cembra* stand on the Kékes slope was a small and isolated population, and the area can be designated as a Holocene refugium.

The role of local settings in the formation of the cold refugium

Based on our findings, the question may arise: what made the area capable of preserving the coniferous species (most importantly the Swiss stone pine) until the mid-Holocene? The decline of coniferous trees in the Carpathian Basin was triggered by climate change: in the Early Holocene the climate became warmer and the growing season longer, which allowed the deciduous trees to outcompete the previously dominant boreal taiga elements (Tóth et al., 2015). Coniferous trees, in general, were driven back to colder areas and/or areas that had a more continental climate with frequent late frosts, often with otherwise unfavourable soil conditions, e.g., poor in nutrients, mildly acidic, shallow, or with bad water supply (Huntley, 1990; Leuschner and Ellenberg, 2017). The long local existence of a coniferous forest around the Nagy-forrás forest hollow could be supported by the shallow soil layer of the steep slope or by the waterlogged soil in the hollow.

In addition to the edaphic reasons, the presence of *P. cembra* suggests that the area had a colder and more humid mesoclimate. Compared to the deciduous trees and to other coniferous species, *P. cembra* requires a colder (9-16 °C summer average temperature), and more humid (min. 700 mm yearly precipitation) climate (Leuschner and Ellenberg, 2017). Although it can also appear in areas with slightly warmer conditions that are still not suitable for deciduous trees, but it generally cannot compete in these areas with *Picea abies* or even with *Larix decidua*, which otherwise forms mixed forests with Swiss stone pine (Casalegno et al., 2010; Caudullo and de Rigo, 2016). Moreover, *P. cembra* tolerates frost exceptionally well (until -10 °C in summer, and -70 °C in winter), but the summer warm period can be lethal for its populations, if it reaches 30 °C (Leuschner and Ellenberg, 2017). Based on these facts, the local persistence of Swiss stone pine suggests that the Nagy-forrás forest hollow and its neighbourhood have been decoupled from the regional climate and represented a cooler and more humid environment.

There is no direct evidence for the present-day cooler micro/mesoclimate in absence of microclimate measurements in this area. However, the cold microclimate and the possibility of a cold refugium is supported by the presence of the cold-tolerant montane and subalpine plant species, that would be otherwise absent at this altitude in Hungary (e.g. _*Polygonatum verticillatum, Woodsia alpine, Rosa pendulina, Valeriana tripteris*_, Vojtkó et al., 2010). In addition, the topography of the area (e.g. north facing slope and local depression) theoretically makes a slightly colder microclimate possible: the north facing slopes are generally characterized by shorter growing seasons, less solar radiation and lower maximum temperature (Dobrowski, 2011; Geiger and Bouyoucos, 1951; Körner, 2003). On the one hand, the steep slopes can also be dry, as the soil layer is shallow and water runoff is high (Dobrowski, 2011), on the other hand, the convergent environments (basins, local depressions, sinks) pool cool air and accumulate soil and water (Dobrowski, 2011). Thus the combination of north facing slope and local depression together could facilitate a cool and humid micro/mesoclimate in case of Nagy-forrás forest hollow too.

This possible decoupling from the macroclimate of the northern slope of Kékes might be especially important in the light of recent climate change. The discovery of areas with cool and humid microclimate is a hot topic in conservation biology (Suggitt et al., 2018), not only because they can preserve glacial relict species, but also because they are able to buffer the effects of the warming climate (Maclean et al., 2015; Suggitt et al., 2011), and thus they can potentially function as refugia for species threatened by present-day climate change (Dobrowski, 2011; Suggitt et al., 2011, 2018). In absence of other disturbances, the stands of these areas are also more resistant to the invasions triggered by climate change (Suggitt et al., 2011, 2018). The identification of past microrefugia could be a helpful tool in conservation biology, but in most cases their exact landscape positions are difficult to localize (Dobrowski, 2011). This fact underlines the importance of the conifer refugium around the Nagy-forrás forest hollow. The significance of these findings is further strengthened by the fact that the northern slope of Kékes is covered by a relatively undisturbed beech forest today (Czájlik, 2009), and beech is threatened by climate change in Hungary (Czúcz et al., 2013; Mátyás et al., 2010).

When did beech colonize the local forest? What are the chances for its survival under global warming?

*Fagus sylvatica* survived the LGM both in Southern European and in small Central European northern (cryptic) refugia, and started to spread at the beginning of Holocene (Huntley, 1990; Magri, 2008; Magri et al., 2006). On the basis of our current knowledge, the Carpathians were colonized both from southern refugia and from cryptic refugia. The first signs of the beech presence in the Holocene are from Moravia (8900-10 200 cal yr BP, Magri, 2008), from the Vihorlat (11 500 cal yr BP, Wiezik et al., 2019), from the Little Carpathians (11 000 - 10 000 cal yr BP, Wiezik et al., 2019) and from Western Hungary (8200-11 400 cal yr BP, Magyari, 2002).

In the northern part of the Carpathians (Tatra) its first detection times (>2%) date back to 9700 - 8900 cal yr BP (Magyari, 2002; Wiezik et al., 2019), while apparent local presence in Apuseni Mountains dates to ca. 9400-9000 cal yr BP (Bodnariuc et al., 2002; Grindean et al., 2015). There are signs of the presence of beech stands from 7000 cal yr BP in Rodna (Grindean et al., 2019; Tanţău, Geantă, et al., 2014), from 6500-6700 cal yr BP in the South Carpathians (Magyari et al., 2018) and from *ca.* 5100-4800 cal yr BP in Maramureş and Gutin Mts., (Björkman et al., 2003; Fărcaş et al., 2013).

Based on sites from similar altitude as the Nagy-Forrás (600-1200m), beech became present at ca. 5-6000 cal yr BP (Apuseni Mts., Retezat hivatkozások). (Bodnariuc et al., 2002) (Magyari et al., 2018).

Beech started to expand at the mid altitudes of Eastern and Southern Carpathians between 5200 – 4500 cal yr BP (Feurdean, 2005, 2010; Grindean et al., 2014, 2019; Tanţău, Geantă, et al., 2014) and became dominant ca. 4000 cal yr BP ago (Feurdean et al., 2011). At the lower altitudes of mountains (300-600 m a.s.l.), in the plains and more continental parts of the Carpathians, F. sylvatica expanded around 4800-4000 cal yr BP (Czerwiński et al., 2019; Grindean et al., 2014) or between 3700-3000 cal yr BP (Magri, 2008; Magyari, 2002; Tanţău, Feurdean, et al., 2014) at latest.

In the North Hungarian Mountains *F. sylvatica* became remarkable between 7900-4500 cal yr BP, then it attained its present day distribution by 3100 cal yr BP when it replaced temperate deciduous tree (mostly *Ulmus sp.*, *Corylus avellana* and *Quercus sp.*) species (Gardner, 2002; Magyari, 2002; Magyari et al., 2010; Willis et al., 1998). *F. sylvatica* might have been present from 9000-8000 cal yr BP according to the pollen record (exceeded 10%) at the Nagy-forrás forest hollow; however, the formation of the beech-dominated mixed forest cannot be pinpointed on the timeline because of the hiatus. The first direct evidence of the beech-dominated forest is after the hiatus (from 2710 cal yr BP), but most likely beech overtook dominance on the northern slope of Kékes earlier, at latest 3100 year ago.

Fagus sylvatica has reached its maximum distribution in Europe by present (Bradshaw et al., 2010; Giesecke et al., 2006; Magri, 2008; Saltré et al., 2013), and dominates almost all physiologically suitable habitats by outcompeting other deciduous tree species (Leuschner and Ellenberg, 2017). However, beech is sensitive to late frosts and summer drought (Fang and Lechowicz, 2006; Leuschner and Ellenberg, 2017; Packham et al., 2012), so most of the beech population is found in areas with Atlantic climate, mild winters (minimum -2.3 °C coldest-month mean temperature) and humid summers with minimum 520-1000 mm annual precipitation (Leuschner and Ellenberg, 2017; Magyari et al., 2010; Packham et al., 2012; Sykes et al., 1996). Nevertheless, beech populations in the Carpathian Basin grow close to their xeric limits, and therefore they are threatened by warming climate (Garamszegi and Kern, 2014; Salamon-Albert et al., 2016). Climate models for the Carpathian

Basin predict the disappearance of the so-called 'beech climate' from Hungary until AD 2100 (Czúcz et al., 2013; Mátyás et al., 2010). The frequency of late frost can also have a significant role in the long-term survival of beech (Fang and Lechowicz, 2006; Leuschner and Ellenberg, 2017), and both model results (Rigby and Porporato, 2008) and field observations (Augspurger, 2013) show the increasing risk of late spring frosts in the future in the Carpathian Basin. However, these models use only the regional climate parameters and do not take into consideration the adaptive potential of beech and the effect of cold and humid microclimatic patches (Lenoir et al., 2017; Suggitt et al., 2018) and the human-induced changes of distribution in the past several centuries.

If the northern slope of Kékes Mount was decoupled from the regional climate in the Early Holocene, it could preserve a cooler and more humid micro- and mesoclimate during the ongoing climate change too. As the distribution of beech is limited by drought (Fang and Lechowicz, 2006; Leuschner and Ellenberg, 2017; Packham et al., 2012), it is plausible to suggest that an area with a humid mesoclimate could support the survival of local beech populations. In addition, it was shown previously that undisturbed communities are more resistant against the effects of climate change (Suggitt et al., 2018), and the area is covered by a relatively undisturbed primary beech forest today (Czájlik, 2009).

Based on the vegetation history of the studied area, the combination of a more humid microclimate and the lack of strong human disturbances can make the northern slope of Kékes an important target for the long-term conservation of beech forests in Hungary.

Conclusions

The macrofossil, pollen and stomata analyses of the sediment of Nagy-forrás forest hollow are the first stand-scale paleoecological studies in Hungary. Since small and undisturbed forest hollows are rare at mid-altitudes under continental climate, Nagy-forrás forest hollow (685 m a.s.l) provided a rare opportunity to analyze the local vegetation patterns. The studied sediment profile showed an unidirectional vegetation trajectory from an open boreal forest and wet tundra-like habitat (15 500-14 600 cal yr BP) to a European larch-Swiss stone pine (*Larix decidua-Pinus cembra*) forest (14 600-7050 cal yr BP) and later, after a hiatus between c. 7050 and 2710 cal yr BP, to a beech (*F. sylvatica*) dominated mixed temperate deciduous forest, similar to the current forest cover. Anthopogenic influence was indicated by the presence of cereal pollen from 175 cal yr BP, while modern deforestation and artificial plantations started from 110 cal yr BP.

The most important finding of our study is that coniferous trees (*Pinus sylvestris*, *P. cembra*, *Larix decidua* and *Picea abies*) survived until the mid-Holocene on the northern slope of Kékes Mount. Swiss stone pine macrofossils have never been found in Holocene sediments in Hungary before. The long-lasting presence of the coniferous tree species suggests that the study area was decoupled from the regional climate and did not follow the patterns of regional vegetation changes. Given that our study area was a cold conifer refugium during the Holocene, we assume it can play the same role for present day beech forests which are threatened by recent climate change in Hungary.

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The Authors declare that there is no conflict of interest.

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Figure legend:

Fig.1. **Location of Nagy-forrás forest hollow in the Carpathian Basin and in the Mátra Mountains.**

Fig.2. **The results of age-depth modelling, lithostratigraphical description and loss on ignition measurements of the Nagy-forrás forest hollow, core PM-1.** The symbols of the lithography follow the Troels-Smith nomenclature: Th-<u>*Turfa herbacea*</u>, Ld-<u>*Limus humosus*</u>, Ag-<u>*Argilla granosa*</u>, As-<u>*Argilla steatodes*</u>, Ga-<u>*Grana arenosa*</u>, Gs-<u>*Grana saburralia*</u>, Gg-<u>*Grana glaerosa*</u> (min)

Fig. 3. **Plant macrofossil remains from Nagy-forrás forest hollow**. **A.** *Larix sp*. dwarf shoot **B.** *Larix sp*. needle tip **C.** *Larix decidua* cone **D.** *Larix decidua* seed **E.** *Pinus sylvestris* needle **F.** *Pinus cembra* needle **G.** *Betula pubescens* fruit **H.** *Fagus sylvatica* twigs **I.** *Populus sp*. budscales **J.** deciduous leaf fragments **K.** *Batrachium sp*. seed **L.** *Carex sp*. perigynium **M.** *Caltha palustris* seed **N.** *Scirpus sylvaticus* fruit **O.** *Solanum sp*. seed. The pictures were taken with a Zeiss SteREO Discovery.V12 microscope in the Institute of Archaeology of the Research Centre for the Humanities (Hungarian Academy of Sciences)

Fig. 4. **Pollen percentage diagrams of selected tree and shrub pollen types and concentration diagrams of the selected plant macrofossils.**

A. Coniferous trees and cold-tolerant deciduous trees.

B. Temperate deciduous trees, wet woodland trees and shrubs.

The stacked bar chart shows the relative proportion of the different vegetation types (based on pollen record). Filled line charts represent the pollen proportions in percentage, where 100% is the sum of all terrestrial taxa (see total terrestrial pollen), the exaggeration factor (black line) was 3. Grey bar charts: stomata concentrations (pieces in 1 cm^3). Bar charts: macrofossil concentrations (pieces in 5 cm^3). Line charts: the total pollen concentration (in 1 cm3) and charcoal records

Fig. 5. **Pollen percentage diagram of selected herb pollen types and concentration diagrams of selected plant macrofossils.** Filled line charts represent the pollen proportions in percentage, where 100% is the sum of all terrestrial taxa (see total terrestrial pollen), the exaggeration factor (black line) was 3. Bar charts: macrofossil remains concentrations (pieces in 5 cm^3)

Fig. 6. **Principal component analysis (PCA) biplot of main terrestrial taxa.** Only the taxa with loadings higher than 0.1 for both axes were plotted. PH 1-5 represents the local pollen zones.

Table legend:

Table 1. Results of AMS ^{14}C measurements from Nagy-forrás forest hollow (core PM-1) – in text

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