

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

## Global Ecology and Conservation

journal homepage: [www.elsevier.com/locate/gecco](http://www.elsevier.com/locate/gecco)

# Vegetation and land snail-based reconstruction of the palaeocological changes in the forest steppe eco-region of the Carpathian Basin during last glacial warming

Pál Sümegei<sup>a,b,\*</sup>, Dávid Molnár<sup>a,b,\*</sup>, Katalin Náfrádi<sup>a,b</sup>, László Makó<sup>a,b</sup>, Péter Cseh<sup>a,b</sup>, Tünde Töröcsik<sup>a,b</sup>, Mihály Molnár<sup>c</sup>, Liping Zhou<sup>d</sup>

<sup>a</sup> Department of Geology and Paleontology, University of Szeged, Egyetem u. 2-6., H-6722 Szeged, Hungary

<sup>b</sup> University of Szeged, Interdisciplinary Excellence Centre, Institute of Geography and Earth Sciences, Long Environmental Changes Research Team, Egyetem u. 2-6., H-6722 Szeged, Hungary

<sup>c</sup> INTERACT AMS Laboratory Nuclear Research Center, Bem tér 18/c., H-4026 Debrecen, Hungary

<sup>d</sup> Institute of Ocean Research, Peking University Leo KoGuan Building, Room 511, 100871, China

## ARTICLE INFO

## Keywords:

Carpathian Basin

Last deglacial warming

Long-term climatic and environment impacts

Terrestrial molluscs assemblage succession

change

Forest steppe habitat developing

## ABSTRACT

In the present work, well radiocarbon-dated Quaternary malacological and palynological analyses were implemented on 4 cm samples deriving from one of the thickest and best developed last glacial sequences of Central Europe the Madaras brickyard and the borehole of Kolon Lake in the southern part of Hungary. Using a combination of mollusc, anthracological, palynological and climatic proxies evidence preserved within loess, we demonstrate that long-term changes (e.g. the last 39,000 (28,000) years) in paleoclimatic dynamics on the northern edge of the Bácska-Titel loess plateau, on the southern part of the Great Hungarian Plain. These proxy data are reflected in the following ecological changes: a turnover from predominantly cold-tolerant mollusc fauna in a boreal type forest-steppe context under cold conditions during the last glacial then followed by a shift to a predominantly xerothermophilous land snail fauna in a temperate forest-steppe context under a warm temperate climate in the early Holocene. Certain warm-adapted, Central and SSE European distribution mollusc species such as *Caucasotachea vindobonensis* and *Granaria frumentum*, were found to have been associated with temperate forest-steppe in both the Holocene record and the present-day ecosystem.

## 1. Introduction

It can be noted based on the analysis of the recent climate changes and the marine and terrestrial ecosystems, that terrestrial communities are rapidly transforming as a result of global warming (Meir et al., 2006; Tylianakis et al., 2008; Zhou and Tung, 2013; Franzke, 2014). This process results the modification of the entire ecosystem (Agiadi and Albano, 2020; Albano et al., 2021). Today's ongoing and rapid global warming is rapidly transforming both plant communities and faunal associations under the influence of climate-induced transformation of their environment, resulting in changes in ecological community interactions and whole ecosystem processes (Agiadi and Albano, 2020; Albano et al., 2021). This contemporary warming process, the transformation of terrestrial

\* Corresponding authors at: Department of Geology and Paleontology, University of Szeged, Egyetem u. 2-6., H-6722 Szeged, Hungary.  
E-mail addresses: [sumegi@geo.u-szeged.hu](mailto:sumegi@geo.u-szeged.hu) (P. Sümegei), [molnard@geo.u-szeged.hu](mailto:molnard@geo.u-szeged.hu) (D. Molnár).

<https://doi.org/10.1016/j.gecco.2021.e01976>

Received 24 June 2021; Received in revised form 14 December 2021; Accepted 14 December 2021

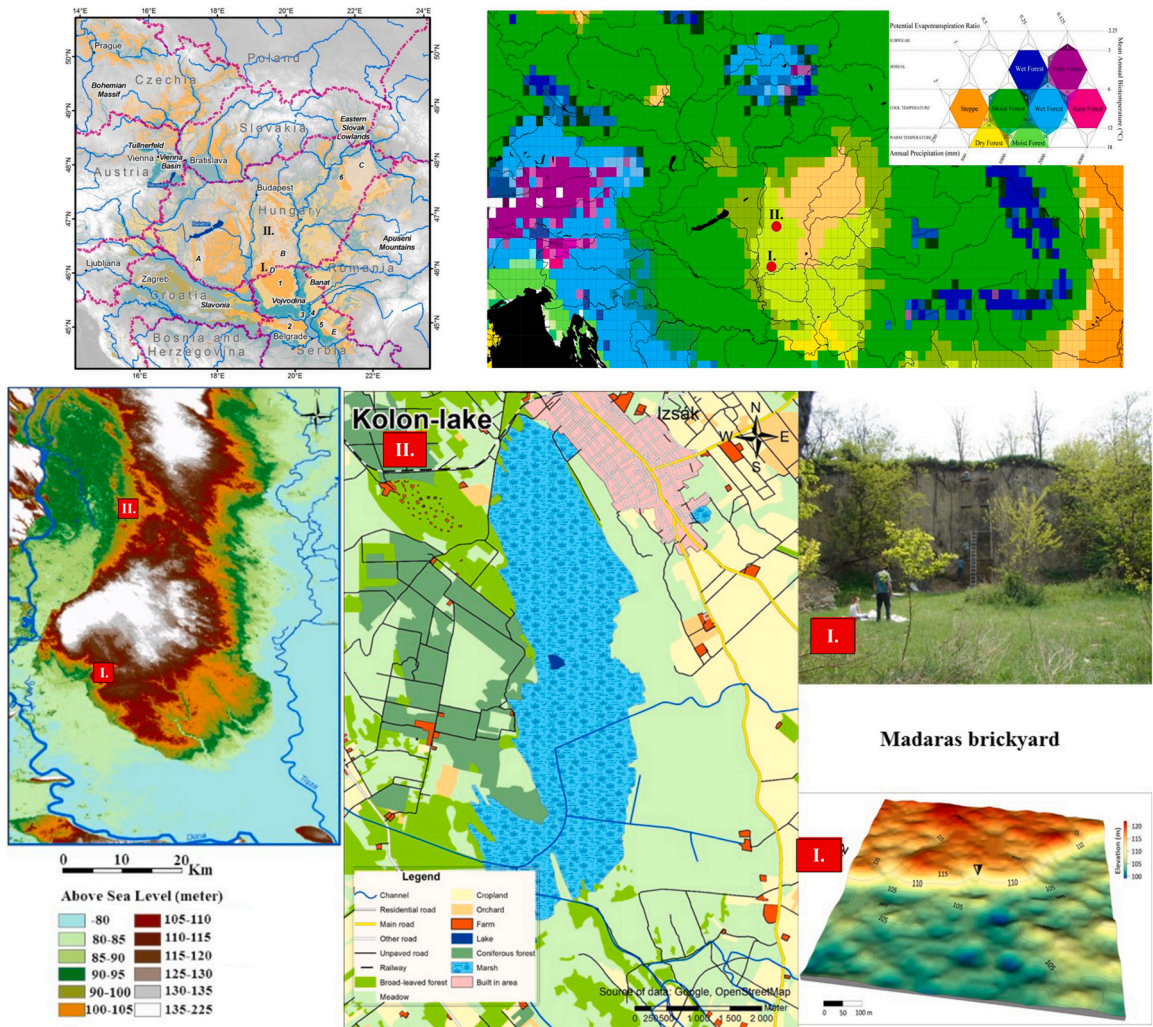
Available online 17 December 2021

2351-9894/© 2021 The Author(s).

Published by Elsevier B.V. This is an open access article under the CC BY license

(<http://creativecommons.org/licenses/by/4.0/>).

vegetation and fauna, can be excellently reconstructed by the environmental transformation that occurred at the end of the Glacial period, following the 7–8 °C temperature increase from the end of the Last Glacial Maximum (LGM) (Dong et al., 2020b), and the associated vegetation and mollusk fauna transformation. Although many publications have addressed the environmental transformations induced by climate change in the Carpathian Basin at the end of the Late Glacial/Early Holocene (e.g. Magyari et al., 2012b; Feurdean et al., 2014), these analyses have mainly focused on plant and animal remains in temperate wetlands. Dryland environmental transformations in response to Late Glacial and Early Holocene climate change in the approximately 30,000–35,000 km<sup>2</sup> of loess area in the 320,000 km<sup>2</sup> area of the Carpathian Basin have not yet been modelled. Its reason is that these sections were sampled in every 25 cm (Sümegei, 2005; Sümegei et al., 2019) according to the sampling protocol developed in the 1950 s (Krolopp, 1961, 1965, 1973, 1983; Ložek, 1964, 1965, 1990, 2001), which resulted in relatively low resolution and each sample covered thousands of years. Thus, despite the existing data, the correlation between pollen material extracted from lake/marsh sediments and mollusc material from dryland loess sediments couldn't have been established.



**Fig. 1.** Overview maps of the research area showing places of interest mentioned in the text (Lehmkuhl et al., 2018, 2020) (I. = Madaras brickyard, II. = borehole in the Lake Kolon; A = Inner Somogy, B = Little Cumania, C = Nyírség, D = Bácska loess plateau, E = Deliblat; 1 = Vojvodina (Vajdaság) loess area, 2 = Stem Loess plateau, 3 = Titel Loess plateau, 4 = Temes Loess plateau, 5 = Banat Loess plateau, 6 = Hajdúság region) and Holdridge modified bioclimatic areas of the Carpathian Basin and Carpathians, Alps, Dinaric Alps (Szelepcsényi et al., 2014, 2018) (1 = subpolar humid dry – moist tundra, 2 = subpolar perhumid moist-wet tundra, 3 = subpolar superhumid moist-wet tundra, 4 = subpolar subhumid dry – moist tundra, 5 = subpolar humid moist-wet tundra, 6 = subpolar perhumid wetrain tundra, 7 = boreal subhumid desert – dry scrub, 8 = boreal humid dry scrub – moist forest, 13 = boreal humid moist wet forest, 14 = boreal perhumid wet-rain forest, 15 = cool temperate semiarid desert – desert scrub, 16 = cool temperate subhumid desert scrub – steppe, 17 = cool temperate subhumid forest steppe, 18 = cool temperate perhumid moist-wet forest, 19 = cool temperate subhumid wet-rain forest, 20 = cool temperate arid desert – desert scrub, 21 = cool temperate subarid desert scrub – steppe, 22 = cool temperate subhumid forest steppe, 23 = cool temperate humid moist-wet forest, 24 = cool temperate perhumid moist-wet forest).

The comparative recent malacological and vegetation data (Bába, 1983, 1987, 1997a,b) from the analysed region, the central and southern parts of the Great Hungarian Plain (GHP) (Fig. 1) suggests a clear ecological interdependency between specific vegetation types and mollusc assemblages. Because today the area of the central part of the Carpathian Basin hosts a lower (Ødum, 1979) or dry treeline (Stevens and Fox, 1991) with an unusually wide ecotone (Fig. 1), where the actual steppe zone is not uniform (Molnár et al., 2007). At dry treelines, the deep roots of trees may put them at a competitive disadvantage, compared to grasses, when rains are infrequent and fail to fully saturate the soil. The shallow and diffuse root systems of grasses are probably better at harvesting water under these circumstances (Stevens and Fox, 1991). There is a drastic fall in total biomass in the transition zone between the actual woodland and the tree line from ca. 20 kg/m<sup>2</sup> to 0.6 kg/m<sup>2</sup> due to the replacement of trees by smaller bushes and non-arboreal elements (Stevens and Fox, 1991). Based on the bioclimatic models (Szelepcsényi et al., 2014, 2018), the decrease of the humidity limiting the spread of the trees in the Carpathian Basin caused the development of the Pannonian forest-steppe region, this unusually wide ecotone. Therefore, the emergence of transitional zones between woodlands and grasslands is generally controlled by the availability of humidity as a limiting factor (Szelepcsényi et al., 2014, 2018). The origin of this modern unusually wide woodland-grassland transition, the Pannonian forest-steppe region, which covers an area of ca. 100,000 km<sup>2</sup> nestled in the heart of the Carpathian Basin, is disputed (Varga et al., 2000). Three prevailing theories are available in the literature for the development of the so-called Pannonian forest-steppe (Molnár et al., 2012).

According to the first theory, the forest-steppe in the heart of the Carpathian Basin is an interim continuation of the Eastern European forest-steppe belt, which emerged as a result of the extreme drought is literally exterminating arboreal elements in the area (Kerner, 1863). This concept, held for over 150 years with only slight modifications (Soó, 1929; Borhidi, 1956; Varga, 1989), considers the modern Pannonian forest-steppe as an independent westernmost island-like fragment of the European continental oak forest-steppe, which emerged at the transitional climatic zone of closed woodlands and grasslands separated from the main belt by the ranges of the Carpathian Mts. According to the analysis of the terrestrial sections covering most of the Quaternary (Sümegei et al., 2018, 2019), the mountain range surrounding the Carpathian Basin rose to such a height between 450 and 600 thousand years ago that the inner parts of the basin could have been rain-shaded, and the drying of the area and the development of the Pannonian forest-steppe could have started. Based on these data, the Pannonian forest-steppe is not part of the Eurasian forest-steppe zone, but a vegetation unit that developed in the rain shadow of the mountains surrounding the Carpathian Basin (Sümegei et al., 2012a, 2018).

The second theory considers so-called edaphic factors (soil, geomorphology) that are responsible primarily for the emergence of forest-steppe ecotone in the basin (Zólyomi, 1957, 1987; Zólyomi and Fekete, 1994). According to this concept, the heart of the Carpathian Basin is considered to be a part of the woodland belt from the point of climate-zonal classification. Thus, the opening of closed woodland and the appearance of parkland and grassland patches must be attributed to local abiotic ecological factors. This idea is completely contradicted by the results of the bioclimatic model of the Carpathian Basin, which was developed by Holdridge (Holdridge, 1947, 1967) and shows the relationship between vegetation and climate (Szelepcsényi et al., 2016, 2018; Fig. 1). Based on the Holdridge bioclimatic model (Holdridge, 1947, 1967), not a forest but a forest-steppe environment has developed in the centre of the Carpathian Basin, as a result of the relationship between vegetation, and climate/humidity values (Szelepcsényi et al., 2016, 2018; Fig. 1). The third explanation claims human activities were responsible for the opening of the original woodland vegetation and the emergence of a Pannonian forest-steppe (Bernátsky, 1914; Rapaics, 1918; Magyarai et al., 2012a; Chapman, 2018; Moskal-del Hoyo

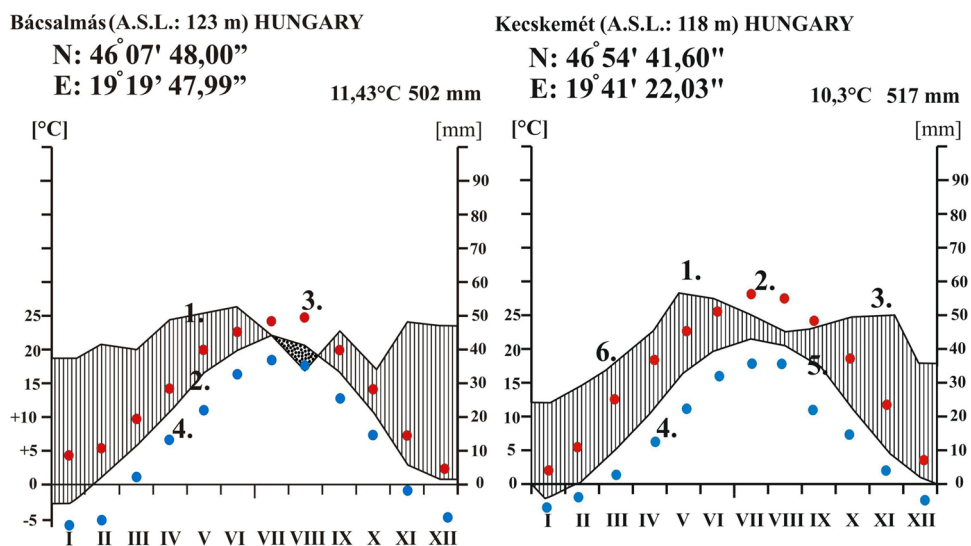


Fig. 2. Recent Walter-Lieth diagram from Bácsalmás (Madaras) and Kecskemét (Lake Kolon) settlements (For Bácsalmás diagram: 1 = annual monthly rainfall, 2 = annual average monthly temperature curve, 3 = annual warmest monthly temperature, 4 = annual coldest monthly temperature. For Kecskemét diagram: 1 = first (Atlantic) rainfall maximum, 2 = annual warmest monthly temperature, 3 = second (Sub-mediterranean) rainfall maximum, 4 = annual coldest monthly temperature, 5 = annual average monthly temperature curve, 6 = annual monthly rainfall).

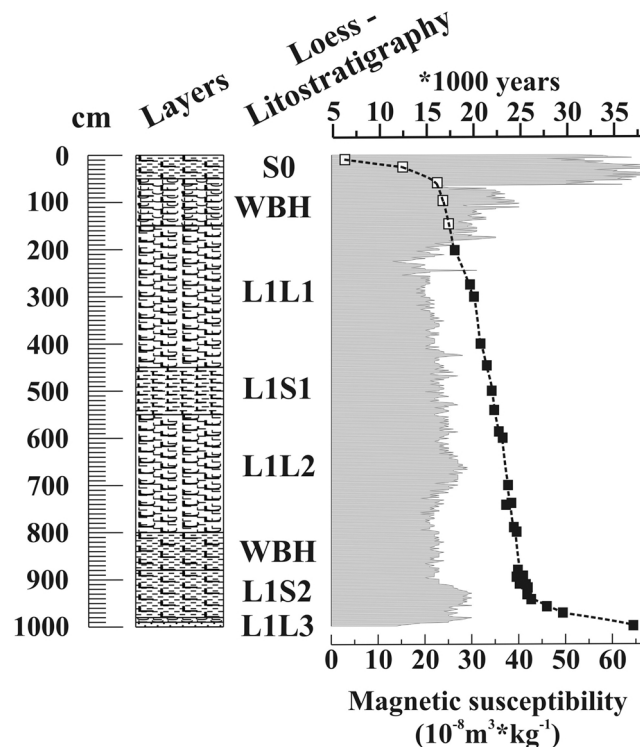
et al., 2018). The first such disturbances are linked to the first farming cultures settling in the basin (ca. 8000 cal BP = 6000 cal BC). Initial clearings gradually expanded as human activities intensified parallel with cyclical population growth. These activities thus contributed to the sustainment of a highly variegated, mosaic-like forest-steppe vegetation in the Great Hungarian Plains as early as prehistoric times (Magyari et al., 2012a; Chapman, 2018; Moskal-del Hoyo et al., 2018).

The question naturally arises: which theoretical approach to the formation of the Carpathian forest steppes is right? To answer this question, we chose a plateau loess section on the edge of the Loess Plateau in Bácska, which is dated by radiocarbon data, where only minimal differences can be observed between microclimate and regional climate (Sümegei, 2005; Náfrádi et al., 2013; Sümegei et al., 2016) and where typical forest-steppe vegetation is dominant today (Molnár et al., 2007).

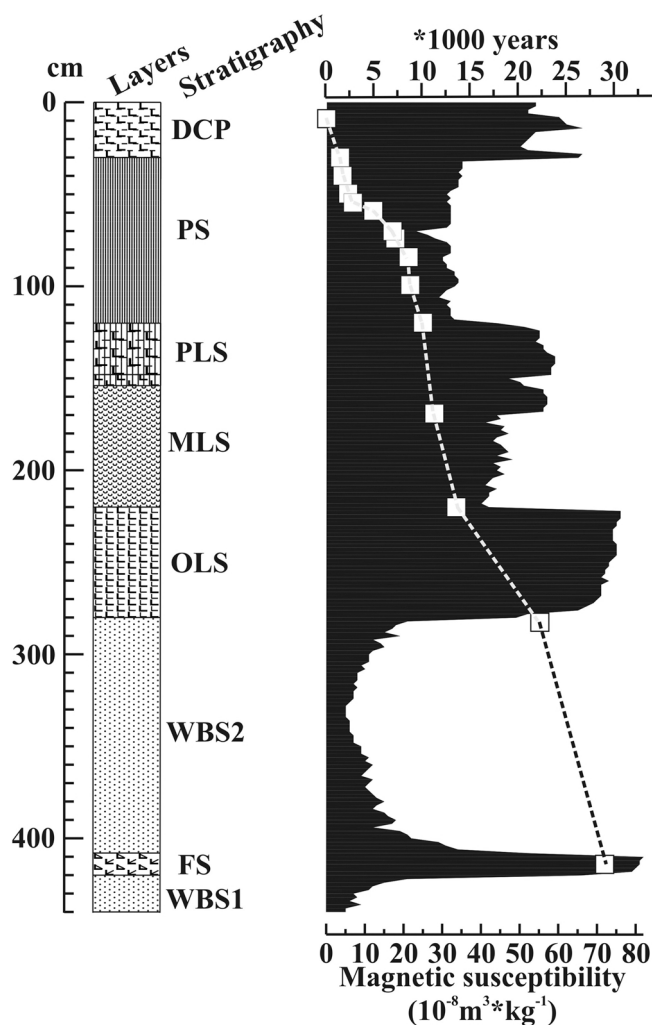
The paleoenvironmental analysis of the Late Glacial loess sequence and the overlying soil, which started to develop during the Early Holocene, was chosen because palaeolithic and mesolithic fish-hunter-gatherer communities (Dobosi, 1975) had not yet regionally transformed the vegetation of their environment in this period (Sümegei et al., 2004). Thus, the evolution of the vegetation cover in the area could be modelled by palaeoenvironmental analysis. In addition, well-radiocarbon dated univariate pollen and macrobotanical results from the region were used (Sümegei et al., 2011b, 2020) to extend the vegetation changes to a regional scale. Paleoclimatological changes between 28,000 and 10,000 thousand years were also modelled based on the changes in the dominance of temperature-sensitive snail species.

As such, the long-term vegetation-mollusc fossil records highlight the indirect impacts of climate change on soil fauna turnover via such as plant-derived food structure and habitat routes and have major implications for understanding how these ecosystems are likely to respond to future climate changes (Kis et al., 2017, 2020). The recent climatic models suggest the local and regional impact of the expected 2–5 °C annual mean temperature increase (Krüzselyi et al., 2011; Bartholy et al., 2014; Ács et al., 2020). Based on the changes in the analysed vegetation and fauna similar changes occur as a result of the climate changes that evolved at the end of the Pleistocene and beginning of the Holocene.

In the present work, we aim to fill this gap by using a decade-resolution of malacological, phytological and anthracological analysis of a 10 m loess section covering the last 39,000 years (practically the last 28,000 years – Figs. 3 and 5) of changes in the Danube-Tisza interfluvial region in the centre of the Carpathian Basin, and a decade-resolution analysis of the same period, also with a significant amount of radiocarbon data (Sümegei et al., 2011b).



**Fig. 3.** Lithology, magnetic susceptibility of samples taken at 2 cm intervals, and radiocarbon-dated sedimentation rate from the studied loess profile at Madaras settlement with potential interpretation on incipient pedogenesis (S0 = Recent Soil Horizon, WBH = Weakly Brunified Horizon, L1L1 = post LGM Loess Layer, L1L2 = Early LGM Loess, L1S1 = Weakly Developed Humic Layer, L1S2 = Paleosol, L1L3 = Loess from MIS2/MIS3 transition).



**Fig. 4.** Lithology, magnetic susceptibility of samples taken at 2 cm intervals, and radiocarbon-dated sedimentation rate from the studied undisturbed core sequence of Kolon Lake at Izsák settlement with potential interpretation on incipient pedogenesis (WBS1 = Wind-blown sand 1 layer, FS = Fossil soil within *Pinus sylvestris* (Norway pine) charcoal fragments, WBS2 = Wind-blown sand 2 layer, OLS = Oligotrophic Lake Stage, MSL = Mesotrophic Lake Stage, PLS = Peat-Lake Stage, PS = Peatland Stage, DCP = Decomposed Peat (Hydromorphic soil layer)).

## 2. Study area

### 2.1. Madaras

The Madaras loess area (N: 46° 02' 14.39" E: 19° 17' 15.01") is located in the Carpathian Basin, in the southern part of Hungary, close to the Hungarian-Serbian borderline, on the northern edge of the Bácska Loess Plateau, which is a loess plateau of 2800 km<sup>2</sup> (Fig. 1). The investigated Madaras area, is one of the driest areas of the Carpathian Basin, with air humidity below 60% and frequent air storms in July and August (Horváth et al., 2006). The Walter-Lieth (Walter and Lieth, 1967) diagram (Fig. 2), which provides an excellent illustration of the climatic conditions of the area, shows that a sharp decrease in precipitation in the second half of summer, and the concomitant development of an annual temperature maximum, leads to severe drought even in years with average temperatures. This air drought has a profound effect on the water balance, vegetation and soil conditions in the area. According to data from the climate station established in the area (Bácsalmás), the mean annual temperature is 11.43 °C, while the annual precipitation is 502 mm based on averages for the last decades (Horváth et al., 2006).

The area is covered by several metres of loess and the overlying layers are the sandy alluvial fans sediments of Danube River origin, which have developed into aeolian sand dunes (Molnár and Krolopp, 1978; Molnár and Geiger, 1995). Thus, in addition to the predominantly loessy surface, wind-blown-sand occurs as the bedrock of the study area. Moreover, alluvial sediments are also presented with incised stream valleys that divide the loess surfaces and forms a chessboard pattern (Fig. 1). As a result of the mesoclimatically uniform climatic conditions, the soil conditions predominantly follow the bedrock conditions, with hydromorphic (World Reference

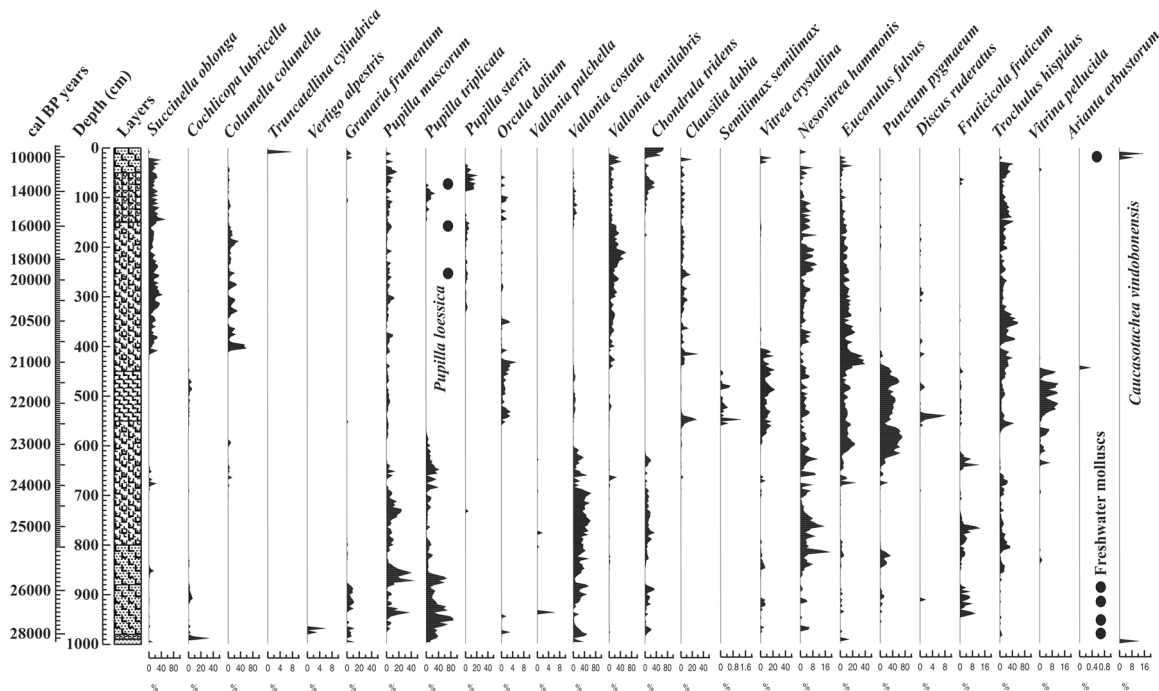


Fig. 5. Dominance changes of Quaternary snail species for the studied profile loess profile at Madaras settlement.

Base for soil resources 2006: Fluvisol, Baxter, 2007) and saline soils (WRB: Solonetz, Solonchaks) developing on the alluvial sediments, typical black soils (WRB: Chernozems) on the loess plateaus and sandy valley soils (WRB: Arenosols) on the sandy areas. However, in the area, from the Early Neolithic onwards, the productive human agriculture of the last 8000 years, and in particular the intensive mechanised agriculture of the last 200 years, has transformed all soil types into anthropogenic soils (WRB: Anthrosols), regardless of bedrock or climatic conditions and vegetation.

In the loess areas, forest-steppe elements considered to be original have been preserved (Horváth et al., 2006; Molnár et al., 2007). On the loess surfaces, the plant communities of the typical closed loess scrub grassland (*Salvio-Festucetum sulcatae*) are presented in mosaic and patchy form. The characteristic elements in these associations suggest Balkan - Eastern Mediterranean links. The most important herbaceous elements of loess grasslands, *Festuca rupicola*, *Festuca valesiaca*, *Stipa capillatata*, *Agropyron pectinatum*, *Euphorbia pannonica*, *Salvia nemorosa*, *Salvia austriaca*, *Salvia pratensis*, occur in mass stands. In addition to loess grasslands, isolated natural forest vegetation elements (*Convallario-Quercetum*) are also presented subordinately. The original surface of the Madaras brickyard at the northern end of the Bácska Loess Plateau (Telecska hills), 117 m above sea level, also contains loess grassland vegetation, besides the installed acacia (*Robinetea*).

## 2.2. Kolon Lake

The undisturbed borehole of the pollen site (N: 46° 46' 12.85" E: 19° 20' 43.47") is also located in the Danube-Tisza Interfluves, in a depression between sand dunes covered with sandy skeletal soils (WRB: Arenosols). It is situated on the edge of a glacial alluvial fan, in the centre of the Pannonian forest-steppe vegetation area (Fig. 1).

The Kolon Lake system (now a marshland with marsh patches due to recharge and river and groundwater control (1929)), has known in Latin written historical sources from 1055, was formed in an abandoned Danube riverbed (Molnár et al., 1979). The lake has a centre line at 94.5 m and a shoreline at 97 m a.s.l. It now covers about 30 km<sup>2</sup> but it was more extensive before the groundwater regulation (1929). The western edge of the lake is dominated by sand dunes, while the eastern edge is a sandy loess plateau. The swamp with marshy lake patches (Kolon Lake) is a dry terrigenous area, which entire north-south oriented area with a width of 1.5–4 km is covered by peat.

Based on historical maps and floristic analyses (Tölgyesi, 1981; Szujkó-Lacza, 1993; Hollósi et al., 2015), which include recent vegetation changes, the shallow lake - swamp system is almost entirely covered by reed (*Phragmitetalia*) in the Kolon Lake basin. In the reedbeds, besides *Phragmites australis*, *Typha latifolia*, *T. angustifolia*, *Sparganium erectum*, *Alisma plantago-aquatica* were predominant, while in the deeper water cover areas *Nymphaea alba*, *Lemna trisulca*, *Persicaria amphibia*, *Potamogeton natans*, *Hydrocharis morsuranae*, *Ceratophyllum submersum*, *Carex pseudocyperus*, *Mentha aquatica* were scattered. On the wetland edge of Kolon Lake, Orchideaceae species of outstanding importance (*Orchis laxiflora*, *Orchis militaris*, *Dactylorhiza incarnata*, *Anacamptis coriophora*) and remnants of hardwood gallery forest are known.

The bird fauna of Kolon Lake and its surroundings is of outstanding importance, even though human activities include grazing,

haymaking and reed-harvesting. The whole area is protected and is part of the Little Cumanian National Park.

The climatic conditions of the area are very similar to those of the Madaras area, as shown in the Walter-Lieth diagram (Fig. 2). Temperature and precipitation patterns are similar, but drought is less significant in the warmest months of July and August (Fig. 2). The level of the Kolon Lake follows the seasonal rainfall changes, thus the seasonal lake level fluctuating process forms in this catchment area. The average annual mean temperature is 10.3 °C and the annual precipitation is 517 mm based on public data from the Kecskemét climate station (Fig. 2).

### 3. Material and methods

#### 3.1. Methods for loess profile at Madaras

Conventional radiocarbon ages were derived from Sümeği et al. (2020, in press) which study is presented in Table 1 within now converted using the Intcal20 calibration curve (Reimer et al., 2020).

The 10 m high loess wall of the Madaras brickyard was sampled by using scaffolds. The section was cleaned from the scaffolds to a depth of 1.5 m. Samples were taken in every 2 cm for magnetic susceptibility measurements (Sümeği et al., 2012b) and sedimentological analysis, moreover, in every 4 cm for malacological analysis.

The sedimentological results were used to characterise the section by the following methods. The colour of the sediments was determined by using the Munsell Colour Scale (Munsell, 1954).

Environmental magnetic analyses were carried out on bulk samples (An et al., 1991; Rousseau and Kukla, 1994; Sun and Liu, 2000; Zhu et al., 2004). Before the measurements, all samples were crushed in a glass mortar after weighing. Then samples were cased in plastic boxes and dried in an oven at 40 °C for 24 h. Afterwards, magnetic susceptibilities were measured at a frequency of 2 kHz using an MS2 Bartington magnetic susceptibility metre with a MS2E high-frequency sensor (Dearing et al., 1996). All samples were measured five times and the average values of magnetic susceptibility were used.

One charcoal sample, 31 gastropod shell samples and a single soil organic matter sample from the northern part of the loess wall were submitted for radiocarbon dating (Sümeği et al., 2020). AMS <sup>14</sup>C dating measurements were performed in the AMS laboratory of Seattle, WA, USA, and in the Institute for Nuclear Research of the Hungarian Academy of Sciences at Debrecen (Table 1).

Certain herbivorous gastropods are known to yield reliable ages for dating deposits of the past 40 ka with minimal estimates of shell age offsets on the scale of perhaps a couple of decades which allow the construction of highly reliable millennial and even centennial,

**Table 1**  
Radiocarbon chronological data from loess section of the brickyard at Madaras village.

cm	Material	Sample	uncal BP	+/-	cal BP (2 σ)	Code
4–8	<i>Granaria frumentum</i>	AMS	5 390	26	6 333–6 083	DeA-2248
16–20	<i>Granaria frumentum</i>	AMS	10 986	57	13 001–12 724	D-AMS 4172
60–64	<i>Trochulus hispidus</i>	AMS	12 891	46	15 201–15 609	DeA-11787
100–104	<i>Granaria frumentum</i>	AMS	13 561	41	16 540–16 162	D-AMS 4173
148–152	<i>Trochulus hispidus</i>	AMS	14 498	81	17 915–17 449	DeA-1467
200–204	<i>Trochulus hispidus</i>	AMS	14 891	53	18 288–17 922	DeA-11908
248–252	<i>Trochulus hispidus</i>	AMS	16 133	63	19 656–19 245	DeA-11907
272–276	<i>Fruticicola fruticum</i>	AMS	16 541	54	19 735–20 152	DeA-20947
300–304	<i>Trochulus hispidus</i>	AMS	16 628	63	20 280–19 847	DeA-11906
400–404	<i>Columella columella</i>	AMS	17 150	50	20 879–20 510	D-AMS 4174
448–452	<i>Trochulus hispidus</i>	AMS	17 368	63	21 200–20 718	DeA-11905
500–504	<i>Vallonia tenuilabris</i>	AMS	17 858	64	21 859–21 413	DeA-11903
548–552	<i>Trochulus hispidus</i>	AMS	17 870	71	21 418–21 377	DeA-11904
548–552	<i>Granaria frumentum</i>	AMS	17 935	66	22 118–21 502	DeA-11902
588–592	<i>Columella columella</i>	AMS	18 528	121	22 669–22 031	DeA-1466
600–604	<i>Euconulus fulvus</i>	AMS	18 942	71	23 035–22 552	DeA-11901
648–652	<i>Chondrula tridens</i>	AMS	19 288	72	23 497–22 974	DeA-11900
700–704	<i>Chondrula tridens</i>	AMS	20 193	93	24 513–24 000	DeA-11860
748–752	<i>Trochulus hispidus</i>	AMS	20 503	75	25 013–24 375	DeA-11898
748–752	<i>Chondrula tridens</i>	AMS	20 544	79	25 075–24 419	DeA-11896
892–896	<i>Trochulus hispidus</i>	AMS	21 266	159	25 892–25 246	DeA-1465
896–900	<i>Chondrula tridens</i>	AMS	21 381	82	25 896–25 526	DeA-11895
900–904	<i>Granaria frumentum</i>	AMS	21 415	86	25 921–25 573	DeA-11897
900–904	fossil soil material	AMS	21 899	126	25872–26432	DeA-19221
904–908	<i>Granaria frumentum</i>	AMS	21 518	98	26 004–25 627	DeA-8796
900–908	Pinus charcoal	bulk	21 937	252	26 876–25 718	Deb-3104*
908–912	<i>Granaria frumentum</i>	AMS	21 968	84	26 427–25 939	DeA-8799
920–924	<i>Granaria frumentum</i>	AMS	22 062	106	26 568–26 008	DeA-11861
924–928	<i>Chondrula tridens</i>	AMS	22 066	82	26 535–26 034	DeA-20946
948–952	<i>Granaria frumentum</i>	AMS	23 636	104	27 927–27 552	D-AMS 005122
952–956	<i>Planorbis planorbis</i>	AMS	23 899	102	28 206–27 706	DeA-11790
996–1000	<i>Granaria frumentum</i>	AMS	34 654	264	39 790–38 582	D-AMS 004636

\* Bulk charcoal sample.

sub-centennial scale age models with high precision (Hertelendi et al., 1992; Sümeği and Hertelendi, 1998; Preece and Day, 1994; Pigati et al., 2004, 2010, 2013; Újvári et al., 2014; Xu et al., 2011).

Conventional radiocarbon ages were converted to calendar ages using the software Bacon (Blaauw and Christen, 2011; Blaauw et al., 2018) and the most recent IntCal20 calibration curve (Reimer et al., 2020). Calibrated ages are presented at the 2-sigma confidence level (95.4%).

According to the Central European protocol (Sümeği and Krolopp, 2002), 2 dm<sup>3</sup> (ca. 5.7 kg) of sediment was extracted from every 4 cm to yield malacological material. All samples were washed and sieved using a 0.5 mm mesh sieve to remove fine wind-blown sand, loessy and soil material. After sieving, mollusc shells were dried, sorted and identified. The malacofauna was divided into different palaeoecological groups following the palaeoecological classifications of Ložek (1964), Krolopp and Sümeği (1995), Sümeği and Krolopp (2002), Alexandrowicz (2014) and Sümeği (2005). The malacological record was also classified according to the recent geographical distribution of the species (Boycott, 1934; Soós, 1943; Evans, 1972; Kerney et al., 1983; Krolopp, 1983; Welter-Schultes, 2012; Horsák et al., 2010a, 2010b), and on the basis of paleoclimatological indicator roles (Sümeği and Krolopp, 2002; Sümeği, 2005; Sümeği et al., 2013b).

The recovered mollusc material was compared with the material from our Quaternary malacological database (Krolopp and Sümeği, 1995; Sümeği and Hertelendi, 1998; Sümeği and Krolopp, 2002; Sümeği, 2005; Sümeği et al., 2015, 2016; Molnár et al., 2010, 2019, 2021) and, as a result, the presence, dominance and distribution of bioindicator species of outstanding importance, we have been able to delineate biogeographical, palaeoclimatological and palaeoecological past changes of regional significance. Although preliminary data without geochronological data on the malacological material of the Madaras loess section have been published (Hupuczki and Sümeği, 2010), new and fundamental malacological approaches (Horsák et al., 2010a, 2010b, 2012, 2013; Nekola et al., 2015; Haase et al., 2020) have led to a reanalysis, redefinition and re-enumeration of the *Pupilla* fauna, which constitutes the major part of the entire mollusc material. The first results of this comprehensive Quaternary malacological analysis are reported here.

The French malacologist, Rousseau was the first who used the detrended correspondence analysis (DCA) method (Rousseau, 1986, 1987, 1990, 1991, 2001; Rousseau and Puisségur, 1990, 1999) for determining climate trends using loess malacofauna. This method has been used for snail fauna analyses from Chinese loess and soil formations (Dong et al., 2020b, 2020a). The critique of the statistical use of this method was formulated in the 1980 s (Wartenberg et al., 1987). DCA analysis was used to characterise the changes and plot the trends of the paleoenvironmental changes in the mollusc fauna of the Madaras loess section and the Kolon Lake core sequence. The malacology-based DCA data was presented on a radiocarbon-dated geochronological scale.

Principal components analysis (PCA) was applied to the 26 terrestrial percentage pollen data from the undisturbed core sequence of the Kolon Lake to extract the main gradient changes in terrestrial vegetation, using Psimpoll (Bennett, 1992, 2005). This method was developed in the 1970 s and 1980 s (Webb III, 1974; Birks and Birks, 1980; Prentice, 1985; Birks and Gordon, 1985). The linear ordination technique PCA was used to analyse the variation in the most important terrestrial pollen data set and correlation between pollen taxa (Birks, 1985). The pollen-based PCA data were presented on a radiocarbon-dated geochronological scale.

The plotting of the sedimentological, malacological data was done using Psimpoll (Bennett, 1992, 2005) software.

### 3.2. Methods for undisturbed core sequence of Lake Kolon at Izsák

Conventional radiocarbon ages were derived from Sümeği et al. (2011b) which study is presented in Table 2 within now converted using the Intcal20 calibration curve (Reimer et al., 2020).

Double overlapping undisturbed cores of a total 440 cm were retrieved using a 5 cm diameter Russian corer (Belokopytov and Beresnevich, 1955; Aaby and Digerfeldt, 1986) in the centre part of the Kolon Lake system (Sümeği et al., 2011b). This core sequence

**Table 2**  
Radiocarbon chronological data from undisturbed core sequence of the Kolon Lake at Izsák settlement.

cm	Material	Sample	uncal BP	+/-	cal BP (2 σ)	Code
5	Phragmites	AMS	117	1	259–31	Poz-23346
30	Phragmites	AMS	410	30	519–328	Poz-23344
40	Phragmites	AMS	1005	35	961–793	Poz-23345
50	Phragmites	AMS	2668	40	2853–2738	AA79670
55	Phragmites	AMS	2864	36	3140–2870	AA79671
60	Phragmites	AMS	4137	38	4824–4530	AA79669
65	Phragmites	AMS	4396	39	5267–4856	AA79668
70	Phragmites	AMS	4777	41	5592–5509	AA79667
75	Phragmites	AMS	5585	41	6445–5295	AA79666
80	Phragmites	AMS	6559	43	7569–7358	AA79665
85	Phragmites	AMS	7578	45	8514–8216	AA79664
100	Phragmites	AMS	8763	57	10 118–9548	AA79663
120	Phragmites	AMS	9149	58	10 496–10 216	AA79662
170	Phragmites	AMS	9678	51	11 215–10 790	AA79661
221	Phragmites	AMS	11573	58	13 577–13 317	AA79660
279	<i>Pinus</i> charcoal	AMS	17871	99	22 019–21 402	AA79659
279	<i>Pinus</i> humin acid	AMS	19700	118	23 972–23 319	AA79657
415	<i>Pinus</i> charcoal	AMS	21047	134	25 715–25 093	AA79658
415	<i>Pinus</i> humin acid	AMS	21907	155	26 447–25 879	AA79656



was gained from the deepest part of the basin and was used for pollen, plant macrofossil, malacological and radiocarbon analyses. Detailed sedimentological description of the peat cores follows the system described by Troels-Smith (1955), the colours of sediment layers were written using the Munsell Colour Chart (Munsell, 1954).

Mollusc shells were collected from 4 cm thick subsamples taken at regular intervals throughout the core. The aquatic malacofauna was divided into three groups following the palaeoecological classifications of Boycott (1936), Sparks (1961), Ložek (1964), Krolopp and Sümeği (1995): 1./moving-water habitat preferring species (rheophilous species, such as *Bithynia leachii*), 2./species demanding steady water inundation (ditch group, e.g. *Gyraulus crista*, *Stagnicola palustris*, *Viviparus contectus*), 3./species tolerant to periodic water supply (slum group, for example *Anisus leucostoma*, *A. spirorbis*, *Galba truncatula*). The terrestrial fauna was grouped as follows: water bank (hygrophilous), mesophilous, xerophilous, cold-resistant, mesophilous, thermophilous, open habitat preferring, ecotone habitat preferring and woodland habitat preferring species (Sümeği and Krolopp, 2002; Sümeği, 2005). The malacological record was also classified according to the recent geographical distribution of the species (Soós, 1943; Evans, 1972; Kerney et al., 1983; Krolopp, 1983; Økland, 1990; Alexandrowicz, 2004; Welter-Schultes, 2012; Horskák et al., 2013), and based on palaeoclimatological indicator roles (Sümeği and Krolopp, 2002; Sümeği, 2005; Sümeği et al., 2015). The malacological (local) zones were identified by cluster analysis with the squared Euclidean distance and Ward aggregation method (Zar, 1984; Rousseau, 1990, 1991, 2001; Rousseau and Kukla, 1994; Rousseau and Keen, 1989; Rousseau and Puisségur, 1990, 1999; Rousseau et al., 2002).

The retrieved cores were also subsampled at 1 cm intervals for pollen analysis. A volumetric sampler was used to obtain 2 cm<sup>3</sup> samples, which were then processed for pollen recovery (Berglund and Ralska-Jasiewiczowa, 1986). *Lycopodium* spore tablets of known volume were added to each sample to determine pollen concentrations. A known quantity of exotic pollen was added to each sample to determine the concentration of the identified pollen grains (Stockmarr, 1971).

A minimum count of 500 grains per sample (excluding exotics) was made to ensure a statistically significant sample size (Faegri and Iversen, 1989; Punt et al., 1976–1995; Moore et al., 1991). Micro-charcoal (flying ash) abundances were determined using the point count method (Clark, 1982; Hu et al., 2020). The pollen types were identified and modified according to Moore et al. (1991), Beug (2004) and Punt et al. (1976–1995), supplemented by the examination of photographs in Reille (1992, 1995, 1998) and the reference material in the Hungarian Geological Institute in Budapest. Percentages of terrestrial pollen taxa, excluding *Cyperaceae*, were calculated using the sum of all those taxa. Percentages of *Cyperaceae*, aquatics and pteridophyte spores were calculated relative to the main sum plus the relevant sum for each taxon or taxon group. Calculations, numerical analyses and graphing of pollen diagrams were performed using the Psimpoll 4.26 software package (Bennett, 1992, 2005). Local pollen assemblage zones (LPAZs) were defined using the optimal splitting of information content (Birks and Gordon, 1985), while zonation was performed using the terrestrial pollen taxa that reached at least 5% in at least one sample.

Palaeovegetation examinations were executed on 4 cm subsamples of the core, similarly to the malacological analysis. Paleovegetation was reconstructed using the works of Sugita (1994), Soepboer et al. (2007), Jacobson and Bradshaw (1981), Prentice (1985) and Magyari et al. (2010). The different vegetation types, indicator elements and weed types were separated according to Allen et al. (2000), Behre (1981, 1986), Tarasov et al. (1998, 2000), Magyari et al. (2010), Prentice et al. (1996), Prentice and Webb (1998). We distinguished the species of the warm steppe, cold steppe, cold-mixed forest-steppe, cold mixed forest, temperate deciduous forest and deciduous forest-steppe. For the description of macrofossils from undisturbed core sequence, modified version of the QLCMA technique (Barber et al., 1994; Jakab et al., 2004; Jakab and Sümeği, 2004, 2011) was used. Psimpoll programme was used to plot the analytical results of macrobotanical analyses (Bennett, 1992, 2005; Podani, 1993).

The biomisation procedure translates pollen and plant macrofossil spectra into biome assignments. The biomisation method is an objective method based on assigning taxa to one or more plant functional types (PFTs). The concept and the different steps of this method are fully described in Prentice et al. (1996) and Prentice and Webb (1998).

## 4. Results

### 4.1. Geochronological results

#### 4.1.1. Geochronological results of the Madaras section

The calibration of radiocarbon ages dates back the age of the bedrock sand to 39,843 ± 602 cal BP years (Fig. 3; Table 1). The age of the top of the profile at 6 cm has also been slightly modified thanks to the new calibration from 6208 ± 175.5 cal BP years to 6208 ± 125 cal BP. Thus, the Madaras section captures the malacofaunal changes from approximately 40,000 years to 6000 years. From the 32 radiocarbon data presented here, 16 were published previously (Sümeği et al., 2020), but they were calibrated with an older radiocarbon calibration method. In another publication currently under review (Sümeği et al., in press), radiocarbon data were compared with the OSL data measured in the same section, and the differences and their reason were investigated. In both publications, we focused mainly on the geochronological delineation of the LGM development in the southern Carpathian Basin and it did not address especially the Late Glacial / post-Glacial transition, which is the main issue of this paper.

#### 4.1.2. Kolon Lake borehole

The <sup>14</sup>C calibration dates back the age of the bedrock sand to 25–27 cal BP years (Fig. 4; Table 2). The Kolon Lake sequence is highly variable in its evolution, and the formation of the surface peat spans the last 10–10.5 thousand years and is still ongoing today. The studied profile covers the changes of the last 26 kyr, thus it provides an excellent opportunity to reconstruct the vegetation changes by supplement the Madaras section's snail-based reconstruction with background pollen data during the Late Glacial and Early Holocene. The previously reported raw radiocarbon data had to be recalibrated using the latest calibration method (Reimer et al., 2020). The

main objective of the geochronological studies was to reconstruct the changes in the Late Glacial and transitional Late Glacial/post-Glacial malacology, vegetation and paleohydrology of the Kolon Lake sedimentary system, taking into account the geochronological data provided by the calibrated radiocarbon data.

## 4.2. Magnetic susceptibility (MS)

### 4.2.1. Results of magnetic susceptibility and sedimentological studies of the Madaras section

Although the measured MS data from the Madaras loess section have already been reported (Sümeği et al., 2012b), radiocarbon dates were not yet available for these data, so it was impossible to define the MS changes in time. In the analysis here, changes in MS values can be shown along a geochronological scale constructed from the calibrated radiocarbon data in the Madaras section (Fig. 3).

The profile of Madaras was deposited on wind-blown-sand formation and can be characterised as plateau loess. Below the wind-blown-sand, a fossil soil horizon developed between 28,000 and 25,000 cal BP years with the thickness of half a metre (Fig. 3). On the surface of the fossil soil horizon, a yellowish-brown loess layer was deposited. In its middle part, a strongly weathered horizon (L1S1) developed between 23,000 and 21,000 cal BP years with significant organic matter, fine silt and clay content. Then a loess horizon (L1L1) can be found with high coarse silt content. The Holocene chernozem soil developed on its surface. The soil horizon is rich in organic matter, clay and fine silt (Fig. 3). Based on the high-resolution MS record from Madaras loess section seems to display a good correspondence with stratigraphical boundaries observed on the field with one exception. The zone representing the weakly developed humic layer (L1S1) in the middle of the profile must be extended in the knowledge of the new findings.

### 4.2.2. Kolon Lake

The bottom of the undisturbed core sequence of the Kolon Lake between 4.4 and 2.9 m is a well-graded, fine and tiny sand fraction rich wind-blown sand layer, with low MS values (Fig. 4). Within the wind-blown-sand layer, a fossil soil layer can be found, which is rich in organic matter, clay and fine silt fractions, containing burnt Scotch pine (*Pinus sylvestris*), with an age ranging between 25 and 26 kyr years. On the surface of the wind-blown-sand layer, oligotrophic lake sediments developed (280 cm), which dates back to approximately 22,000 cal BP years ago. Thus, the formation of the wind-blown-sand was interrupted by soil formation between 27,000 and 22,000 cal BP years. At the end of the Ice Age, an oligotrophic mineral-organic recharged lake system developed, with significant MS values. At the end of the Glacial period, the formation of calcareous mud begun in a mesotrophic lake environment, and these *Chara* lake conditions continued during the Early Holocene. The MS values were reduced in this layer (Fig. 4). At the end of the Early Holocene, the *Chara* lake phase was terminated, the organic matter increased and an organic matter-rich eutrophic marshy phase developed. From about 9000 years onwards, a closed peat layer developed in the section and MS values continued to decrease.

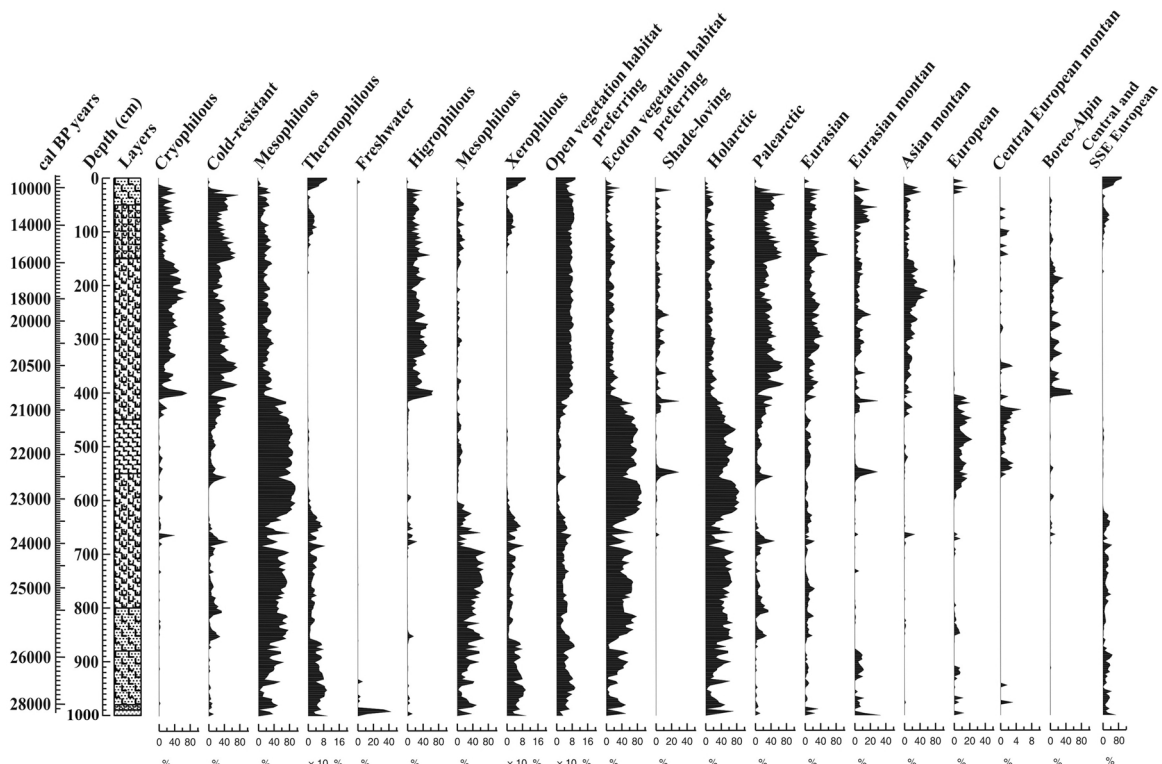


Fig. 6. Dominance changes of Quaternary malacological palaeocological groups for the studied loess profile at Madaras settlement.

Although the development of the peat layer still characterizes this environment, groundwater regulation has caused the near-surface part of the peat to dry out cyclically and hydromorphic soil formation has started in the near-surface peat horizon. As a result, organic matter content decreased, inorganic matter, including iron, increased and MS values also became more significant. In the Kolon Lake section, changes in macrobotanical, pollen and malacological material were used to trace changes in the aquatic, waterfront environment over the last 22,000 years and to compare changes in terrestrial pollen material with changes in terrestrial snail material on the Madaras loess Section.

### 4.3. Malacological, macrobotanical and pollen results

#### 4.3.1. Madaras loess section

The fossil soil (L1S2; Fig. 3) in the wind-blown-sand layer at the base of the Madaras section, moreover the loess layer deposited on the wind-blown-sand layer was dominated by a xerophilous open habitat preferring snail fauna with a predominantly Central and SSE European distribution (Figs. 5 and 6; Supplementary Table 1). Characteristic elements of this fauna are the species *Granaria frumentum*, *Cochlicopa lubricella*, *Chondrula tridens* and *Caucasotachea vindobonensis*, which are widespread in the present-day Pannonian forest-steppe areas (Bába, 1980, 1983, 1987, 1997). In this level (900–770 cm), shade-loving species are absent, open vegetation and ecotone habitat preferring snails are dominant. Paleotemperatures in July varied between 17 and 20 °C. That is, they were 2–5 °C colder than the present-day mean July temperature (Fig. 2). However, even at this horizon, short periods of cooling were detected, with Eurasian taxa, and Asian montane species, notably *Vallonia tenuilabris*, and *Vertigo alpestris* (Figs. 5 and 6). Paleotemperatures of 14–16 °C in July were recorded during short cooling waves. The most distinctive feature of the malacofauna of the area is the presence of thermomesophilous species in addition to the gradually dominant cold-tolerant elements at the end of MIS3 and the lead-up to MIS2. It is no coincidence that the maximum diversity (23 species; 19 terrestrial, 4 freshwater) in the snail fauna of the section was reached at this time. The 4 freshwater mollusc species also played an important role in the development of the diversity maximum.

From 25,000 cal BP the proportion of warmth-loving, Central and SSE European, xerophilous elements gradually decreased, and from 23,000 cal BP they fully disappeared from the profile. At the same time, the proportion of mesophilous Holarctic elements of high tolerance (*Vallonia costata*, *Pupilla muscorum*) became dominant. This can be considered as the beginning stage of the LGM, a change in fauna that has been transformed during the gradual cooling. It was also the time when the first significant cooling phase developed at 24,000 cal BP year when the former mean July temperature was around 12 °C based on the malacothermometer (Sümeği, 1989, 2005, 2019). Thus, summer temperatures developed in this cooling phase was 10 °C colder than the recent mean July temperature (Fig. 2).

In the next layer (600–430 cm; 23–21,000 cal BP ys) the thermomesophilous species disappeared, the LGM horizon development can be characterised with a cool but not particularly cold climate, and more dense vegetation cover (ecotone vegetation habitat preferring vegetation). It was dominated by snail species recently widespread in European and Central European forests (*Vitrina*

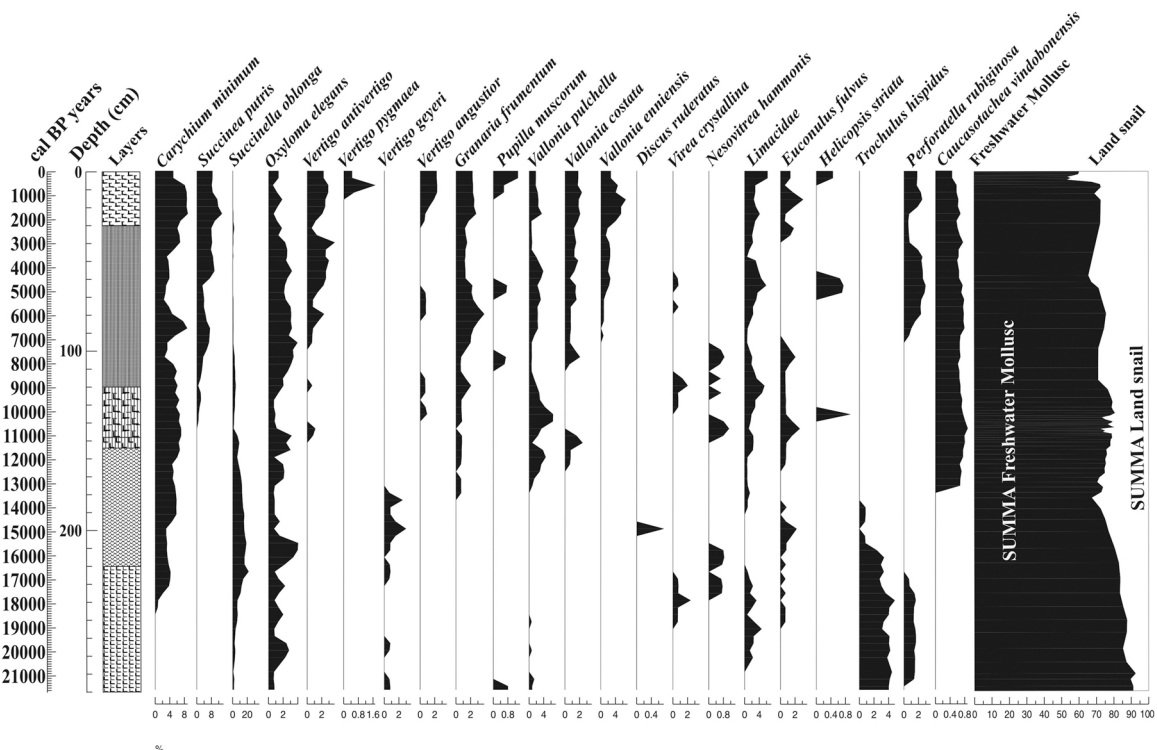


Fig. 7. Dominance changes of Quaternary terrestrial mollusc species for the studied undisturbed core profile of Kolon Lake at Izsák settlement.

*pellucida*, *Punctum pygmaeum*, *Semilimax semilimax*, *Vitrea crystallina*, *Orcula dolium*). This snail fauna forms a characteristic horizon in the Carpathian Basin loesses (Krolopp and Sümeği, 1990, 1991, 2002; Sümeği and Krolopp, 1995, 2002). This malacological level contains two extinct paleoassociations (*Semilimax semilimax* - *Punctum pygmaeum* - *Vitrea pellucida* and *Orcula dolium* - *Vitrea crystallina* - *Punctum pygmaeum*). Based on the fauna association, boreal-type open parkland (Larsen, 2013) vegetation can be reconstructed (Sümeği, 1989, 1996, 2005; Sümeği et al., 2012a, 2013b). This mixed-leaved boreal open parkland structured vegetation is typical in the present-day southern Siberian areas (Sümeği, 1989, 1996, 2005; Sümeği et al., 2012a, 2013b; Horsák et al., 2010a, 2010b; Chytrý et al., 2019) but there were some European distribution snail elements (e.g. *Orcula dolium*) in this LGM open parkland around the loess section at Madaras. Despite the predominance of snail species, which suggests the development of a relatively cooler climatic phase (with paleotemperatures of 13–16 °C in July), very insignificant, subordinate presence of elements of the central and south-eastern European temperate steppe-forest-steppe elements also occurred, including the index snail taxa of these vegetation units, the *Granaria frumentum*.

From 22,000 cal BP years, distinctly cold-tolerant (Rousseau, 1986, 1987, 1989, 1990, 1991, 2001; Horsák et al., 2009, 2010a, 2010b; Hoffmann et al., 2011) Asian, Eurasian montane, Palearctic, Boreo-Alpin, Eurasian species (*Columella columella*, *Vallonia tenuilabris*) were dominant, while the widespread, highly tolerant Holarctic mesophilous species have declined, and warmth-loving ones have disappeared. At the same time, cold-tolerant shade-loving and hygrophilous species appeared in the section with a relatively strong dominance (Figs. 5 and 6). The most significant cooling (between 24,000 and 18,000 cal BP years) occurred in the local environment at this time, and the paleotemperature in July was between 11 and 13 °C. The composition of the malacofauna suggests that a boreal taiga steppe developed in the study area, with tundra-like vegetation patches (*Betula nana* - dwarf birch, and *Pinus mugo* - bog pine).

By the Holocene, the composition of the malacofauna had changed, with xerophilous warmth-loving and mesophilous steppe species (*Chondrula tridens*, *Granaria frumentum*, *Pupilla msucorum*) become dominant in the section (Figs. 5 and 6).

#### 4.3.2. Kolon Lake

From 22,000 cal BP years, the analysis of the malacological, pollen and macrobotanical material of the Kolon Lake section (Sümeği et al., 2011b) provided an opportunity for regional vegetation reconstruction (Figs. 7–10; Supplementary Tables 2 and 3). As a result, the presence of an open parkland type boreal type forest-steppe in the cold maximum is well supported. The former tundra-like patches are proven by the macrobotanical remains of *Betula nana* excavated in this time horizon of the Kolon Lake section and the presence of pollen and spores of tall herb meadows (*Thalictrum*, *Sanguisorba*, *Angelica*, *Campanula*, *Filipendula*) and arctic fens (*Armeria maritima*, *Selaginella selaginoides*) (Sümeği et al., 2011b). At this time, the Kolon Lake core sequence was characterised by the aquatic mollusc fauna (Figs. 8 and 10), with a significant proportion of *Valvata macrostomata*, *Bithynia leachii*, *Anisus leucostoma*, *Gyraulus riparius*, in addition to Holarctic species with a significant distribution and tolerance. The terrestrial elements of the Kolon Lake malacofauna were dominated by cold-tolerant Euro-Siberian and hygrophilous elements (Fig. 7). The reconstructed July paleotemperatures were

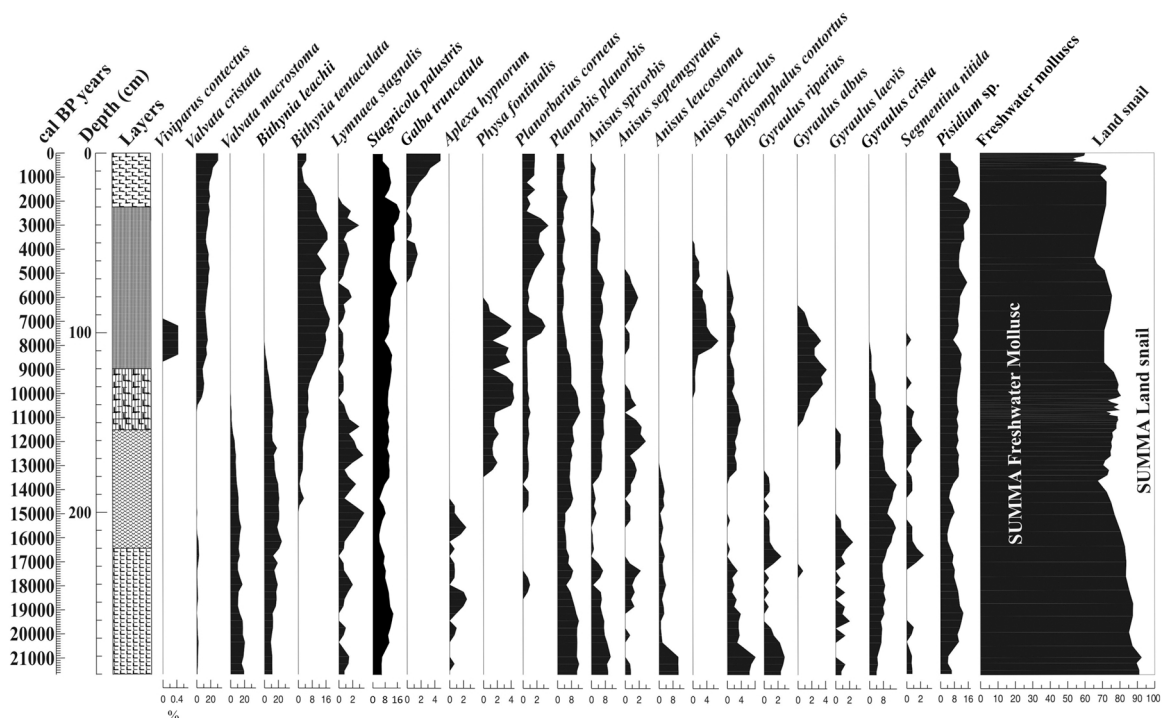


Fig. 8. Dominance changes of Quaternary freshwater mollusc species for the studied undisturbed core profile of Kolon Lake at Izsák settlement.

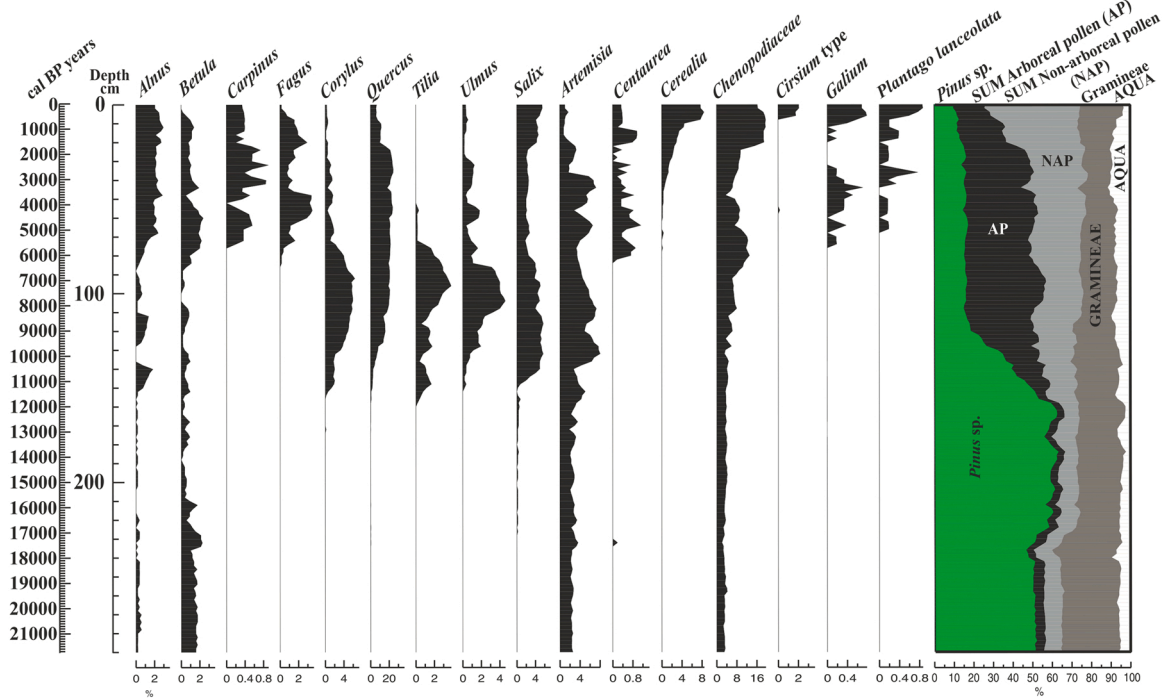


Fig. 9. Dominance changes of pollen species for the studied undisturbed core profile of Kolon Lake at Izsák settlement.

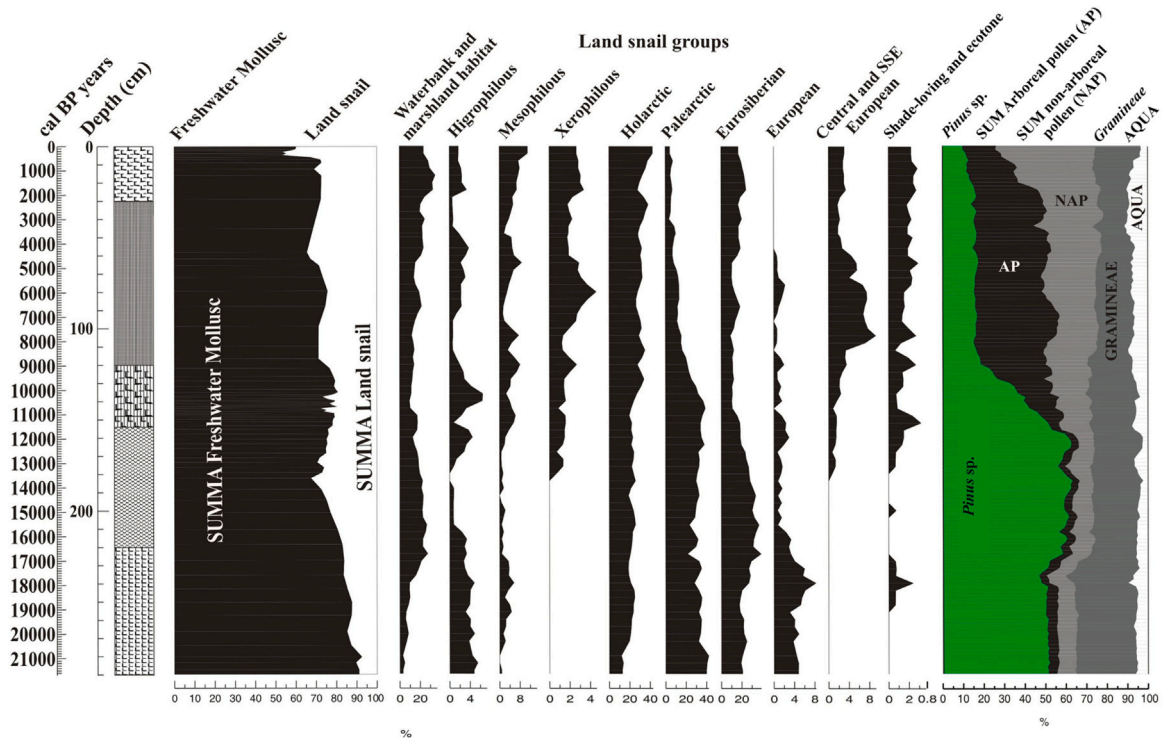


Fig. 10. Dominance changes of terrestrial snail-based palaeoecological groups for the studied undisturbed core profile of Kolon Lake at Izsák settlement with summary pollen sequence.

between 15 and 16 °C, which was 6–7 °C colder than today's July temperatures (Fig. 2).

Following the most significant cooling phase (LGM), the temperatures started to gradually rise. The cold-loving elements gradually declined and the cold-tolerant, hygrophilous, Palearctic, Eurasian (Eurosiberian) elements became the dominant elements in the terrestrial snail fauna (Fig. 7). Temperatures in July exceeded 15 °C. Pollen of *Pinus* became dominant (ca. 60%) in the pollen material of Kolon Lake, indicates the transformation of the open parkland. The local cover of coniferous trees and pines increased and a boreal forest-steppe with a higher density of arboreal elements can be reconstructed in the study region.

Although the post-LGM period is characterised by increasing temperatures, one of the most significant climatic changes is associated with a cold phase. This cooling phase was also reflected in the pollen material of the Kolon Lake (Fig. 9) with a decline in *Pinus* pollen and the increase of the proportion of the herbaceous elements.

Following that cooling phase, the Kolon Lake section show gradual warming in all palaeoecological factors. The terrestrial snail fauna underwent a fundamental change, which is reflected in the detrended correspondence analysis (DCA) values of these faunas but is also detectable in the changes in the pollen section and in the changes in the PCA values of the pollen material (Figs. 7, 9, 11).

Thus, the boreal forest-steppe that evolved at the end of the Ice Age was gradually transformed into temperate forest-steppe vegetation between 13,000 and 10,500 cal BP years. The mosaic-like forest-steppe structure of the Late Glacial has been preserved, but other thermomesophilous, xerophilous, Holocene-dispersing mid- and SSE European species have taken the place of the Late Glacial boreal structure. The transition between the two vegetation formations was between 15,000 and 10,000 cal BP years ago. A diversity minimum developed in a drier environment at higher temperatures, and the 25–36 species at the end of the Ice Age were reduced to 9–10 species at the Holocene. These changes took place over a period of approximately 5,000 years, during which time summer temperatures increased by approximately 9–10 °C, resulting in a 2 °C increase in summer temperatures over 1000 years between the Late Glacial cold maximum and the Early Holocene temperature maximum.

The charcoal record of the Kolon Lake from this period suggests that burning ceased in this mixed woodland and probably emphasises both the different flammability levels of the two forest steppe types and also climatic change (Dryness et al., 1986; Clark, 1988; Flannigan and Harrington, 1988).

## 5. Discussion

### 5.1. Terminal phase of MIS3 and transition phase of MIS3/MIS2 (between 40,000 and 26,000 cal BP years)

This phase could be reconstructed only in the Madaras loess-paleosol section. During this phase, wind-blown-sand movement took place throughout the Danube-Tisa interfluvium region and based on the dominance of the malacofauna (*Cochlicopa lubricella*, *Chondrula tridens*, *Pupilla triplicata*, *Granaria frumentum*) mild, dry environment can be reconstructed in the area. Wind-blown-sand accumulated during this phase, probably at the time of the Greenland Interstadial (GI) 8 warming phase (Rasmussen et al., 2014), forming the bedrock of both of the 10 m thick Madaras loess section and the catchment basin of the Kolon Lake. These geological data show that on the alluvial fan surface of the Danube-Tisa interfluvium region a particularly dry, open parkland environment developed. In this dry, less vegetated stage, the fluvial, Danube-originated sand was easily transported by aeolian processes and wind-blown-sand formed on the surface of the alluvial fan.

The wind-blown-sand movement was interrupted by the formation of a finer, loessy sediment at the end of the MIS3 phase, and then at the transition phase of MIS3/MIS2, a fossil soil layer with clayey silt containing charcoals of Norway pine (*Pinus sylvestris*), birch (*Betula*) was formed in both the Madaras and Kolon Lake areas. This fossil soil horizon was detected in several locations (Sümeği and Krolopp, 2002; Sümeği et al., 2013b, 2015, 2019) in the study region (southern and central GHP) and forms a macroscopically well-traced regional leader level. It is likely that the soil formation, dated between 28,000 and 25,000 cal BP years, is synchronous with Greenland Interstadial (GI) 3 phase (Rasmussen et al., 2014), which evolved between 28,000 and 27,000 cal BP years (Rasmussen et al., 2014). This fossil soil formation concludes the MIS3 stage and marks the beginning of the MIS2 stage in the study region.

The summer temperature at the end of MIS3, at the beginning of MIS2, delimited by marine sediments and ice sheet boreholes (Voelker, 2002; Voelker et al., 1998; Weinelt et al., 2003; Andersen et al., 2006; Suggate and Almond, 2005; Svensson et al., 2006; Rasmussen et al., 2006, 2008, 2014), fluctuated strongly. During longer periods with temperatures 1–2 °C lower than recent July temperatures, the characteristic elements *Granaria frumentum* and *Caucasotachea vindobonensis* were the index fossils, which are typical of the Central and S-SE European forest-steppe environments in the recent Hungarian Plain forest-steppe. This level of warming may be identified as Dansgaard Oeschger event 4 (D-O4) Cacho et al., 1999. At the same time, during short periods of intense cooling lasting several hundred years, *Vertigo alpestris*, widespread in mountainous and hilly forests in central Europe, and the xeromontane *Vallonia tenuilabris* from central Asia, appeared.

### 5.2. LGM horizon (26,000–19,000 cal BP years)

The cold maximum of the Last Glacial (within the MIS2 phase) was formed at this time, but this phase cannot be characterised with a uniform climate. In both the Madaras and Kolon Lake mollusc faunas, cold-loving (*Columella columella*, *Pupilla sterrii*, *Vallonia tenuilabris*), cold-tolerant (*Valvata macrostomata*, *Bithynia leachii*, *Anisus leucostoma*, *Gyraulus riparius*, *Succinella oblonga*, *Vertigo geyeri*) elements were occurred in significant proportions. At the same time, the fluctuation in the proportion of cold-tolerant elements and the subordinate presence of thermophilous species (*Cochlicopa lubricella*, *Granaria frumentum*, *Fruticicola fruticum*) indicate that the temperature of the growing season has changed in this climate phase. The malacothermometer-based July paleotemperature ranged from 14 to 16°C, which is a decrease of 6–8°C compared to the recent July temperatures (Fig. 2). However, in the coldest phases, a

paleotemperature of 11–13°C was reconstructed for July, which represents a decrease of 9–11°C compared to the recent warmest month (Fig. 2).

At the same time, humidity varied more strongly in this phase: wetter periods alternated with drier ones. The wetter periods and consequently wetter surfaces could also have developed as a result of the decrease in temperature, as it demonstrated in several loess-paleosol section from around the Carpathian Basin (e.g. Sümegei et al., 2011b, 2015, 2019; Molnár et al., 2010, 2019, 2021). The same increase in humidity could also have developed as a result of the increase in precipitation. Ice sheet analyses have also indicated this temperature fluctuation in the LGM horizon and reconstructed two short milder periods (GI2.1 and GI2.2) (Rasmussen et al., 2014). These changes are supported by the terrestrial record of some Pyrenean glaciers which have advanced during the LGM (González-Sampérez et al., 2006). However, in northern Spain, at latitude 43°, stalagmites formed even during the LGM, suggesting a locally/regionally more precipitous climate (Moreno et al., 2010), since much of the European stalagmites did not form during the dry, cold climate of the LGM (Genty et al., 2006). These regional differences highlight that even the LGM level cannot be interpreted as uniform. The LGM horizon is considered to be a cold and dry period in general, but temperature and precipitation (humidity) varied over a wide spectrum within this horizon as well. Thus, regional differences were very significant in some areas of Europe during the LGM. Short-term climate variability during the LGM is supported by ice sheet analyses (Johnsen et al., 2001; Rasmussen et al., 2014), as well as by land-based data and proxy data from loess (Rousseau et al., 2007) and lakes (Wohlfarth et al., 2008).

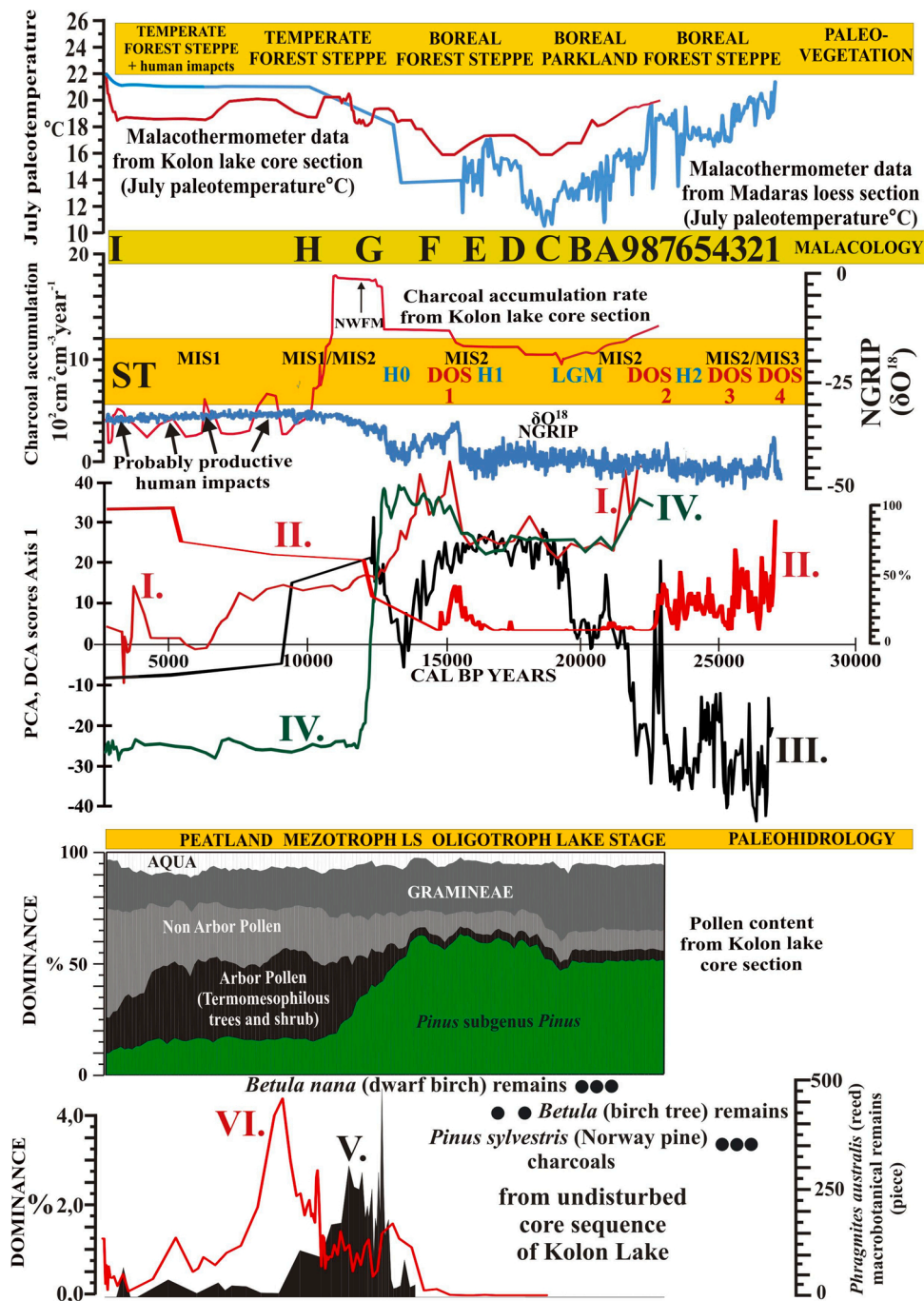
Thus, our data support these temporally and spatially differences in regional climate variations during the LGM. The study area of Madaras was a dust accumulation zone with significant thicknesses of loess plateaus, while the Kolon Lake catchment basin system accumulated weathered silicates and mineral-organic sediments. The most significant feature of the LGM horizon is that the area did not develop a homogeneous, completely open vegetation, cold loess steppe, but a boreal open parkland type forest-steppe with a mosaic structure and scattered trees (Norway pine - *Pinus sylvestris*, Swiss stone pine - *Pinus cembra*, birch - *Betula*). In this open parkland vegetation with mosaic structure, surfaces with tall herbaceous occurred among the patchy trees and shrubs and scattered subordinate patches of bog pine (*Pinus mugo*) and dwarf birch (*Betula nana*) were also present in the cold draughts, with diffuse tundra patches. The mosaic and open parkland structure of the boreal forest-steppe that developed in the area, with occasionally central and south-eastern European elements, was extremely species-rich. Snail fauna was four times richer at the LGM phase.

Our data suggest that the cooling phase (and cyclical cold but wetter climatic phases) in the area were particularly favourable for the development of higher humidity. During the higher humidity phase, more vegetation cover and more phytomass developed in the area than today, and more species- and abundance-rich snail communities may have developed. The LGM mixed-leaved boreal open parkland forest with tall-herbs habitat was favourable for the shade-loving habitat preferring (e.g. *Semilimax semilimax*) and ecotone habitat preferring (*Vitrea crystallina*) taxa during this cold maximum. This open parkland structured mixed-leaved forest type with mosaic vegetation structure and relative humid soil surface with vapour-retaining tall herbs were favourable for shade-loving habitat and ecotone vegetation habitat preferring mollusc taxa. Our data suggest that the present-day open parkland type forest-steppe vegetation structure was already developed in the LGM horizon, but different species constituted the vegetation (and fauna) communities then and now.

At the beginning of the MIS2 phase, between 26,000 and 25,000 cal BP years, a fossil soil with *Pinus sylvestris* (Norway pine) and *Betula* (birch) charcoals formed in the accumulated loess layer. In the fossil soil layer, the mollusc paleoassociation *Granaria frumentum* - *Chondrula tridens* developed. Both the fossil soil type, the charcoals, and the malacofauna revealed that the fossil soil level developed like the recent mixed forest-steppe of the western part of the Eastern European Plain (Marcuzzi, 1979; Rodwell et al., 1995; Novenko et al., 2009; Welter-Schultes, 2012; Baliuk et al., 2017; Tóth et al., 2021), although with significant individual, local-regional features. In the Kolon Lake section, this fossil soil layer developed by interrupting the development of the wind-blown-sand and contained significant amounts of burnt *Pinus sylvestris* (Norway pine) remains. Thus, it allowed the paleoenvironmental and chronological synchronisation of this fossil soil layer (Sümegei, 1988; Szöör et al., 1991; Sümegei and Krolopp, 2002; Verpoorte et al., 2013; Sümegei et al., 2015). Based on the analysis of charcoal (Willis et al., 2000; Rudner and Sümegei, 2001; Sümegei and Rudner, 2001; Sümegei, 2005) and the malacological data, it is clear that the fossil soil was formed in a boreal forest-steppe environment and that natural wildfires (Viereck, 1973; Payette, 1992; Agee, 1996; Whitlock and Millsaugh, 1996) played a considerable role in the development of the mosaic vegetation. Thus, globally at the end of MIS3 and the beginning of MIS2 (Dansgaard et al., 1982; Alley et al., 1993; Bond et al., 1992, 1993, 1999; Kreveld et al., 2000), and locally/regionally in the studied sections, widespread natural forest fires induced by decreasing humidity in drier climate stages also played a prominent role in the development of boreal-type mosaic-covered forest-steppe in the study area. The environment and age of the fossil soil development can be traced back to Dansgaard-Oeschger Event 3 (D-O3), but the terrestrial malacological data suggest that the local environment was not uniform at either D-O4 or D-O3 events, with significant temperature changes and consequent strong environmental transformations that had taken place in these relatively mild climate zones in the study section.

On the surface of fossil soil developed at the beginning of MIS2 aeolian dust accumulated in the second half of MIS2, mainly during the LGM, which diagenised into a loess sequence (Pécsi, 1990). The dust material accumulated on a plateau surface, but the environment (vegetation, humidity and temperature) of this area was not uniform but showing very significant changes in the terrestrial malacofauna during MIS2. The accumulation of dust material lasted for about 12,000 years and a very thick loess section of 9 m was formed during this time, but during this time the local environment was repeatedly altered by the microclimate led by the trends of global temperature changes.

Between 25,000 and 24,000 cal BP years, Holarctic steppe/forest-steppe elements were widespread, then a cold maximum formed based on the maximum of the cold-lover and cold-tolerant Eurasian boreo-alpine and Asian xeromontane elements at 24,000 cal BP years during the formation of the Madaras sequence. This cold maximum has been identified as the Heinrich 2 cold event (Bond et al., 1992, 1993, 1999; Grootes et al., 1993; Meese et al., 1997; Chaco et al., 1999). Uniquely, even after this cold maximum,



(caption on next page)



**Fig. 11.** Comparative analyses for lithological, malacological, pollen, macrobotanical, statistical results from investigated profiles and the ecosystem change during the last 30 kyr in the analysed region between Danube and Tisza rivers (**Malacology:** 1 = *Granaria frumentum* - *Caucasotachea vindobensis* paleoassociation, 2 = *Vertigo alpestris* - *Vallonia tenuilabris* paleoassociation, 3 = *Granaria frumentum* - *Fruticicola fruticum* paleoassociation, 4 = *Granaria frumentum* - *Vallonia costata* paleoassociation, 5 = *Pupilla muscorum* - *Vallonia costata* paleoassociation, 6 = *Columella columella* - *Vallonia tenuilabris* paleoassociation, 7 = *Vallonia costata* - *Trochulus hispidus* paleoassociation, 8 = *Columella columella* - *Euconulus fulvus* paleoassociation, 9 = *Punctum pygmaeum* - *Vitrina pellucida* paleoassociation, A = *Discus ruderratus* - *Clausilia dubia* - *Trochulus hispidus* paleoassociation, B = *Semilimax semilimax* - *Punctum pygmaeum* - *Vitrina pellucida*, and *Orcula dolium* - *Vitrea crystallina* - *Punctum pygmaeum* paleoassociations, C = *Columella columella* - *Vallonia tenuilabris* paleoassociation, D = *Succinella oblonga* - *Trochulus hispidus* paleoassociation, E = *Pupilla sterrii* - *Pupilla loessica* - *Trochulus hispidus* paleoassociation, F = *Succinella oblonga* - *Trochulus hispidus* paleoassociation, G = *Granaria frumentum* - *Caucasotachea vindobensis* paleoassociation, H = *Truncatellina cylindrica* - *Granaria frumentum* paleoassociation, I = *Granaria frumentum* - *Helicella obvia* paleoassociation, J = DCA values of terrestrial Mollusc from undisturbed core sequence of Kolon Lake, K = Central and SSE European species dominance values from loess section at Madaras, L = DCA values of terrestrial Mollusc from loess section at Madaras, M = PCA values of 26 most important pollen taxa from undisturbed core sequence of Kolon Lake, N = *Chara vulgaris* macrobotanical remains dominance from undisturbed core sequence of Kolon Lake O = *Phragmites australis* (reed) macrobotanical remains (piece) from undisturbed core sequence of Kolon Lake, P = NWFM = Natural wild fire maximum, Q = stigraphy, R = MIS1 = Marine Isotope Stage 1 (Holocene), S = MIS2 = Marine Isotope Stage 2 (Upper Pleniglacial)).

thermomesophilous steppe/forest-steppe elements persisted in the Carpathian Basin, although their proportions were subordinate. Recently these elements can be found in Central and South - South-Eastern Europe. At 23,000–21,000 cal BP years, the next cold peak were formed, also dominated by boreo-alpine and Asian xeromontane elements. Following the decline of thermomesophilous species, while between the two cold maxima, Holarctic, ecotone habitat preferring, paleartic elements dominated. These Quaternary malacological data with a resolution of ~20 years (Sümeği et al., 2019), due to the 4 cm sampling, show that the former climate and environment of the LGM in the study area was not homogeneous and cannot be characterised by a single cold maximum. Unfortunately, only very few sections are available with this kind of resolution (Sümeği et al., 2012b, 2020) in the Carpathian Basin, but these data from Madaras support what was reported earlier at another 4 cm resolution sampling, that the globally determined warming (Dansgaard-Oeschger events) and cooling (Heinrich events) waves at the end of MIS3 and the beginning of MIS2, were not uniform in either climatic or environmental terms. At the LGM between 23,000 and 21,000 cal BP years, one of the most significant malacofauna developed, consisting predominantly of holartic snail species with high tolerance. At the same time, a typical dominance level of snail species with ecotone habitat preferring species of modern European, central European distribution developed. In this time horizon, the spread of modern shade-loving and ecotone habitat preferring snail fauna can be observed in other Carpathian loess areas (Sümeği and Krolopp, 2002; Sümeği, 2005; Molnár et al., 2021). It is assumed that during this relatively cool/cold and perhaps wetter climate phase, humidity increased in the Carpathian Basin and consequently vegetation density and cover increased. As a result, ecotone habitat preferring snail elements spread and became dominant. The more significant vegetation cover and the wetter understory is also supported by a more heavily weathered layer, a weakly developed humic layer, both in the study section and in the rest of the Carpathian Basin (Sümeği, 2005; Sümeği et al., 2019). The peculiarity of this horizon is that one of the Upper Palaeolithic waves in the Carpathian Basin (Dobosi, 1967, 1989, 1994) is associated with this time horizon. The analysis of charcoal from these Upper Palaeolithic sites (Stieber, 1967a, 1967b; Rudner and Sümeği, 2001; Sümeği and Rudner, 2001; Willis et al., 2000; Willis and Van Andel, 2004) suggests that the so-called Sub-Carpathian region (Sümeği et al., 2012a), a predominantly *Picea parkland* with scattered *Pinus sylvestris* trees developed. In the southern part of the basin, a boreal forest-steppe with *Pinus sylvestris* - *Betula* mixed species and patches of taiga developed, with occasional and scattered *Pinus cembra* and *Abies*. Thus, in this boreal forest-steppe areas developed between 23,000 and 21,000 cal BP years ago preferring Holarctic, European and Central European montane ecotone habitat.

From 22,000 cal BP years, in the catchment basin of Kolon Lake, the pollen and macrobotanical material started to accumulate, thus the changes in the terrestrial malacological material of Madaras loess section can be compared with the changes in the terrestrial vegetation of the region (Fig. 11). At the same time, a cold maximum developed based on the dominance maximum of cold-tolerant, cold-tolerant boreo-alpine and Eurasian, Asian montane elements. From 21,000 cal BP years the overall character of the Madaras snail fauna changed. The Holarctic ecotone habitat preferring molluscan taxa declined, and the cold, open-habitat preferring, paleartic, Eurasian, Asian montane elements became dominant in the fauna, with cold maxima marked by peaks of the dominance of species preferring boreo-alpine, tundra-like environments besides the basic fauna elements.

### 5.3. Post-LGM horizon (19,000–13,000 cal BP years)

At the beginning of the post-LGM horizon, a mixed-leaved boreal open parkland forest with tall-herbs habitat with a distinct cold climate phase, which was established during the LGM horizon prior to the Late Glacial period, was preserved in parallel with the Greenland Stadial (GS) horizon 2.1 (Rasmussen et al., 2014). It was in this stadial horizon that the Asian xeromontane (Horsák et al., 2010a, 2010b; Hoffmann et al., 2011), cold-loving (Rousseau, 1986) taxon *Vallonia tenuilabris* reached its maximum dominance besides significant dominance of the boreal-alpine, cold-loving *Columella columella* (Rousseau, 1989, 1990, 1991, 2001). These data suggest that the cold maximum may have developed in the southern and central lowland region between 18,000 and 17,000 cal BP years, after the LGM horizon. Thus, it can be assumed that the environment and climate of the LGM persisted in this region for a longer period than previously assumed. At the same time, the shade-loving and ecotone vegetation habitat preferring snail elements (*Vitrina pellucida*, *Semilimax semilimax*, *Vitrea crystallina*, *Punctum pygmaeum*, *Discus ruderratus*) dominance decline in the post-LGM horizon. Although some new shade-loving and ecotone habitat preferring land snail elements (e.g. *Clausilia dubia*) spread in the post-LGM

horizon. However, the dominance of pine species (*Pinus* sp.) increased during this phase in the Kolon Lake section (Figs. 9 and 10). Therefore, the post-LGM stage remained cold/cool but became wetter and this may have triggered the closure of the boreal forest-steppe, but the tree pollen sum was between 60% and 70%. This tree pollen sum dominance suggests (Prentice, 1985; Prentice et al., 1996; Allen et al., 2000) that a boreal forest-steppe formed in the analysed region during the post-LGM phase. A significant area was covered by trees, but still, a mosaic structure of boreal forest-steppe persisted in the area. Cold-resistant and hygrophilous species (*Succinella oblonga*, *Trochulus hispidus*), which gradually became dominant after the cold maximum of 18,000–17,000 cal BP years, also reflect the climate precipitation (Figs. 7 and 10) in the post-LGM horizon.

In the previous quarter-malacological literature (Krolopp, 1961, 1965, 1973, 1983; Ložek, 1964, 1965, 1990, 2001), that almost homogeneous malacological stage was described as a cold loess steppe fauna, which developed between 21,000 and 13,000 cal BP years cold maxima in the Madaras loess section (Fig. 11). Stieber (1967a) pointed out that trees, including *Betula* (birch), *Pinus sylvestris* (Norway pine), *Pinus cembra* (Swiss pine), *Larix* (larch) species, are known to occur in this cold maximum. Thus, it is not coincidental that the pollen section of Kolon Lake was used in the comparison of vegetation development of the boreal-type open parkland vegetation in the cold maxima, with *Betula nana* (dwarf birch) remnants demonstrating tundra-like patches. Between 21,000 and 13,000 cal BP years, the pollen composition revealed a mosaic of mixed forest-steppe structure (birch, alder, willow, Norway pine) with patches of taiga and cold steppe, but also scattered tundra-like vegetation (bog pine, dwarf birch, tall herb meadows and arctic fens). Besides the malacofauna (Rousseau, 2001; Frank et al., 2011; Moine, 2014; Moine et al., 2005), the study area showed a different vegetation development compared to German, French, Czech or Austrian areas (Peyron et al., 1998; Bartlein et al., 2011; Antoine et al., 2013; Heiri et al., 2014; Rybníčková and Rybníček, 2014; Nerudová et al., 2016; Duprat-Oualid et al., 2017; Novák et al., 2018) during the LGM period.

#### 5.4. Late Glacial phase (13,000–11,700 cal BP years)

The main environment change formed during the Late Glacial phase in the analysed region. Temperatures increased based on the malacothermometer-based reconstruction, cryophilous elements (*Vallonia tenuilabris*, *Columella columella*) decline, and the appearance and spreading of thermophilous elements (*Caucasotachea vindobonensis*, *Chondrula tridens*, *Granaria frumentum*) (Figs. 5 and 7) can be observed. The overall environmental transformation in the Kolon Lake catchment basin is marked by the closure of the oligotrophic environment and the onset of lake chalk sediment accumulation rich in *Chara* remains (Fig. 11). Parallel to the change in the faunal composition, the pollen composition also changed, with the gradually decreasing proportion of pine (*Pinus* sp.) and the gradually increasing proportion of thermomesophilous trees (Fig. 9). The Arboreal Pollen and Non-Arboreal Pollen ratio did not change, i.e. the mosaic forest-steppe structure was maintained, but the woody vegetation was gradually replaced. As the vegetation transitioned and temperatures increased, the ash content in the Kolon Lake section began to increase (Fig. 11). This suggests that the change in arboreal vegetation during the higher temperatures of the Late Glacial was due to the burning of pine trees, and their replacement with thermomesophilous broad-leaved trees. The burning of pine trees and the colonisation of thermomesophilous broad-leaved trees at higher temperatures in the Late Glacial is supported by previous publications (Willis et al., 1995, 1997, 2000). The new element in this process is that the boreal open parkland structured forest-steppe has been transformed into a temperate open parkland structured forest-steppe environment. The vegetation structure was retained, but at that time thermomesophilous vegetation elements formed the mosaic structure. The process started in the Late Glacial Period and culminated in the transition phase of the Late Glacial - Postglacial phase (12,000–11,000 cal BP years). The formation of the soil level (S0 – Fig. 3) on the surface of the loess layer also started in this phase.

Based on the malacological record of the Madaras section, the Last Glacial cold peak developed between 14,000 and 12,000 cal BP years, parallel to the North Atlantic H0 event (Kirby, 1998), also known as the Younger Dryas (Hemming and Hajdas, 2003; Keigwin and Lehman, 1994). This was the last glacial phase in which significant proportions of Boreo-alpine, Asian montane and Eurasian montane species occurred in masses in the Hungarian Great Plains. The terrestrial malacofauna, pollen material and the composition of the freshwater mollusc fauna in the Kolon Lake sediment basin also indicate the development of a colder phase.

From this layer, both the fauna and the pollen composition have changed fundamentally. The xeromezophilous and thermomesophilous forest-steppe elements, already present in the terrestrial fauna at both the LGM and post-LGM levels, became dominant in the Late Glacial period, both in the developing soil layer of the Madaras section and in the terrestrial gastropod fauna from the Kolon Lake sedimentary basin. Specimens of the characteristic elements *Granaria frumentum* and *Caucasotachea vindobonensis*, typical of Pannonian forest-steppes, were found on this Late Glacial-Early Holocene transition horizon in both the Madaras and Kolon Lake sections. The faunal composition shows that the mosaic forest-steppe structure of the Late Glacial period was preserved, but the thermomesophilous elements dispersed during the Holocene and replaced the cold-loving - cold-tolerant faunal elements. This process resulted that a mosaic temperate forest-steppe replaced the boreal forest-steppe. In parallel, an ash maximum developed in the Kolon Lake core sequence. Based on the ash maximum, a wild natural fire maximum (WNFM) can be assumed during the transition from Late Glacial into post-Glacial according to global and regional data (Johnsen et al., 1995; Rousseau et al., 1998; Voelker et al., 1998; Demske et al., 2005; Magyari et al., 2006; Mackay et al., 2011; Brooks et al., 2012; Magyari et al., 2012b; Tóth et al., 2012). The local malacothermometer, pollen composition and macrobotanical data indicate that this ash maximum developed when the temperature rose. The present-day fire-ecological studies in boreal forest ecosystems suggest that the effect of burning upon the coniferous vegetation would not in itself have been detrimental (Payette, 1992).

In the pollen composition, the proportion of pines decreased drastically, thermomesophilous deciduous trees appeared and gradually increased, in parallel with the microcharcoal maximum. This suggests that the flammability elements of the boreal forest-steppe, e.g. pines, could burn out in a very short time and could not be regenerated at higher temperatures, and they were replaced by

deciduous trees, which can accumulate Ca and Mg (Willis et al., 1995, 1997; Packham et al., 1992) in their leaves like *Betula* (birch), *Quercus* (oak), *Tilia* (linden), *Ulmus* (elm). It can be assumed that the significant amount of ash, which was found in the transition layer of Late Glacial and post Glacial sediments in the Kolon Lake sedimentary basin, was released by the burning of the predominantly coniferous vegetation, which became unstable at rising temperatures. The change of pollen composition suggests the transformation of the boreal forest-steppe vegetation into temperate forest-steppe vegetation, i.e. the mosaics of herbaceous and forest patch structure was preserved, but the species composition was replaced. This is the most significant in the case of woody vegetation, in which pollen of the genus *Pinus* has declined while the proportion of temperate tree pollen has increased. Evidence for a forest-steppe condition is provided by the fact that the combined proportion of woody pollen was between 50% and 70% (Figs. 9 and 10) at both the end of the Glacial and the beginning of the Holocene. This pollen assemblage (Prentice et al., 1996; Allen et al., 2000; Magyari et al., 2010) suggests a forest-steppe condition in the sedimentary environment of the study site. Changes in pollen composition revealed in the Kolon Lake sediment assemblage show good agreement with the Madaras terrestrial snail fauna. Thus, the mosaic structure of the Pannonian forest-steppe was already established at the transition of the Glacial period and the Holocene, between 12,000 and 11,000 cal BP years ago.

In parallel with the ash maximum, the previously mineral-rich (inorganic) oligotrophic lake system was transformed into a calcareous-rich Chara Lake mesotrophic lake system, and this geological change also marks the transformation of the complex ecosystem in the area.

Based on the principal component analyses (PCA) curves of the pollen composition of the most important taxa and detrended component analyses (DCA) curves of the terrestrial snail fauna (Fig. 11) show the transition of the two forest-steppe types. It may have occurred over a period of about 1000 years. During it, the average temperature of the warmest month of the growing season increased by a minimum of 5 °C between 12,000 and 11,000 cal BP years and increased from 13 °C at the end of the Ice Age to 18 °C, and then from 10,500 cal BP years to 20–22 °C in the present. This temperature rising and the accompanying decrease in precipitation (COHMAP: Kutzbach and Guetter, 1986; Kutzbach et al., 1993; Willis et al., 1995; Regional Climatic Model (RCM): Strandberg et al., 2011) first created and then stabilised the temperate forest-steppe environment in the region, as the temperature rise was accompanied by a very significant decrease in humidity. The decrease in humidity likely caused the decrease of water level in the Kolon Lake, transforming the lake system into a eutrophic peat-forming marsh environment (Sümegei et al., 2011b) and peat accumulated in the area from the beginning of the Holocene.

The gradual temperature increase appears to be causing a decrease in humidity and significant environmental and vegetation changes in the region. Moreover, this isolated, basin-scale environmental situation in the middle-south of the basin is suffering from the most significant regional threat (Huang et al., 2016; Burrell et al., 2020), the ongoing process of global temperature rise due to human impacts (Poortinga et al., 2011; Anderson et al., 2012) in the area.

##### 5.5. Early Holocene phase (11,700–8000 cal BP years)

The *Chara* remains accumulated in the analysed basin from Late Glacial but the *Chara* lake phase (Blindow et al., 2002; Apolinska, 2009; Pelechata et al., 2015) formed during the Early Holocene phase (Fig. 11). After the wild natural fire and microcharcoal maximum, the pollen of the broad-leaved trees dominated together with Gramineae and Non-Arboreal Pollens. Changes in the pollen composition (Prentice, 1985; Prentice et al., 1996; Allen et al., 2000) suggest that a temperate forest-steppe dominated the region during the Early Holocene. Vegetation changes started from the Late Glacial but developed fully during the Early Holocene. At that time, the late glacial ecosystem was completely transformed, with the development of the temperate forest-steppe. The oligotrophic lake environment was transformed into a mesotrophic calcareous lake system composed of *Chara* remains (Fig. 11). Similar changes have been reconstructed in the Carpathian Basin, in the eastern part of the Hungarian Great Plain (Willis et al., 1995), in its centre (Sümegei et al., 2013b) and in its western part (Töröcsik et al., 2018). In the Early Holocene phase even the Mesolithic hunting - fishing - gathering communities lived in the analysed area (Sümegei, 2013a; Sümegei et al., 2002, 2004, 2013c), who did not transform the vegetation in a regionally permanent way. Thus, the development of the Early Holocene vegetation was still characterised by natural evolution which was influenced by climatic factors. It was also during this phase that the formation of the surface soil layer (S0) has begun.

##### 5.6. The second half of the Holocene (after 8000 cal BP years)

Productive human communities settled from 8000 years in some waves (Bánffy, 2013, 2020). Thus, some microcharcoal maximums formed in the Kolon Lake section during the second half of the Holocene can be observed, with the Neolithic deforestation, then the wide-spread of the Yamnaya (Pit Grave) culture formed. After then the Iron Age settlement of the Eastern European large-scale pastoral culture such as Mezöcsát culture, and Scythians spread on the Great Hungarian Plain, and in the analysed region (Ecsedy, 1979; Vaday, 2004; Sümegei, 2001; Sümegei and Szilágyi, 2011a).

During the Roman Imperial Age, Sarmatian tribes immigrated to the analysed region (Tugya et al., 2020), then in the Dark and Medieval Ages, some large animal keeper communities (Avars, Magyars, Cumans) settled there (Vaday, 2004). These productive communities are associated with economic activities, a strong increase in grazing areas, the reduction of forest cover in the forest-steppe region, and the establishment of cultivated steppe (Fig. 11) during the Late Holocene. Following the emergence of large pastoral populations during the Late Glacial phase, the surface soil (S0), which had already been developed during the Early Holocene phase, was eroded. Thus, the soil horizon between the soil level that developed in the Early Holocene and the surface soil level that developed after the medieval land-use change, fertilisation agriculture and ploughing (Nyári et al., 2012, 2014) may be missing,

eroded during the Iron Age to the Roman Imperial Age, the Dark Age due to the large animal keeper communities that appeared in the area.

The entire lake system of Kolon Lake was transformed in the last 8000 years and a peaty lake stage developed in the basin, with wider or narrower marsh margins and lower or higher water levels as a result of precipitation and flooding. As the Kolon Lake system is dependent on groundwater levels, groundwater was also dependent on the Danube floods and on changes in the Danube catchment, or even in the Alps (snow and glacier melt, precipitation) (Kiss, 2007, 2009). Thus, in addition to precipitation in the study region, Danube floods have also influenced changes in the water level of the marsh lake over the last 8000 years. The gradual recharge of the basin is indicated by a slow increase in the proportion of terrestrial gastropod (*Galba truncatula*, *Succinea putris*, *Oxytoma elegans*, *Vallonia ennensis*) and xeromesophilous (*Granaria frumentum*, *Vallonia costata*, *Helicopsis striata*) species within the section towards the Late Holocene period. The surface soil formation on the peat layer is probably a result of the hydroregulation of the 19th century, when the water level of the Kolon Lake was lowered by draining (Molnár, 2015).

These archaeological, geological and environmental-historical data are the most alarming signs of climate change and land use in the region today. The current intensive mechanised and chemical-based agriculture has resulted in the development of open vegetation and areas without vegetation in spring on several km<sup>2</sup> and in some places, 10–20 km<sup>2</sup> of surface, and the conservation strategy of the National Park in the region (Tóth, 1979; Molnár, 2015) cannot compensate for the increased human impacts on the rising local and regional temperatures. As a consequence, the vegetation cover, especially at the beginning of the growing season, is fatally reduced, resulting in a strong soil degradation on loess surfaces and a patchy but intense wind-blown-sand formation on sand surfaces. At the end of the glacial period, beginning of the Holocene, although a cascade-type gradual change developed between the LGM and the Early Holocene, an increase of 5 °C over 1000 years between 12 and 11 kyr developed, geologically speaking abruptly. Based on current climate scenarios for the region (Krüzselyi et al., 2011; Bartholy et al., 2014; Kis et al., 2017, 2020; Ács et al., 2020), a similar mean temperature increase will play out over the coming decades, over approximately a century. That is, ten times faster than at the end of the Ice Age, at the beginning of the Holocene. This is likely to be one of the major problems in the area, as the natural elements of the local biota, with their significant human impact, may find it difficult to adapt to these changes (Dobrowski, 2011). Because these will be the warmest months of the new average temperatures, precipitation, especially in the breeding season, will be drastically reduced (Pálfai, 2002, 2010; and Führer and Járó, 2000), and as a consequence humidity will be drastically reduced (Pálfai, 2002, 2010), especially in the breeding season. The first signs of this can be seen in the change in the composition of the snail fauna, the impoverishment of the fauna, the decline in species and number of individuals over the last 50–60 years, the dominance and dominance of xerothermophilous elements and the anabiosis that occurs during the summer (Bába, 1969, 1997a, 1997b; Bába and Bagi, 1997). It is likely that these processes will be exacerbated by modern human-induced temperature changes and that the study region will become the driest area of the Carpathian Basin. This will certainly require changes in land use and agricultural activity, especially in the Bácska loess plateau, one of the most important areas for crop and livestock production, because the current intensive agricultural activity will become unsustainable as a result of the current climatic changes.

## 6. Conclusions

A comparative analysis of the 32 radiocarbon dated section of Madaras and 21 radiocarbon dates of Kolon Lake section allowed us to reconstruct the following series of changes.

These data, as well as recent bioclimatic results, demonstrate that the central and southern parts of the Carpathian Basin belong to different vegetation and environmental regions, different ecoregions (Sümegei et al., 2012a) than the north-western and western margins of the Eurasian loess belt. The specificities of the ecoregion made it distinct from the eastern European loess region in terms of faunal and vegetation development (Gerashimenko and Rousseau, 2008; Alexandrowicz, 2011, 2014; Alexandrowicz et al., 2014; Magyari et al., 2014; Feurdean et al., 2014; Haesaerts et al., 2020). Based on the palaeoecological data available so far, the most important process in the development of this ecoregion was the uplift of the mountain range surrounding the Carpathian Basin (Sümegei et al., 2018), the closure of the basin and its rain shadow (Sümegei et al., 2012a).

The July paleotemperature values reconstructed by the malacothermometer data (Sümegei, 1989, 2019; Sümegei et al., 1991; Hertelendi et al., 1992) for the Hungarian Great Plain in the LGM period show good correlation with the mathematical-statistical models for the area, which reconstructed the temperature values from the ice cover distance in the same area (COHMAP: Kutzbach and Guetter, 1986; Kutzbach et al., 1993). The quartermalacological and distance models resulted in paleotemperatures of 11–14 °C in July, the warmest summer month, in the cooling phases. Climate models suggest that the strong cooling effects occurred in the winter (December to February) and in January mean temperatures when mathematical models suggest a climate 20–25 °C colder than recent temperatures.

At the same time, the changes of the mollusc fauna prove the almost continuous presence of Central and SSE European thermomesophilous open vegetation habitat preferring elements, especially *Granaria frumentum*, and the European and Central European ecotone vegetation habitat preferring and shade-loving snail taxa, which are abundant at the LGM level. The occurrence, persistence and dominance of both faunal groups in the cooling phase of the LGM are related to the role of the Carpathian Basin refugium (Stieber, 1956, 1967a; Willis et al., 1995, 2000; Willis and Whittaker, 2000; Brewer et al., 2002; Petit et al., 2003; Willis and Van Andel, 2004; Magyari et al., 2011; Juříčková et al., 2019; Pató et al., 2020).

Malacological data suggest that both temperate forest-steppe elements (*Granaria frumentum*, *Chondrula tridens*: Sümegei et al., 2016) and shade-loving, ecotone habitat preferring, recently forest and ecotone snail faunas (e.g. *Clausilia dubia*, *Semilimax semilimax*: Sümegei, 2003) with sporadic refugia continuously inhabited by these species may have been located on the margins of the study region and colonised the study area only intermittently when suitable environmental and climatic conditions developed. Thus, the study

region is referred to as a fluctuation zone (Varga, 1981; Sümeği, 1999; Deli and Sümeği, 2004), and these shade-loving and ecotone vegetation habitat preferring European, Central European and Central SSE European open habitat preferring mesothermophilous snail taxa appeared only periodically and sporadically in the centre of the Carpathian Basin, the Hungarian Great Plain, in the horizon of MIS2, following cyclical climatic changes. Local palaeoecological data show that the cold phase of the LGM and Heinrich 1 cold event were completely merged in both the Madaras and Kolon Lake sections and in the study area. However, during and after the Heinrich 1 event in the post-LGM phase, the local July temperature varied over a wide range (1–5 °C).

Following the Early Holocene, less significant temperature fluctuations occur during the Holocene based on changes in the composition of the malacofauna but ash maximum also developed. However, these ash maxima have always been associated with the appearance of more massively productive farming communities and with the production technology changes (mainly the appearance of large pastoralists). The increase in grazing areas, the reduction of forest patches by burning (Neolithic, late Bronze Age/early Bronze Age, Iron Age, Roman Imperial, Dark, Medieval Ages) can be assumed during that time. Human impacts were so strong during the Imperial period that the development of the Danubian Roman limes, as a result of the anthropogenic environment, including the destruction of forest vegetation (Willis, 1994), led to the colonisation of species, especially *Xerolenta obvia*, which were widespread in the limestone steppe areas of the northern Balkans, first in the Danube valley and then on the loess surfaces of the study region (Sümeği, 1999, 2013a). These burning processes and the homogenisation of vegetation by burning and overgrazing resulted in the development of characteristic wind-blown-sand movement levels on the surface of the Danube-Tisza alluvial cone (Sümeği, 2001; Nyári et al., 2014). Thus, as a result of this strong human influence, the vegetation has been transformed to such an extent that the natural forest-steppe has been converted into a cultivated steppe, a cultivated desert, and in the absence of vegetation cover, sand movement levels, sometimes metres thick sand layers, have developed in the study region in historical times.

### CRedit authorship contribution statement

P.S., D.M., K.N.: Conceptualization. P.S., D.M., L.M., M.M.: Methodology. P.S., D.M., K.N., L.M., P.Cs.: Software. P.S. D.M., L.Z.: Validation. P.S., D.M., K.N., L.M., P.Cs. T.T.: Investigation. P.S., D.M.: Writing – original draft. D.M., K.N., L.M., P.Cs., L.Z.: Writing – review & editing. P.S., M.M.: Resources. D.M., P.Cs., T.T.: Formal analysis. P.S., L.Z.: Supervision. M.M., P.S., D.M.: Funding acquisition.

### Declaration of Competing Interest

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

### Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

### Acknowledgements

This research was supported by the Hungarian Government, Ministry of Human Capacities (20391-3/2018/FEKUSTRAT) and the European Regional Development Fund (GINOP-2.3.2-15-2016-00009 'ICER') and the University of Szeged Open Access Fund (no. 5386). D. Molnár would like to thank the support of the Hungarian National Excellence Programme grant (NTP-NFTÖ-19-B-0158).

### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01976](https://doi.org/10.1016/j.gecco.2021.e01976).

### References

- Aaby, B., Digerfeldt, G., 1986. Sampling techniques for lakes and bogs. In: Berglund, B.E. (Ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology*. Wiley, New York, pp. 181–194.
- Ács, F., Zsákai, A., Kristóf, E., Szabó, A.I., Breuer, H., 2020. Human thermal climate of the Carpathian Basin. *Int. J. Climatol.* <https://doi.org/10.1002/joc.6816>.
- Agee, J.K., 1996. *Fire Ecology of Pacific Northwest Forests*. Island Press.
- Agiadi, K., Albano, P.G., 2020. Holocene fish assemblages provide baseline data for the rapidly changing eastern Mediterranean. *Holocene*, 0959683620932969.
- Albano, P.G., Steger, J., Bošnjak, M., Dunna, B., Guifarro, Z., Turapova, E., Hua, Q., Kaufman, D.S., Rilov, G., Zushin, M., 2021. Native biodiversity collapse in the eastern Mediterranean. *Proc. R. Soc. B* 288 (1942), 20202469.
- Alexandrowicz, W.P., 2011. Molluscan communities in Vistulian loess located in Chobrzany, a village near Sandomierz (Southern Poland). *Geol. Geophys. Environ.* 37 (3), 357.
- Alexandrowicz, W.P., 2014. Malacological sequence of Weichselian (MIS 5-2) loess series from a profile in Grodzisko Dolne (southern Poland) and its palaeogeographic significance. *Quat. Int.* 319, 109–118.
- Alexandrowicz, W.P., Łanczont, M., Boguckij, A.B., Kulesza, P., Dmytruk, R., 2014. Molluscs and ostracods of the Pleistocene loess deposits in the Halych site (Western Ukraine) and their significance for palaeoenvironmental reconstructions. *Quat. Sci. Rev.* 105, 162–180.

- Allen, J.R., Watts, W.A., Huntley, B., 2000. Weichselian palynostratigraphy, palaeovegetation and palaeoenvironment; the record from Lago Grande di Monticchio, southern Italy. *Quat. Int.* 73, 91–110.
- Alley, R.B., Meese, D.A., Shuman, C.A., Gow, A.J., Taylor, K.C., Grootes, P.M., White, J.W.C., Ram, M., Waddington, E.D., Mayewski, P.A., Zielinski, G.A., 1993. Abrupt increase in Greenland snow accumulation at the end of the Younger Dryas event. *Nature* 362 (6420), 527–529.
- An, Z., Kukla, G.J., Porter, S.C., Xiao, J., 1991. Magnetic susceptibility evidence of monsoon variation on the Loess Plateau of central China during the last 130,000 years. *Quat. Res.* 36, 29–36.
- Andersen, K.K., Svensson, A., Johnsen, S.J., Rasmussen, S.O., Bigler, M., Röthlisberger, R., Ruth, R., Siggaard-Andersen, M.-L., Steffensen, J.P., Jensen, D.D., Vinther, B.M., 2006. The Greenland ice core chronology 2005, 15–42ka. Part 1: constructing the time scale. *Quat. Sci. Rev.* 25, 3246–3257.
- Anderson, J.T., Panetta, A.M., Mitchell-Olds, T., 2012. Evolutionary and ecological responses to anthropogenic climate change: update on anthropogenic climate change. *Plant Physiol.* 160 (4), 1728–1740.
- Antoine, P., Rousseau, D.D., Degeai, J.P., Moine, O., Lagroix, F., Fuchs, M., Hatté, C., Lisá, L., 2013. High-resolution record of the environmental response to climatic variations during the Last Interglacial–Glacial cycle in Central Europe: the loess-palaeosol sequence of Dolní Věstonice (Czech Republic). *Quat. Sci. Rev.* 67, 17–38.
- Apolinarska, K., 2009.  $\delta^{18}O$  and  $\delta^{13}C$  isotope investigation of the Late Glacial and early Holocene biogenic carbonates from the Lake Lednica sediments, western Poland. *Acta Geol. Pol.* 59, 111–121.
- Bába, K., 1969. Malacocological investigation some sandy grassland and forest in the Danube – Tisza Interfluve. Szeged. Tanárk. Főiskola Tud. Közleményei 14, 83–92.
- Bába, K., 1980. A history and present-day situation of the investigation of the recent land snails in the Great Hungarian Plain. *Tiscia* 15, 93–102.
- Bába, K., 1983. History of the investigation of the terrestrial snails of the Great Hungarian Plain and its present situation. II. *Tiscia* 18, 83–95.
- Bába, K., 1987. Mollusca from the Kiskunság National Park. In: Mahunka, S. (Ed.), *The Fauna of the Kiskunság National Park*. Magyar Természettudományi Múzeum Kiadványa, Budapest, pp. 47–62.
- Bába, K., 1997. Changes in terrestrial snail assemblages in the organogenic successional sere in response to antropogenic influences. *Heldia* 4 (5), 125–129.
- Bába, K., 1997. Characteristic processes in the succession of snail assemblages in the plant associations of continental sand dunes of the Danube-Tisza mid-region and of the Kiskunság National Park (Hungary). *Nachr. Ersten Vorarlb. Malakol. Ges.* 5, 45–56.
- Bába, K., Bagi, I., 1997. Snail communities associated to swampy meadows and sedgy marshy meadows plant communities of the Great Hungarian Plain. Comunidades de moluscos asociadas a comunidades vegetales de praderas pantanosas y junqueras en la Gran Llanura Húngara. *Soc. Esp. Malacol. Iberus* 15, 83–93.
- Baliuk, S., Medvedev, V., Kucher, A., Solovey, V., Levin, A., Kolmaz, Y., 2017. Ukrainian chernozems as a factor in global food security and resilience of agriculture to climate change. In: Shedeekar, V.S., Islam, R. (Eds.), *Proceedings of the Global Symposium on Soil Organic Carbon 2017, Rome, Italy, 21–23 March*. Food and Agriculture Organization of the United Nations (FAO), pp. 423–428.
- Bánffy, E., 2013. *The Early Neolithic in the Danube-Tisza Interfluve*. Archaeopress (British Archaeological Reports), 2584, Oxford, p. 189.
- Bánffy, E., 2020. *The Environmental History of the Prehistoric Sárköz Region in Southern Hungary*. Confinia et horizontes 1, Harrassowitz Verlag, Darmstadt, p. 250.
- Barber, K.E., Chambers, F.M., Maddy, D., Brew, J., 1994. A sensitive high resolution record of the Holocene climatic change from a raised bog in northern England. *Holocene* 4, 198–205.
- Bartholy, J., Pongrácz, R., Pieczka, I., 2014. How the climate will change in this century? *Hung. Geogr. Bull.* 63 (1), 55–67.
- Bartlein, P.J., Harrison, S.P., Brewer, S., Connor, S., Davis, B.A.S., Gajewski, K., Guiot, J., Harrison-Prentice, T.I., Henderson, A., Peyron, O., Prentice, L.C., Scholze, M., Seppä, H., Schuman, B., Sugita, S., Thompson, R.S., Viau, E.A., Williams, J., Wu, H., 2011. Pollen-based continental climate reconstructions at 6 and 21 ka: a global synthesis. *Clim. Dyn.* 37 (3), 775–802.
- Baxter, S., 2007. *World Reference Base for Soil Resources*. World Soil Resources Report 103. Rome: Food and Agriculture Organization of the United Nations (2006), pp. 1–132, *Experimental Agriculture*, 43(2), 264–264.
- Behre, K.E., 1981. The interpretation of anthropogenic indicators in pollen diagrams. *Pollen Spores* 23, 225–245.
- Behre, K.E. (Ed.), 1986. *Anthropogenic Indicators in Pollen Diagrams*. Balkema, Rotterdam.
- Belokopytov, I.E., Beresnevich, V.V., 1955. Giktorf's peat borers. *Torfyannya Promyhlennost* 8, 9.
- Bennett, K.D., 1992. PSIMPOLL: a quickBASIC program that generates PostScript page description files of pollen diagrams. INQUA Commission for the study of the Holocene: working group on data handling methods. *Newsletter* 8, 11–12.
- Bennett, K.D., 2005. *Documentation for psimpoll 4.25 and pscomb 1.03: C Programs for Plotting Pollen Diagrams and Analysing Pollen Data*. Department of Earth Sciences, University of Uppsala, Uppsala.
- Berglund, B.E., Ralska-Jasiewiczowa, M., 1986. *Handbook of Holocene Palaeoecology and Palaeohydrology*. J. Wiley and Sons, Chichester, p. 869.
- Bernátsky, J., 1914. The tree vegetation of the Great Hungarian Plain. *Erd. Kísérletek* 16, 129–180.
- Beug, H.J., 2004. *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete*. Verlag Dr. Friedrich Pfeil, München.
- Birks, H.J.B., 1985. Quantitative palaeoenvironmental reconstructions. In: Maddy, D., Brew, J.S. (Eds.), *Statistical Modelling of Quaternary Science Data*. Technical Guide. Quaternary Research Association, Cambridge, pp. 161–254.
- Birks, H.J.B., Birks, H.H., 1980. *Quaternary Palaeoecology*. Arnold Press, London, p. 289.
- Birks, H.J.B., Gordon, A.D., 1985. *Numerical Methods in Quaternary Pollen Analysis*. Academic Press, London.
- Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Anal.* 3, 457–474.
- Blaauw, M., Christen, J.A., Bennett, K.D., Reimer, P.J., 2018. Double the dates and go for Bayes- Impacts of model choice, dating density and quality of chronologies. *Quat. Sci. Rev.* 188, 58–66.
- Blindow, I., Hargeby, A., Andersson, G., 2002. Seasonal changes of mechanisms maintaining clear water in a shallow lake with abundant Chara vegetation. *Aquat. Bot.* 72 (3–4), 315–334.
- Bond, G., Heinrich, H., Broecker, W., McManus, J., Labeyrie, L., Andrews, J., 1992. Evidence for massive discharges of icebergs into the North Atlantic ocean during the last glacial period. *Nature* 360, 245–249.
- Bond, G., Broecker, W., Johansen, S., Labeyrie, L., McManus, J., Jouzel, J., Bonani, G., 1993. Correlation between climate records from North Atlantic sediments and Greenland ice. *Nature* 365, 245–249.
- Bond, G.C., Showers, W., Elliot, M., Evans, M., Lotti, R., Hajdas, I., Bonani, G., Johnson, S., 1999. The North Atlantic's 1–2 Kyr climate rhythm: relation to Heinrich Events, Dansgaard/Oeschger Cycles and the Little Ice Age. In: Clark, P.U., Robert, S.W., Lloyd, D.K. (Eds.), *Mechanisms of Global Climate Change at Millennial Time Scales*. Geophysical Monographs, 112. American Geophysical Union, Washington, USA, pp. 35–58.
- Borhidi, A., 1956. Die Steppen und Wiesen im Sandgebiet der Kleinen Ungarischen Tiefebene. *Acta Bot. Acad. Sci. Hung.* 2, 241–274.
- Boycott, A.E., 1934. The habitats of land Mollusca in Britain. *J. Ecol.* 22, 1–38.
- Boycott, A.E., 1936. The habitats of freshwater molluscs in Britain. *J. Anim. Ecol.* 5, 118–186.
- Brewer, S., Cheddadi, R., De Beaulieu, J.L., Reille, M., 2002. The spread of deciduous Quercus throughout Europe since the last glacial period. *For. Ecol. Manag.* 156 (1–3), 27–48.
- Brooks, S.J., Matthews, I.P., Birks, H.H., Birks, H.J.B., 2012. High resolution Lateglacial and early-Holocene summer air temperature records from Scotland inferred from chironomid assemblages. *Quat. Sci. Rev.* 41, 67–82.
- Burrell, A.L., Evans, J.P., De Kauwe, M.G., 2020. Anthropogenic climate change has driven over 5 million km<sup>2</sup> of drylands towards desertification. *Nat. Commun.* 11 (1), 1–11.
- Cacho, I., Grimalt, J.O., Pelejero, C., Canals, M., Sierro, F.J., Flores, J.A., Shackleton, N., 1999. Dansgaard-Oeschger and Heinrich event imprints in Alboran Sea paleotemperatures. *Paleoceanography* 14 (6), 698–705.
- Chapman, J., 2018. Climatic and human impact on the environment?: A question of scale. *Quat. Int.* 496, 3–13.

- Chytrý, M., Horsák, M., Danihelka, J., Ermakov, N., German, D.A., Hájek, M., Hájková, P., Kočí, M., Kubešová, S., Lustik, P., Nekola, J.C., Řičánková, V.P., Preislerová, Z., Resl, P., Valachovič, M., 2019. A modern analogue of the Pleistocene steppe-tundra ecosystem in southern Siberia. *Boreas* 48 (1), 36–56.
- Clark, J.S., 1988. Effect of climatic change on fire regimes in northwestern Minnesota. *Nature* 334, 233–235.
- Clark, R.L., 1982. Point count estimation of charcoal in pollen preparations and thin sections of sediments. *Pollen Spores* 24, 523–535.
- Dansgaard, W., Clausen, H.B., Gundestrup, N., Hammer, C.U., Johnsen, S.F., Kristinsdottir, P.M., Reeh, N., 1982. A new Greenland deep ice core. *Science* 218 (4579), 1273–1277.
- Dearing, J.A., Dann, R.J.L., Hay, K., Lees, J.A., Loveland, P.J., Maher, B.A., O'Grady, K., 1996. Frequency-dependent susceptibility measurements of environmental materials. *Geophysical Journal International* 124, 228–240.
- Deli, T., Sümegi, P., 2004. Late Pleistocene forest refugia in the Carpathian Basin and glacial relict elements in the gastropod fauna of the analyzed region. In: Sümegi, P., Gulyás, S. (Eds.), *The Geohistory of Bátorliget Marshland*. Archaeolingua Press, Budapest, pp. 207–212.
- Demske, D., Heumann, G., Granoszewski, W., Nita, M., Mamakowa, K., Tarasov, P.E., Oberhänsli, H., 2005. Late glacial and Holocene vegetation and regional climate variability evidenced in high-resolution pollen records from Lake Baikal. *Glob. Planet. Chang.* 46 (1–4), 255–279.
- Dobosi, T., 1967. A recent Upper Palaeolithic settlement in the Great Hungarian Plain. *Archaeol. Értesítő* 94, 184–193.
- Dobosi, T., 1975. Register of palaeolithic and mesolithic sites in Hungary. *Archaeol. Értesítő* 102, 64–76.
- Dobosi, T., 1994. Contribution to the Upper Palaeolithic topography. *Acta Archaeol. Acad. Sci. Hung.* 46, 3–20.
- Dobosi, T., 1989. Upper Paleolithic settlement at Madaras-Téglavető. *Régészeti feldolgozás. Cumania*, 11, 45–65. (in Hungarian).
- Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Glob. Chang. Biol.* 17 (2), 1022–1035.
- Dong, Y., Wu, N., Jiang, W., Li, F., Lu, H., 2020. Cascading response of flora and terrestrial mollusks to last deglacial warming. *Glob. Ecol. Conserv.* 24, e01360.
- Dong, Y., Wu, N., Li, F., Zhang, D., Zhang, Y., Huang, L., Chen, X., Wu, B., Lu, H., 2020. Anthropogenic modification of soil communities in northern China for at least two millennia: evidence from a quantitative mollusk approach. *Quat. Sci. Rev.* 248, 106579.
- Dryness, C.T., Viereck, L.A., Van Cleve, K., 1986. Fire in taiga communities of interior Alaska. In: Van Cleve, K., Chapin, F.S., I.I.I., Flanagan, P.W., Viereck, L.A., Dryness, C.T. (Eds.), *Forest Ecosystems in the Alaskan Taiga*. Springer-Verlag, New York, pp. 74–88.
- Duprat-Oualid, F., Riud, D., Bégeot, C., Magny, M., Millet, L., Wulf, S., Appelt, O., 2017. Vegetation response to abrupt climate changes in Western Europe from 45 to 14.7 k cal a BP: the Bergsee lacustrine record (Black Forest, Germany). *J. Quat. Sci.* 32 (7), 1008–1021.
- Ecsedy, I., 1979. The people of the pit-grave kurgans in Eastern Hungary. *Fontes archaeologici Hungariae. Akadémiai Kiadó, Budapest*.
- Evans, J.G., 1972. *Land Snails in Archeology*. Seminar Press, London.
- Faegri, K., Iversen, J., 1989. *Textbook of Pollen Analysis*. John Wiley and Son, Chichester, p. 328.
- Feurdean, A., Persoiu, A., Tanjäu, I., Stevens, T., Magyari, E.K., Onac, B.P., Marković, S., Andrić, M., Connor, S., Fărcaș, S., Gaika, M., Gaudenyi, T., Hoek, W., Kolaczek, P., Kuneš, P., Lamentowicz, M., Marinova, E., Michczyńska, D.J., Persoiu, I., Plóciennik, M., Slowiński, M., Stancikaite, M., Sümegi, P., Svensson, A., Tămaș, T., Timar, A., Tonkov, S., Tóth, M., Veski, S., Willis, K.J., Zernitskaya, V., 2014. Climate variability and associated vegetation response throughout Central and Eastern Europe (CEE) between 60 and 8 ka. *Quat. Sci. Rev.* 106, 206–224.
- Flannigan, M.D., Harrington, J.B., 1988. A study of the relationship of meteorological variables to monthly provincial area burned by wildfire in Canada (1953–1980). *J. Appl. Meteorol.* 27, 441–452.
- Frank, C., Terhorst, B., Damm, B., Thiel, C., Frechen, M., Peticzka, R., 2011. Pleistocene loess deposits and mollusc assemblages in the Eastern Pre-Alps. *EG Quat. Sci. J.* 60 (1), 126–136.
- Franzke, C.L., 2014. Warming trends: nonlinear climate change. *Nat. Clim. Chang.* 4 (6), 423–424.
- Führer, E., Járó, Z., 2000. The effectiveness of drought and drainage water in the silviculture of the Great Plain I. *Erdészeti Tudományos Intézet Kiadványai*, 12, 1–144 (in Hungarian).
- Genty, D., Blamart, D., Ghaleb, B., Plagnes, V., Causse, C., Bakalowicz, M., Zouari, K., Chkri, N., Hellstrom, J., Wainer, K., Bourges, F., 2006. Timing and dynamics of the last deglaciation from European and North African  $\delta^{13}C$  stalagmite profiles—comparison with Chinese and South Hemisphere stalagmites. *Quat. Sci. Rev.* 25 (17–18), 2118–2142.
- Gerasimenko, N., Rousseau, D.D., 2008. Stratigraphy and paleoenvironments of the last Pleniglacial in the Kyiv loess region (Ukraine). *Quat. Rev. l'Assoc. Fr. pour l'étude Quat.* 19 (4), 293–307.
- González-Sampériz, P., Valero-Garcés, B.L., Moreno, A., Jalut, G., García-Ruíz, J.M., Martí-Bono, C., Delgado-Huertas, A., Navas, A., Otto, T., Dedoubat, J.J., 2006. Climate variability in the Spanish Pyrenees during the last 30,000 yr revealed by the El Portalet sequence. *Quat. Res.* 66 (1), 38–52.
- Groote, P.M., Stuiver, M., White, J.W.C., Johnsen, S., Jouzel, J., 1993. Comparison of oxygen isotope records from the GISP2 and GRIP Greenland ice cores. *Nature* 366 (6455), 552–554.
- Haase, M., Meng, S., Horsák, M., 2020. Tracking parallel adaptation of shell morphology through geological times in the land snail genus *Pupilla* (Gastropoda: Stylommatophora: Pupillidae). *Zool. J. Linn. Soc.* 20, 1–28.
- Haesaerts, P., Gerasimenko, N., Dambon, F., Yurchenko, T., Kulakovska, L., Usik, V., Ridush, B., 2020. The Upper Palaeolithic site Doroshivtsi III: a new chronostratigraphic and environmental record of the Late Pleniglacial in the regional context of the Middle Dniester-Prut loess domain (Western Ukraine). *Quat. Int.* 546, 196–215.
- Heiri, O., Koinig, K.A., Spötl, C., Barrett, S., Brauer, A., Drescher-Schneider, R., Gaar, D., SusanIvy-Ochs, S., Kerschner, H., Luetscher, M., Moran, A., Nicolussi, K., Preusser, F., Schmidt, R., Schoeneich, P., Schwörer, C., Sprafke, T., Terhorst, B., Tinner, W., 2014. Palaeoclimate records 60–8 ka in the Austrian and Swiss Alps and their forelands. *Quat. Sci. Rev.* 106, 186–205.
- Hemming, S.R., Hajdas, I., 2003. Ice-rafted detritus evidence from 40Ar/39Ar ages of individual hornblende grains for evolution of the eastern margin of the Laurentide ice sheet since 43 14C ky. *Quat. Int.* 99, 29–43.
- Hertelendi, E., Sümegi, P., Szőör, Gy., 1992. Geochronologic and paleoclimatic characterization of Quaternary sediments in the Great Hungarian Plain. *Radiocarbon* 34, 833–839.
- Hoffmann, M.H., Meng, S., Kosachev, P.A., Terechina, T.A., Silanteva, M.M., 2011. Land snail faunas along an environmental gradient in the Altai Mountains (Russia). *J. Molluscan Stud.* 77, 76–86.
- Holdridge, L.R., 1947. Determination of world plant formations from simple climatic data. *Science* 105, 367–368.
- Holdridge, L.R., 1967. *Life zone ecology*. Tropical Science Center, San Jose, Costa Rica.
- Hollósi, A., Biró, Cs., Biró, M., S., Falusi, E., 2015. Landscape historical aspects and macrophyte monitoring of the habitat restoration on the Lake Kolon at Izsák. *Hidrol. Közlöny* 95, 100–101.
- Horsák, M., Chytrý, M., Danihelka, J., Kočí, M., Kubešová, S., Lososová, Z., Otýpková, Z., Tichý, L., 2009. Snail faunas in the Southern Ural forests and their relations to vegetation: an analogue of the Early Holocene assemblages of Central Europe? *J. Molluscan Stud.* 76, 1–10.
- Horsák, M., Chytrý, M., Pokryszko, B.M., Danihelka, J., Ermakov, N., Hájek, M., Hájková, P., Kintrová, K., Kočí, M., Kunešová, S., Lustyk, P., Otýpková, Z., Pelánková, B., Valachovič, M., 2010. Habitats of relict terrestrial snails in southern Siberia: lessons for the reconstruction of palaeoenvironments of full-glacial Europe. *J. Biogeogr.* 37, 1450–1462.
- Horsák, M., Škodová, J., Mýšák, J., Čejka, T., Ložek, V., Hlaváč, J., 2010. *Pupilla pratensis* (Gastropoda: Pupillidae) in the Czech Republic and Slovakia and its distinction from *P. muscorum* and *P. alpica* based on multidimensional analysis of shell measurements. *Biologia* 65 (6), 1012–1018.
- Horsák, M., Schenková, V., Mýšák, J., 2012. The second site of *Pupilla alpica* (Charpentier, 1837) and the first recent record of *Pupilla pratensis* (Clessin, 1871) in Poland. *Folia Malacol.* 20, 1.
- Horsák, M., Juričková, L., Pícká, J., 2013. Mollusc of the Czech and Slovak Republics. *Kabarek*, Zlin.
- Horváth, Z., Sövény, M., Szénásiné Harton, E., 2006. *Bácsalmás*. Chapters from the history of an Upper Bácska small town. *Bácsalmás, Magánkiadás*, p. 271.
- Hu, Y., Zhou, B., Lu, Y., Zhang, J., Min, S., Dai, M., Si, Y.X., Qi, Y., Yang, Q., Bo, H., Zheng, H., 2020. Abundance and morphology of charcoal in sediments provide evidence of massive slash-and-burn agriculture during the Neolithic Kuahuqiao culture, China. *PLoS One* 15 (8), e0237592.
- Huang, J., Yu, H., Guan, X., Wang, G., Guo, R., 2016. Accelerated dryland expansion under climate change. *Nat. Clim. Chang.* 6 (2), 166–171.

- Hupuczki, J., Sümegei, P., 2010. The Late Pleistocene paleoenvironment and paleoclimate of the Madaras section (South Hungary), based on preliminary records from mollusks. *Cent. Eur. J. Geosci.* 2, 64–70.
- Jacobson, G.L., Bradshaw, R.H.W., 1981. The selection of sites for palaeovegetational studies. *Quat. Res.* 16, 80–96.
- Jakab, G., Sümegei, P., 2004. Keys and descriptions for the determination of fossil plant remains occur in peat. *Kitaibelia* 9, 93–129 (in Hungarian with English summary).
- Jakab, G., Sümegei, P., Magyari, E., 2004. New quantitative method for the paleobotanical description of Late Quaternary Organic Sediments (Mire, Development Pathway and Palaeoclimatic Records from Southern Hungary). *Acta Geol. Hung.* 47, 373–409.
- Jakab, G., Sümegei, P., 2011. Quaternary macrobotany. *Geolitera Kiadó, Szeged*, 252 p (in Hungarian with English summary).
- Johnsen, S.J., Dahl-Jensen, D., Gundestrup, N., Steffensen, J.P., Clausen, H.B., Miller, H., Masson-Delmotte, V., Sveinbjörnsdóttir, A.E., White, J., 2001. Oxygen isotope and palaeotemperature records from six Greenland ice-core stations: Camp Century, Dye-3, GRIP, GISP2, Renland and NorthGRIP. *J. Quat. Sci. Publ. Quat. Res. Assoc.* 16 (4), 299–307.
- Juričková, L., Horáčková, J., Jansová, A., Kovanda, J., Harčár, J., Ložek, V., 2019. A glacial refugium and zoogeographic boundary in the Slovak eastern Carpathians. *Quat. Res.* 91 (1), 383–398.
- Keigwin, L.D., Lehman, S.J., 1994. Deep circulation change linked to Heinrich event 1 and Younger Dryas in a middepth North Atlantic core. *Paleoceanography* 9 (2), 185–194.
- Kerner, A., 1863. *Das Pflanzenleben der Donauländer*. Wagner, Innsbruck, 343 p.
- Kerney, M.P., Cameron, R.A.D., Jungbluth, J.H., 1983. *Die Landschnecken Nord- und Mitteleuropas*. Paul Parey Press, Hamburg-Berlin.
- Kirby, M.E., 1998. Heinrich event-0 (DC-0) in sediment cores from the northwest Labrador Sea: recording events in Cumberland Sound? *Can. J. Earth Sci.* 35 (5), 510–519.
- Kis, A., Pongrácz, R., Bartholy, J., 2017. Multi-model analysis of regional dry and wet conditions for the Carpathian Region. *Int. J. Climatol.* 37, 4543–4560.
- Kis, A., Pongrácz, R., Bartholy, J., Gocic, M., Milanovic, M., 2020. Multi-scenario and multi-model ensemble of regional climate change projections for the plain areas of the Pannonian Basin. *Q. J. Hung. Meteorol. Serv.* 124, 157–190.
- Kiss, A., 2009. Historical climatology in Hungary: role of documentary evidence in the study of past climates and hydrometeorological extremes. *Időjárás* 113 (4), 315–339.
- Kiss, A., 2007. “Suburbia autem maxima in parte videntur esse deleta” – Danube ice floods and the pitfalls of urban planning: pest and its suburbs in 1768–1799. In: Kovács, Cs. (Ed.), *From Villages to Cyberspace*. University of Szeged, Szeged, pp. 271–282.
- Krevelde, S.V., Sarnthein, M., Erlenkeuser, H., Grootes, P., Jung, S., Nadeau, M.J., Pflaumann, U., Voelker, A., 2000. Potential links between surging ice sheets, circulation changes, and the Dansgaard-Oeschger cycles in the Irminger Sea, 60–18 kyr. *Paleoceanography* 15, 425–442.
- Krolopp, E., 1965. Mollusc fauna of the sedimentary formations of the Quaternary period. *Hung. Acta Geol. Hung.* 9, 153–160.
- Krolopp, E., 1973. Quaternary malacology in Hungary. *Földrajzi Közlemények* 21, 161–171.
- Krolopp, E., 1983. Biostratigraphic division of Hungarian Pleistocene Formations according to their Mollusc fauna. *Acta Geol. Hung.* 26, 62–89.
- Krolopp, E., Sümegei, P., 1990. Vorkommen von *Vestia turgida* (Rossmässler, 1836) in den Pleistozänen Sedimenten Ungarns. *Soosiana* 18, 5–10.
- Krolopp, E., Sümegei, P., 1991. Dominance level of the species *Punctum pygmaeum* (Draparnaud, 1801) a biostratigraphical and palaeoecological key level for the Hungarian loess sediments of the Upper Würm. *Soosiana* 19, 17–23.
- Krolopp, E., Sümegei, P., 1995. Palaeoecological reconstruction of the Late Pleistocene, based on Loess Malacofauna in Hungary. *GeoJournal* 36 (2–3), 213–222.
- Krolopp, E., Sümegei, P., 2002. The mollusc fauna of the Ságvár loess profile. *Malakol. Tájékoztató* 20, 7–14.
- Krolopp, E., 1961. Upper Pleistocene Mollusc fauna from Tihany. *Földtani Intézet Évi Jelentése 1957–58-ról*, 505–509. (in Hungarian).
- Krüzselyi, L., Bartholy, J., Horányi, A., Pieczka, I., Pongrácz, R., Szabó, P., Szépszó, G., Torma, C., 2011. The future climate characteristics of the Carpathian Basin based on a regional climate model mini-ensemble. *Adv. Sci. Res.* 6, 69–73.
- Kutzbach, L.E., Guetter, P.J., Behling, P.J., Sehling, R., 1993. Simulated climatic changes: results of the COHMAP climate-model experiments. In: Wright Jr., H.E., Kutzbach, L.E., Webb, L.L., T., Ruddiman, W.F., Street-Perrott, F.A., Bartlein, P.J. (Eds.), *Global Climates Since the Last Glacial Maximum*. University of Minnesota Press, Minneapolis, pp. 136–169.
- Kutzbach, J.E., Guetter, P.J., 1986. The influence of changing orbital parameters and surface boundary conditions on climate simulations for the past 18 000 years. *J. Atmos. Sci.* 43 (16), 1726–1759.
- Larsen, J.A., 2013. *The Boreal Ecosystem*. Academic Press, New York, p. 518.
- Lehmkuhl, F., Böskén, J., Hošek, J., Sprafke, T., Marković, S.B., Obrecht, I., Hambach, U., Sümegei, P., Lindner, H., 2018. Loess distribution and related Quaternary sediments in the Carpathian Basin. *J. Maps* 14, 673–682.
- Lehmkuhl, F., Böskén, J., Pötter, S., Sprafke, T., Schulte, P., Jary, Z., Antoine, P., Wacha, L., Wolf, D., Zerboni, A., Hošek, J., Marković, S.B., Obrecht, I., Sümegei, P., Veres, D., Boemke, B., Schaubert, V., Viehweger, J., Hambach, U., 2020. Loess landscapes of Europe – mapping, geomorphology and zonal differentiation. *Earth Sci. Rev.* 211, 1–82.
- Ložek, V., 1964. Quartärmollusken der Tschechoslowakei. *Rozpr. Ústředního ústavu Geol.* 31, 1–374.
- Ložek, V., 1965. The relationship between the development of soils and faunas in the warm Quaternary phases. *Anthropozoikum* 3, 7–51.
- Ložek, V., 1990. Molluscs in loess, their paleoecological significance and role in geochronology - principles and methods. *Quat. Int.* 7, 71–79.
- Ložek, V., 2001. Molluscan fauna from the loess series of Bohemia and Moravia. *Quat. Int.* 76, 141–156.
- Mackay, A.W., Swann, G.E., Brewer, T.S., Leng, M.J., Morley, D.W., Piotrowska, N., Rioual, P., White, D., 2011. A reassessment of late glacial–Holocene diatom oxygen isotope record from Lake Baikal using a geochemical mass-balance approach. *J. Quat. Sci.* 26 (6), 627–634.
- Magny, M., Aalbersberg, G., Bégeot, C., Benoit-Ruffaldi, P., Bossuet, G., Disnar, J.R., Heiri, O., Lagoun-Defarge, F., Mazier, F., Millet, L., Peyron, O., Vanière, B., Walter-Simonnet, A.V., 2006. Environmental and climatic changes in the Jura mountains (eastern France) during the Lateglacial–Holocene transition: a multi-proxy record from Lake Lautrey. *Quat. Sci. Rev.* 25 (5–6), 414–445.
- Magyari, E.K., Chapman, J.C., Passmore, D.G., Allen, J.R.M., Huntley, J.P., és Huntley, B., 2010. Holocene persistence of wooded steppe in the Great Hungarian Plain. *J. Biogeogr.* 37, 915–935.
- Magyari, E.K., Major, Á., Bálint, M., Nédli, J., Braun, M., Rác, I., Parducci, L., 2011. Population dynamics and genetic changes of *Picea abies* in the South Carpathians revealed by pollen and ancient DNA analyses. *BMC Evol. Biol.* 11 (1), 1–16.
- Magyari, E.K., Chapman, J., Fairbairn, A.S., Francis, M., de Guzman, M., 2012. Neolithic human impact on the landscapes of North-East Hungary inferred from pollen and settlement records. *Veg. Hist. Archaeobot.* 21, 279–302.
- Magyari, E.K., Jakab, G., Bálint, M., Kern, Z., Buczkó, K., Braun, M., 2012. Rapid vegetation response to Lateglacial and early Holocene climatic fluctuation in the South Carpathian Mountains (Romania). *Quat. Sci. Rev.* 35, 116–130.
- Magyari, E.K., Kuneš, P., Jakab, G., Sümegei, P., Pelánková, B., Schäbitz, F., Braun, M., Chytrý, M., 2014. Late Pleniglacial vegetation in eastern-central Europe: are there modern analogues in Siberia? *Quat. Sci. Rev.* 95, 60–79.
- Marcuzzi, G., 1979. The Taiga. In: Marcuzzi, G. (Ed.), *European Ecosystems*. Biogeographica Series. Springer, Dordrecht, pp. 186–244.
- Meese, D.A., Gow, A.J., Alley, R.B., Zielinski, G.A., Grootes, P.M., Ram, M., Mayewski, P.A., Bolzan, J.F., 1997. The Greenland Ice Sheet Project 2 depth-age scale: methods and results. *J. Geophys. Res. Oceans* 102 (C12), 26411–26423.
- Meir, P., Cox, P., Grace, J., 2006. The influence of terrestrial ecosystems on climate. *Trends Ecol. Evol.* 21, 254–260.
- Moine, O., 2014. Weichselian Upper Pleniglacial environmental variability in north-western Europe reconstructed from terrestrial mollusc faunas and its relationship with the presence/absence of human settlements. *Quat. Int.* 337, 90–113.
- Moine, O., Rousseau, D.D., Antoine, P., 2005. Terrestrial mollusc records of Weichselian Lower to Middle Pleniglacial climatic changes from the Nussloch loess series (Rhine Valley, Germany): the impact of local factors. *Boreas* 34 (3), 363–380.
- Molnár, B., Geiger, J., 1995. Possibility for subdividing apparently homogeneous depositional sequences by combined use of sedimentological, palaeontological and mathematical methods. *GeoJournal* 36 (2–3), 169–177.



- Molnár, B., Krolopp, E., 1978. Latest Pleistocene geohistory of the Bácska loess area. *Acta Minerol. Petrogr.* 23, 245–264.
- Molnár, B., Iványosi-Szabó, A., Fényes, J., 1979. Die Entstehung des Kolon-Sees und seine limnogeologische Entwicklung. *Hidrol. Közleány* 59, 549–560.
- Molnár, Cs., Bölöni, J., Pál, R., Türke, J.I., Jakab, G., Kállayné, Szerényi, J., 2007. Plant geography and flora. In: Ilyés, E., Bölöni, J. (Eds.), *Loess Steppes, Slope Steppes and Forest Steppes in Hungary*. Private Edition, Budapest, pp. 170–177 (in Hungarian).
- Molnár, D., Hupuczki, J., Galović, L., Sümegei, P., 2010. Preliminary malacological investigation on the loess profile at Zmajevac, Croatia. *Cent. Eur. J. Geosci.* 2, 52–56.
- Molnár, D., Sümegei, P., Fekete, I., Makó, L., Sümegei, B.P., 2019. Radiocarbon dated malacological records of two Late Pleistocene loess-paleosol sequences from SW-Hungary: paleoecological inferences. *Quat. Int.* 504, 40–55.
- Molnár, D., Makó, L., Cseh, P., Sümegei, P., Fekete, I., Galović, L., 2021. Middle and Late Pleistocene loess-paleosol archives in East Croatia: multi-proxy paleoecological studies on Zmajevac and Šarengrad II sequences. *Stud. Quat.* 38/1, 3–17.
- Molnár, Zs., Biró, M., Bartha, S., Fekete, G., 2012. Past trends, present state and future prospects of Hungarian Forest Steppes. In: Werger, M.J.A., van Staalduinen, M. A. (Eds.), *Eurasian Steppes. Ecological Problems and Livelihoods in a Changing World*. Springer, Dordrecht, Heidelberg, New York, London, pp. 209–252.
- Molnár, B., 2015. *The Geology and Hydrogeology of Kiskunsági (Little Cumania) National Park*. JATEPress, Szeged, 524 p. (in Hungarian).
- Moore, P.D., Webb, J.A., Collinson, M.E., 1991. *Pollen Analysis*. Blackwell Scientific, Oxford.
- Moreno, A., Stoll, H., Jiménez-Sánchez, M., Cacho, I., Valero-Garcés, B., Ito, E., Edwards, R.L., 2010. A speleothem record of glacial (25–11.6 kyr BP) rapid climatic changes from northern Iberian Peninsula. *Glob. Planet. Chang.* 71 (3–4), 218–231.
- Moskal-del Hoyo, M., Lityńska-Zajac, M., Raczky, P., Anders, A., Magyari, E.K., 2018. The character of the Atlantic oak woods of the Great Hungarian Plain. *Quat. Int.* 463, 337–351.
- Munsell, A.H., 1954. A color notation. *Munsell Color Company Inc.*, 144 p.
- Náfrádi, K., Jakab, G., Sümegei, P., Szelepcsényi, Z., Tórcsik, T., 2013. Future climate impacts in woodland and forest steppe based on holocene paleoclimatic trends paleobotanical change in central part of the Carpathian Basin (Hungary). *Am. J. Plant Sci.* 4 (6), 1187–1203.
- Nekola, J.C., Coles, B.F., Horsak, M., 2015. Species assignment in *Pupilla* (Gastropoda: Pulmonata: Pupillidae): integration of DNA-sequence data and conchology. *J. Molluscan Stud.* 81 (2), 196–216.
- Nerudová, Z., Doláková, N., Novák, J., 2016. New information augmenting the picture of local environment at the LGM/LGT in the context of the Middle Danube region. *Holocene* 26 (9), 1345–1354.
- Novák, J., Abraham, V., Houfková, P., Kočár, P., Vaněček, Z., Peška, J., 2018. History of the Litovelské Pomoraví woodland (NE Czech Republic): a comparison of archaeo-anthracological, pedoanthracological, and pollen data. *Quat. Int.* 463, 352–362.
- Novenko, E.Y., Volkova, E.M., Nosova, N.B., Zuzanova, I.S., 2009. Late Glacial and Holocene landscape dynamics in the southern taiga zone of East European Plain according to pollen and macrofossil records from the Central Forest State Reserve (Valdai Hills, Russia). *Quat. Int.* 207, 93–103.
- Nyári, D., Knipl, I., Kiss, T., Sipos, G., 2012. Environmental changes in historical times near Kecel on the Danube-Tisza Interfluvium, Hungary. *Archaeological research and optically stimulated luminescence (OSL) dating*. *Archeometriai Műhely* 9 (1), 31–38.
- Nyári, D., Knipl, I., Sipos, Gy., Kiss, T., 2014. Environmental changes in historical times near Apostag on the Danube-Tisza interfluvium, Hungary (a complex research based on archaeological excavation and geomorphological investigations). *J. Environ. Geogr.* 7 (3–4), 39–47.
- Ødum, S., 1979. Actual and potential tree-line in the North Atlantic region, especially in Greenland and the Faroes. *Ecography* 2, 222–227.
- Økland, J., 1990. *Lakes and snails: environment and Gastropoda in 1,500 Norwegian lakes, ponds and rivers*. Universal Book Services, Øegstgeest.
- Packham, J.R., Harding, D.J., Hilton, G.M., Stuttard, R.A., 1992. *Functional Ecology of Woodlands and Forests*. Kluwer Academic Publisher, Dordrecht - Boston - London, p. 407.
- Pálfa, I., 2002. Drought zones of Hungary (in Hungarian). *Vízügyi Közlemények* 84, 323–357.
- Pálfa, I., 2010. The frequency of droughts in the Carpathian Basin in the last three hundred years. *"Klíma-21"* Füzetek 59, 42–45.
- Pató, Z.A., Standovář, T., Galka, M., Jakab, G., Molnár, M., Szomorad, F., Magyari, E., 2020. Exposure matters: forest dynamics reveal an early Holocene conifer refugium on a north facing slope in Central Europe. *Holocene* 30 (12), 1833–1848.
- Payette, S., 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), *A Systems Analysis of the Global Boreal Forest*. Cambridge University Press, Cambridge, pp. 144–169.
- Pécsi, M., 1990. Loess is not just the accumulation of dust. *Quat. Int.* 7–8, 1–21.
- Petechaty, A., Petechaty, M., Pułkacz, A., 2015. Winter temperature and shifts in phytoplankton assemblages in a small Chara-lake. *Aquat. Bot.* 124, 10–18.
- Petit, R.J., Aguinagalde, I., Beaulieu, J.L., Bittkau, C., Brewer, S., Cheddadi, R., Ennos, R., Fineschi, S., Grivet, D., Lascoux, M., Mohanty, A., Muller-Starck, G., Demesure-Musch, B., Palmé, A., Pedro Marti, J., Rendell, S., Vendramin, G.G., 2003. Glacial refugia: hotspots but not melting pots of genetic diversity. *Science* 300, 1563–1565.
- Peyron, O., Guiot, J., Cheddadi, R., Tarasov, P., Reille, M., de Beaulieu, J.L., Bottema, S., Andrieu, V., 1998. Climatic reconstruction in Europe for 18,000 yr BP from pollen data. *Quat. Res.* 49 (2), 183–196.
- Pigati, J.S., McGeehin, J.P., Muhs, D.R., Bettis III, E.A., 2013. Radiocarbon dating late Quaternary loess deposits using small terrestrial gastropod shells. *Quat. Sci. Rev.* 76, 114–128.
- Pigati, J.S., Quade, J., Shanahan, T.M., Haynes Jr., C.V., 2004. Radiocarbon dating of minute. *Quat. Res.* 61, 114–128.
- Pigati, J.S., Rech, J.A., Nekola, J.C., 2010. Radiocarbon dating of small terrestrial gastropod. *Quat. Res.* 74, 114–128.
- Podani, J., 1993. SYN-TAX 5.0: computer programs for multivariate data analysis in ecology and systematics. *Abstr. Bot.* 17, 289–302.
- Poortinga, W., Spence, A., Whitmarsh, L., Capstick, S., Pidgeon, N.F., 2011. Uncertain climate: an investigation into public scepticism about anthropogenic climate change. *Glob. Environ. Chang.* 21 (3), 1015–1024.
- Preece, R.C., Day, S.P., 1994. Special Paper: comparison of post-glacial molluscan and vegetational successions from a radiocarbon-dated tufa sequence in Oxfordshire. *J. Biogeogr.* 21, 463–478.
- Prentice, I.C., 1985. Pollen representation, source area, and basin size: toward an unified theory of pollen analysis. *Quat. Res.* 23, 76–86.
- Prentice, I.C., Webb III, T., 1998. BIOME 6000: reconstructing global mid-Holocene vegetation patterns from palaeoecological records. *J. Biogeogr.* 25, 997–1005.
- Prentice, I.C., Guiot, J., Huntley, B., Jolly, D., Cheddadi, R., 1996. Reconstructing biomes from palaeoecological data: a general method and its application to European pollen data at 0 and 6 ka. *Clim. Dyn.* 12, 185–194.
- Punt, W., Blackmore, S., Hoen, P.P., Stafford, P.J., 1976–1995. *The Northwest European Pollen Flora I–VII*. Elsevier, Amsterdam.
- Rapaics, R., 1918. Phytogeographical characterization of the Great Hungarian Plain. I–II. *Erdészeti Kísérletek*, 20(1–2):1–97, 20(3–4): 183–247 (in Hungarian).
- Rasmussen, S.O., Andersen, K.K., Svensson, A.M., Steffensen, J.P., Vinther, B.M., Clausen, H.B., Siggaard-Andersen, S.J., Larsen, L.B., Dahl-Jensen, D., Bigler, M., Röhrlisberger, R., Fischer, Hansson, M.E., Ruth, U., 2006. A new Greenland ice core chronology for the last glacial termination. *J. Geophys. Res. Atmos.* 111, D06102. <https://doi.org/10.1029/2005JD006079>.
- Rasmussen, S.O., Seierstad, I.K., Andersen, K.K., Bigler, M., Dahl-Jensen, D., Johnsen, S.J., 2008. Synchronization of the NGRIP, GRIP, and GISP2 ice cores across MIS 2 and palaeoclimatic implications. *Quat. Sci. Rev.* 27, 18–28.
- Rasmussen, S.O., Bigler, M., Blockley, S.P., Blunier, T., Buchardt, S.L., Clausen, H.B., Cvijanović, I., Dahl-Jensen, D., Johnsen, S.J., Fischer, H., Gkinis, V., Wim, M.G., Hoek, Z., Joel, J.L., Pedro, B., Inger, T.P., Seierstad, K., Steffensen, J.P., Svensson, M., Vallelonga, P., Vinther, B.M., Walker, J.C., Wheatley, J.J., Winstrup, M., 2014. A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. *Quat. Sci. Rev.* 106, 14–28.
- Reille, M., 1992. *Pollen et Spores d'Europe et d'Afrique du Nord*. Laboratoire Historique et Palynologie, Marseille.
- Reille, M., 1995. *Pollen et Spores d'Europe et d'Afrique du Nord*. Supplement 1. Laboratoire Historique et Palynologie, Marseille.
- Reille, M., 1998. *Pollen et Spores d'Europe et d'Afrique du Nord*. Supplement 2. Laboratoire Historique et Palynologie, Marseille.
- Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T. P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kromer, B., Manning, S.W., Muscheler, R., Palmer, J.G., Pearson, C., van der Plicht, J., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S.M., Fogtmann-Schultz, A., Friedrich, R.,

- Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookedo, A., Talamo, S., 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon* 62 (4), 725–757.
- Rodwell, J.S., Pignatti, S., Mucina, L., Schaminée, J.H.J., 1995. European Vegetation Survey: update on progress. *J. Veg. Sci.* 6, 759–762.
- Rousseau, D.D., 1986. Intérêt paléobiogéographique du *Pupilla loessica* Lozek et du *Vallonia tenuilabris* (A. Braun) pour le Pléistocène ouest-européen. *C. R. l'Acad. Sci.* 303, 257–262.
- Rousseau, D.D., 1987. New approach to the Pleistocene Land Snails. In: Pécsi, M., French, H.M. (Eds.), *Loess and Periglacial Phenomena*. Akadémiai Kiadó, Budapest, pp. 151–163.
- Rousseau, D.D., 1989. Réponses des malacofaunes terrestres quaternaires aux contraintes climatiques en Europe septentrionale. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 69, 113–124.
- Rousseau, D.D., 1990. Statistical analyses of loess molluscs for paleoecological reconstructions. *Quat. Int.* 7, 81–89.
- Rousseau, D.D., 1991. Climatic transfer function from Quaternary molluscs in European loess deposits. *Quat. Res.* 36, 195–209.
- Rousseau, D.D., 2001. Loess biostratigraphy: new advances and approaches in mollusk studies. *Earth Sci. Rev.* 54, 157–171.
- Rousseau, D.D., Keen, D.H., 1989. Malacological records from the Upper Pleistocene at Portelet (Jersey, Channel Islands): comparisons with western and central Europe. *Boreas* 18 (1), 61–66.
- Rousseau, D.D., Kukla, G., 1994. Late Pleistocene climate record in the Eustis loess section, Nebraska, based on land snail assemblages and magnetic susceptibility. *Quat. Res.* 42, 176–187.
- Rousseau, D.D., Puisségur, J.J., 1990. A 350,000-year climatic record from the loess sequence of Achenheim, Alsace, France. *Boreas* 19, 203–216.
- Rousseau, D.D., Puisségur, J.J., 1999. Climatic interpretation of terrestrial malacofaunas of the last interglacial in southeastern France. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 151, 321–336.
- Rousseau, D.D., Preece, R., Limondin-Lozouet, N., 1998. British late glacial and Holocene climatic history reconstructed from land snail assemblages. *Geology* 26 (7), 651–654.
- Rousseau, D.D., Antoine, P., Hatté, C., Lang, A., Zöller, L., Fontugne, M., Ottman, B.D., Luck, J.M., Moine, O., Labonne, M., Bentaleb, I., Jolly, D., 2002. Abrupt millennial climatic changes from Nussloch (Germany) Upper Weichselian eolian records during the Last Glaciation. *Quat. Sci. Rev.* 21, 1577–1582.
- Rousseau, D.D., Sima, A., Antoine, P., Hatté, C., Lang, A., Zöller, L., 2007. Link between European and North Atlantic abrupt climate changes over the last glaciation. *Geophys. Res. Lett.* 34 (L22713) <https://doi.org/10.1029/2007GL031716>.
- Rudner, E., Sümeği, P., 2001. Recurring taiga forest steppe habitats in the Carpathian Basin in the Upper Weichselian. *Quat. Int.* 76/77, 177–189.
- Rybníčeková, E., Rybníček, K., 2014. Palaeovegetation in the Pavlovské vrchy hills region (South Moravia, Czech Republic) around 25,000 BP: the Bulhary core. *Veg. Hist. Archaeobot.* 23 (6), 719–728.
- Soepboer, W., Sugita, S., Lotter, A.F., van Leeuwen, J.F.N., van der Knaap, W.O., 2007. Pollen productivity estimates for quantitative reconstruction of vegetation cover on the Swiss Plateau. *Holocene* 17, 65–77.
- Soó, R., 1929. Die vegetation und die Entstehung der ungarischen Puszta. *J. Ecol.* 17, 329–350.
- Soós, L., 1943. Mollusc fauna of the Carpathian Basin. *Akadémiai Kiadó, Budapest*.
- Stevens, G.C., Fox, J.F., 1991. The causes of treeline. *Annu. Rev. Ecol. Syst.* 22, 177–191.
- Stieber, J., 1967. Hungarian Upper Pleistocene vegetation history in the light of anthracological results until 1957. *Földtani Közlöny* 97, 308–317.
- Stieber, J., 1967. Charcoal analyses of the loess profile at Madaras. *Archaeol. Értesítő* 94, 192–192.
- Stieber, J., 1956. Anthrakotomische Untersuchung. In: Vértes, L. (Hsg.), *Ausgrabungen in der Petényi- und Peskó-Höhle (Bükk -Gebirge)*. Folia Archaeologica, 8, 13–14.
- Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. *Pollen Spores* 13, 614–621.
- Strandberg, G., Brandefelt, J., Kjellström, M., E., Smith, B., 2011. High-resolution regional simulation of last glacial maximum climate in Europe. *Tellus A Dyn. Meteorol. Oceanogr.* 63 (1), 107–125.
- Suggate, R.P., Almond, P.C., 2005. The last glacial maximum (LGM) in western South Island, New Zealand: implications for the global LGM and MIS 2. *Quat. Sci. Rev.* 24, 1923–1940.
- Sugita, S., 1994. Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *J. Ecol.* 82, 881–897.
- Sümeği, P., 1988. Quartermalacological investigation of Lakitelek brickworks profile. *Malakol. Newsl.* 8, 5–7.
- Sümeği, P., 1996. Comparative Paleoeological and Startigraphical Valuation of the NE Hungarian Loess Areas (Ph.D. Thesis), Budapest-Debrecen (Hungary), 120 p. (in Hungarian with English summary).
- Sümeği, P., 1999. Snails and mussels in the archaeological researches. I-II. *Termész. Világa* 130 (454–457), 513–515.
- Sümeği, P., 2001. Little Cuman region in the Medieval Age – through the eyes of a geologist. In: Horváth, F. (Ed.), *The Leader and His People of the Cuman*. Archaeolingua Kiadó, Budapest, pp. 313–317 (in Hungarian).
- Sümeği, P., 2013. Pre-Neolithization: reconstructing the environmental background to life way changes in the late mesolithic of the Carpathian Basin. In: Baldia, M.O., Perittula, T.K., Frink, D.S. (Eds.), *Comparative Archaeology and Paleoclimatology. Socio-cultural Responses to a Changing World*. Archaeopress (British Archaeological Reports), Oxford, pp. 109–117.
- Sümeği, P., 2019. Refuting ideas based on a small batch of data: malacothermometry aid in the reconstruction of mean July paleo-temperatures in the Carpathian Basin for the last glacial of the Pleistocene. *Archeometriai Műhely* XVI/3, 143–166.
- Sümeği, P., Hertelendi, E., 1998. Reconstruction of microenvironmental changes in Kopasz Hill loess area at Tokaj (Hungary) between 15.000-70.000 BP years. *Radiocarbon* 40, 855–863.
- Sümeği, P., Krolopp, E., 1995. Late Quaternary Paleoeology and Historical Geography of Hungary based on quartermalacological and radiocarbon analyses. In: *Proceedings of the 12th International Malacological Congress, Vigo*, pp. 330–331.
- Sümeği, P., Krolopp, E., 2002. Quartermalacological analyses for modeling of the Upper Weichselian palaeoenvironmental changes in the Carpathian Basin. *Quat. Int.* 91, 53–63.
- Sümeği, P., Rudner, E., 2001. In situ charcoal fragments as remains of natural wild fires of the Upper Würm in the Carpathian Basin. *Quat. Int.* 76/77, 165–176.
- Sümeği, P., Szilágyi, G., 2011. A quarter-malacological inventory of Hungarian kurgans. In: Petó, A., Barczai, A. (Eds.), *Kurgan Studies: An Environmental and Archaeological Multiproxy Study of Burial Mounds in the Eurasian Steppe Zone*. British Archaeological Reports, Oxford, pp. 279–291.
- Sümeği, P., Gulyás, S., Stevens, T., Molnár, M., in press. Inconsistency between high-resolution 14C and preliminary luminescence-based chronologies of the MIS 2 Madaras loess/paleosol sequence, Hungary: implications for other chronological studies. *Quaternary Geochronology*.
- Sümeği, P., Kertész, R., Rudner, Z.E., 2004. Paleoenvironmental history of Hungary. In: Visy, Zs. (Ed.), *Hungarian Archeology at the Millennium. Nemzeti Kulturális Örökség Minisztériumának Kiadványa, Budapest*, pp. 51–56.
- Sümeği, P., Szóór, Gy., Hertelendi, E., 1991. Palaeoenvironmental reconstruction of the last period of the Upper Würm in Hungary, based on malacological and radiocarbon data. *Soosiana* 19, 5–12.
- Sümeği, P., Kertész, R., Hertelendi, E., 2002. Environmental Change and Human Adaptation in the Carpathian Basin at the lateglacial/postglacial transition. *Br. Archaeol. Rep.* 1043, 171–177.
- Sümeği, P., Molnár, M., Jakab, G., Persaits, G., Majkut, P., Páll, D.G., Gulyás, S., Jull, A.J.T., Töröcsik, T., 2011. Radiocarbon-dated paleoenvironmental changes on a lake and peat sediment sequence from the central part of the Great Hungarian Plains (Central Europe) during the last 25.000 years. *Radiocarbon* 52, 85–97.
- Sümeği, P., Persaits, G., Gulyás, S., 2012. Woodland-grassland ecotonal shifts in environmental mosaics: lessons learnt from the environmental history of the Carpathian Basin (Central Europe) during the holocene and the last ice age based on investigation of paleobotanical and mollusk remains. In: Myster, R.W. (Ed.), *Ecotones Between Forest and Grassland*. Springer Press, New York, pp. 17–57.
- Sümeği, P., Gulyás, S., Csókmei, B., Molnár, D., Hambach, U., Stevens, T., Markovic, S., Almond, P.C., 2012. Climatic fluctuations inferred for the Middle and Late Pleniglacial (MIS 2) based on high-resolution (~ ca. 20 y) preliminary environmental magnetic investigation of the loess section of the Madaras brickyard (Hungary). *Cent. Eur. Geol.* 55 (3), 329–345.

- Sümegei, P., Magyari, E., Dániel, P., Molnár, M., Töröcsik, T., 2013. 28,000, year record of environmental change in SE Hungary: terrestrial response to Dansgaard-Oeschger cycles and Heinrich-events. *Quat. Int.* 278, 34–50.
- Sümegei, P., Gulyás, S., Kertész, R., Timár, G., 2013. Mesolithic-neolithic transition in the Carpathian Basin: was there an Ecological Trap during the Neolithic? In: Baldia, M.O., Pertulla, T.K., Frink, D.S. (Eds.), *Comparative Archaeology and Paleoclimatology. Socio-cultural Responses to a Changing World*. Archeopress, BAR International Series, Oxford, pp. 119–126.
- Sümegei, P., Náfrádi, K., Molnár, D., Sávia, Sz, 2015. Results of paleoecological studies in the loess region of Szeged-Óthalom (SE Hungary). *Quat. Int.* 372, 66–78.
- Sümegei, P., Markovic, S.B., Molnár, D., Sávai, Sz, Szelepcsényi, Z., Novák, Zs, 2016. Crvenka loess-paleosol sequence revisited: local and regional Quaternary biogeographical inferences of the southern Carpathian Basin. In: *Open Geosci.*, 8, pp. 309–404.
- Sümegei, P., Gulyás, S., Molnár, D., Sümegei, B.P., Almond, P.C., Vandenbergh, J., Liping, Zhou, Pál-Molnár, E., Töröcsik, T., Hao, Q., Smalley, I., Molnár, M., Marsi, I., 2018. New chronology of the best developed loess/paleosol sequence of Hungary capturing the past 1.1 ma: implications for correlation and proposed pan-European stratigraphic schemes. *Quat. Sci. Rev.* 191, 144–166.
- Sümegei, P., Molnár, D., Gulyás, S., Náfrádi, K., Sümegei, B.P., Töröcsik, T., Persaits, G., Molnár, M., Vandenbergh, J., Liping, Zhou, 2019. High-resolution proxy record of the environmental response to climatic variations during transition MIS3/MIS2 and MIS2 in Central Europe: the loess-paleosol sequence of Katymár brickyard (Hungary). *Quat. Int.* 504, 40–55.
- Sümegei, P., Gulyás, S., Molnár, D., Szilágyi, G., Sümegei, B.P., Töröcsik, T., Molnár, M., 2020. 14C dated chronology of the thickest and best resolved loess/paleosol record of the LGM from SE Hungary based on comparing precision and accuracy of age, depth models. *Radiocarbon* 69, 403–417.
- Sümegei, P., 1989. Upper Pleistocene Evaluation of Hajdúság Region Based on Fine, Stratigraphical (Sedimentological, Paleontological, Geochemical) Analyses. Dr. Univ. Thesis, Debrecen (Hungary), 96 p. (in Hungarian).
- Sümegei, P., 2003. Quartermalacological examinations. In: Bognár, A., Schweitzer, F., Szóór, Gy. (Eds.), *Susak. Environmental Reconstruction of a Loess Island in the Adriatic*. MTA Földrajzkutató Kiadványa, Budapest, pp. 110–117.
- Sümegei, P., 2005. Loess and Upper Paleolithic Environment in Hungary. Aurea Press, Nagykovácsi, 312.
- Sun, J., Liu, T., 2000. Stratigraphic evidence for the uplift of the Tibetan Plateau between ~ 1.1 and ~ 0.9 myr ago. *Quat. Res.* 54 (3), 309–320.
- Svensson, A., Andersen, K.K., Bigler, M., Clausen, H.B., Dahl-Jensen, D., Davies, S.M., Sigfus, J.J., Muscheler, R., Rasussen, S.O., Rhöthlisberger, R., Steffensen, J.P., Vinther, B.M., 2006. The Greenland ice core chronology 2005, 15–42ka. Part 2: comparison to other records. *Quat. Sci. Rev.* 25, 3258–3267.
- Szelepcsényi, Z., Breuer, H., Sümegei, P., 2014. The climate of Carpathian Region in the 20th century based on the original and modified Holdridge life zone system. *Cent. Eur. J. Geosci.* 6, 293–307.
- Szelepcsényi, Z., Breuer, H., Kis, A., Pongrácz, R., Sümegei, P., 2018. Assessment of projected climate change in the Carpathian Region using the Holdridge life zone system. *Theor. Appl. Climatol.* 31, 1–18.
- Szóór, Gy, Sümegei, P., Balázs, É., 1991. Sedimentological and geochemical facies analysis Upper Pleistocene fossil soil zones discovered in the Hajdúság region, NE Hungary. In: Pécsi, M., Schweitzer, F. (Eds.), *Quaternary Environment in Hungary. Studies in Geography in Hungary 26*. Akadémiai Kiadó, Budapest, pp. 47–59.
- Szujkó-Lacza, J., 1993. The Flora of the Kiskunság National Park. *Magyar Természet-tudományi Múzeum kiadványa*, Budapest, p. 467.
- Tarasov, P.E., Webb III, T., Andreev, A.A., Afanas'eva, N.B., Berezina, N.A., Bezusko, L.G., Blyakharchuk, T.A., Bolikhovskaya, N.S., Cheddadi, R., Chernovskaya, M. M., Chernova, G.M., Dorofeyuk, N.I., Dirksen, V.G., Elina, G.A., Filimonova, L.V., Glebov, F.Z., Guiot, J., Gunova, V.S., Harrison, S.P., Jolly, D., Khamutova, V.I., Kvavadze, E.V., Osipova, I.M., Panova, N.K., Saarse, L., Sevastyanov, D.V., Volkova, V.S., Zernitskaya, V.P., 1998. Present-day and mid-Holocene biomes reconstructed from pollen and plant macrofossil data from the former Soviet Union and Mongolia. *J. Biogeogr.* 25, 1029–1053.
- Tarasov, P.E., Volkova, V.S., Webb III, T., Guiot, J., Andreev, A.A., Bezusko, L.G., Bezusko, T.V., Bykova, G.V., Dorofeyuk, N.I., Kvavadze, E.V., Osipova, I.M., Panova, N.K., Sevastyanov, D.V., 2000. Last glacial maximum biomes reconstructed from pollen and plant macrofossil data from northern Eurasia. *J. Biogeogr.* 27 (2000), 609–620.
- Tölgyesi, L., 1981. The flora of the Kolon lake and its environs at Izsák (Hungary). *Doktori értekezés*, Budapest, 95 p. (in Hungarian).
- Töröcsik, T., Sümegei, B.P., Sümegei, P., 2018. The environmental history of the Selyemrét from the postLGM at Ócsa. *Rosalia* 10, 81–118.
- Tóth, E.G., Bagnoli, F., Vendramin, G.G., György, Z., Spanu, I., Höhn, M., 2021. Imprints of selection in peripheral and ecologically marginal central-eastern European Scots pine populations. *Gene*, 145509.
- Tóth, K., 1979. National Park in the Little Cumania. *Natura Press*, Budapest, p. 519.
- Tóth, M., Magyari, E.K., Brooks, S.J., Braun, M., Buczkó, K., Bálint, M., Heiri, O., 2012. A chironomid-based reconstruction of late glacial summer temperatures in the southern Carpathians (Romania). *Quat. Res.* 77 (1), 122–131.
- Troels-Smith, J., 1955. Characterization of unconsolidated sediments (in Danish). *Dan. Geol. Under.* 4 (3), 10.
- Tugya, B., Náfrádi, K., Töröcsik, T., Sümegei, B.P., Gulyás, S., Pomázi, P., Sümegei, P., 2020. Environmental historical analysis of the Sarmatian and Gepids settlement of Rákóczi-falva. *Acta Archaeol. Acad. Sci. Hung.* 71, 101–156.
- Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11 (12), 1351–1363.
- Újvári, G., Molnár, M., Novothny, A., Páll-Gergely, B., Kovács, J., Várhegyi, A., 2014. AMS 14C and OSL/IRSL dating of the Dunaszekcső loess sequence (Hungary): chronology for 20 to 150 ka and implications for establishing reliable age-depth models for the last 40 ka. In: *Quat. Sci. Rev.*, 106, pp. 140–154.
- Vadaj, A., 2004. Chronological charts. In: *Visy, Zs. (Ed.), Hungarian Archeology at the Millennium. Nemzeti Kulturális Örökség Minisztériumának Kiadványa*, Budapest, pp. 483–488.
- Varga, Z., 1989. Die Waldsteppen des pannonischen Raumes aus biogeographischer Sicht. *Düsseldorfer Geobot. Kolloquien* 6, 35–50.
- Varga, Z., 1981. The Recent and Historical Dynamic Changes of the Distribution Areas – The Zoogeographical Analyses of the Palearctic Lepidoptera-fauna (Thesis for DSc Degree), Debrecen, 1–23.
- Varga, Z., Borhidi, A., Fekete, G., Debreczy, Z., Bartha, D., Bölöni, J., Molnár, A., Kun, A., Molnár, Z., Lendvai, G., Szodfrid, I., Rédei, T., Facsar, G., Sümegei, P., Kósa, G., Király, G., 2000. The concept, types and their characterization of the forest steppe relicts. In: Molnár, Zs., Kun, A. (Eds.), *Lowland Forest Steppe Relicts in Hungary*. World Wide Foundation, Budapest, pp. 7–19 (in Hungarian).
- Verpoorte, A., Troelstra, S., Beets, K., Sümegei, P., 2013. Stable isotopes of Upper Weichselian land snails from Lakitelek (Hungary): a contribution to understanding the climatic context of the Upper Palaeolithic of the Hungarian basin. *Analecta Praehist. Leiden.* 43/44, 335–345.
- Viereck, L.A., 1973. Wildfire in the taiga of Alaska. *Quat. Res.* 3, 465–495.
- Voelker, A.H., 2002. Global distribution of centennial-scale records for Marine Isotope Stage (MIS3): a database. *Quat. Sci. Rev.* 21, 1185–1212.
- Voelker, A.H.L., Sarnthein, M., Grootes, P.M., Erlenkreuser, H., Laj, C., Mazaud, M., Nadeau, M.J., Slicher, M., 1998. Correlation of marine 14C ages from the Nordic seas with the GISP2 isotope record: implications for 14C calibration beyond 25 ka BP. *Radiocarbon* 40, 517–534.
- Walter, H., Lieth, H., 1967. *Climate Diagram World Atlas*. VEB Gustav Fischer Verlag, Jena, p. 37.
- Wartenberg, D., Ferson, S., Rohlf, F.J., 1987. Putting things in order: a critique of detrended correspondence analysis. *Am. Nat.* 129 (3), 434–448.
- Webb III, T., 1974. Corresponding patterns of pollen and vegetation in Lower Michigan: a comparison of quantitative data. *Ecology* 55 (1), 17–28.
- Weinelt, M., Vogelsang, E., Kucera, M., Pflaumann, U., Sarnthein, M., Voelker, A., Erlenkreuser, H.J., Malmgren, B.A., 2003. Variability of North Atlantic heat transfer during MIS 2. *Paleoceanography* 18. <https://doi.org/10.1029/2002PA000772>.
- Welter-Schultes, F., 2012. *European non-marine mollusc, a guide for species identification*. Planet Poster Edition, Göttingen.
- Whitlock, C., Miltspäugh, S.H., 1996. Testing the assumptions of fire-history studies: an examination of modern charcoal accumulation in Yellowstone National Park, USA. *Holocene* 6, 7–15.
- Willis, K.J., 1994. The vegetational history of the Balkans. *Quat. Sci. Rev.* 13 (8), 769–788.
- Willis, K.J., Van Andel, T.H., 2004. Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. *Quat. Sci. Rev.* 23 (23–24), 2369–2387.
- Willis, K.J., Whittaker, R.J., 2000. The refugial debate. *Science* 287 (5457), 1406–1407.
- Willis, K.J., Sümegei, P., Braun, M., Tóth, A., 1995. The Late Quaternary environmental history of Bátorliget, N.E. Hungary. *Paleoecogr. Palaeoclimatol. Palaeoecol.* 118, 2–47.

- Willis, K.J., Braun, M., Sümeği, P., Tóth, A., 1997. Does soil change cause vegetation change or vice, versa? A temporal perspective from Hungary. *Ecology* 78, 740–750.
- Willis, K.J., Rudner, E., Sümeği, P., 2000. The full-glacial forests of central and southeastern Europe: evidence from Hungarian palaeoecological records. *Quat. Res.* 53, 203–213.
- Wohlfarth, B., Veres, D., Ampel, L., Lacourse, T., Blaauw, M., Preusser, F., Andrieu-Ponel, V., Kéravis, D., Lallier-Vergès, E., Björck, S., Davies, S.M., de Beaulieu, J.-L., Risberg, J., Hormes, A., Kasper, H.U., Possnert, G., Reille, M., Thouveny, N., Zander, A., 2008. Rapid ecosystem response to abrupt climate changes during the last glacial period in western Europe, 40–16 kyr. *Geology* 36 (5), 407–410.
- Xu, B., Gu, Z., Han, J., Hao, Q., Lu, Y., Wang, L., Wu, N., Peng, Y., 2011. Radiocarbon age anomalies of land snail shells in the Chinese Loess Plateau. *Quat. Geochronol.* 6, 383–389.
- Zar, J.H., 1984. *Biostatistical Analysis*, second ed. Prentice Hall, USA.
- Zhou, J., Tung, K.K., 2013. Deducing multidecadal anthropogenic global warming trends using multiple regression analysis. *J. Atmos. Sci.* 70 (1), 3–8.
- Zhu, R., Liu, Q., Jackson, M.J., 2004. Paleoenvironmental significance of the magnetic fabrics in Chinese loess-paleosols since the last interglacial (< 130 ka). *Earth Planet. Sci. Lett.* 221, 55–69.
- Zólyomi, B., 1957. Der Tatarenahorn-Eichen-Lösswald der zonalen Waldsteppe. *Acta Bot. Hung.* 3, 401–424.
- Zólyomi, B., 1987. Coenotone, ecotone and their role in preserving relic species. *Acta Bot. Hung.* 33, 3–18.
- Zólyomi, B., Fekete, G., 1994. The Pannonian loess steppe: differentiation in space and time. *Abstr. Bot.* 18, 29–41.