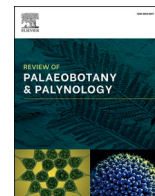




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Holocene vegetation dynamics in southern Ukraine under changing land use and climate

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ABSTRACT

The Holocene vegetation dynamics of the Eurasian steppe are underinvestigated despite its vast extension, chiefly because of the scarcity of suitable sites for palaeoecological research. Here, we present a palaeoecological reinvestigation from Kardashynskiy mire (southern Ukraine), approximately 4 km from a previously cored site. Using pollen, spores and microscopic charcoal, we have reconstructed vegetation dynamics, fire history and land use for the past c. 8300 years. Regionally, steppe vegetation with Poaceae, Chenopodiaceae and *Artemisia* was always dominant. However, pollen assemblages also reflect the presence of floodplain and upland tree stands. At the beginning of the sequence, c. 8300 years ago, *Pinus* stands were growing on the sandy terraces of the Dniipro dry upland sites. Later, at c. 7950 cal yr BP, diverse stands with *Quercus*, *Ulmus*, *Fraxinus*, *Tilia* and *Alnus* established along the riverbanks, where moisture availability was sufficient. Around 6100 cal yr BP, those deciduous broadleaved stands experienced a severe decline, likely in response to changing water table levels. Cultural indicators suggest land use activities after c. 7900 cal yr BP. During the Bronze Age, human impact intensified. Overall, both climate and humans drove vegetation dynamics in the Pontic steppe for millennia. Nowadays, this once extensive biome has almost completely been converted to cropland. Similarly, the wetland vegetation, the riparian forests and, above all, the pine forests growing on the sandy terraces were strongly reduced by millennial-long land use. Under the current conditions, even the last remnants of these special vegetation types are severely threatened.

1. Introduction

Farming, one of the most game-changing innovations in human history, was introduced to mainland Europe more than 8500 years ago (e.g. Lemmen et al., 2011). The onset of production economy laid the foundations for modern societies and had a big impact on the environment and biosphere, for instance through the introduction, propagation, reduction or extirpation of species as well as through increased erosion, fire, and eutrophication (Roberts et al., 2019; Gassner et al., 2020). Agricultural and pastoral farming spread from the Near East into Europe mostly over the Aegean Islands and following the Greek-Balkan routes (e.g. Pashkevich, 2003; Kozłowski, 2005; Lemmen et al., 2011; Hofmanová et al., 2016). In addition to these well-established routes, an

early spread of domesticates into the steppe of Ukraine has been proposed (Kotova, 2003, 2008; Motuzaitė-Matuzevičiute et al., 2009; Motuzaitė-Matuzevičiute and Telizhenko, 2016 and references therein). Specifically, the earliest evidence of Neolithization and early agriculture in southern Ukraine, based on the presence of pottery and imprints of grains on ceramics, could be attributed to the late 7th millennium–early 6th millennium BCE (Kotova and Pashkevich, 2003; Kotova et al., 2021). However, the earliest radiocarbon-dated cereals (*Triticum dicoccum*) in Ukraine were dated to 7420–7180 cal yr BP (5470–5230 BCE) and found in the Linear Pottery Culture (LBK) site Ratniv-2 in western Ukraine (Motuzaitė-Matuzevičiute and Telizhenko, 2016; Endo et al., 2022). The most recent investigation of plant impressions on ancient potsherds using an improved methodology also concludes that the earliest reliable

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evidence of arable farming is found in western and south-western Ukraine and dates to the LBK, i.e. to the second half of the 6th millennium BCE (Motuzaitė-Matuzevičiūtė and Telizhenko, 2016; Salavert et al., 2021; Endo et al., 2022). Trypillia groups (c. 6950–4750 cal yr BP/5000–2800 BCE), inhabiting the forest-steppe mostly west of the Dnipro (Albert et al., 2020), extended agricultural activities to many regions of central and northern Ukraine. In the north-western Black Sea region the Bolgrad-Aldeni culture (a local aspect of the Gumelnița cultural block), dating to the middle of the 5th millennium BCE, were probably the first people to practice arable farming in the steppe (Govedarica and Manzura, 2020). In striking contrast, further east, at the Maiaky site in the Dniester estuary, first evidence of arable farming was only dated to around the second half of the 4th millennium BCE (Endo et al., 2022), though the chronology of the site is somewhat unclear (Nikitin et al., n.d.). Palaeoecological data can significantly contribute to filling the chronological and spatial gaps by providing continuous multi-millennial records of cultural indicator plants and changes in fire occurrence related to farming activities (Lang, 1994; Deza-Araujo et al., 2020; Lang et al., 2023).

To date, little is known about the Holocene vegetation dynamics of the Eurasian steppe in response to climate change and human impact, making it one of Europe's most underinvestigated vegetation types in that regard (Kremenetski, 1995, 2003; Kremenetski et al., 1999; Bezusko, 2010; Matishov et al., 2013; Gobet et al., 2017; Gershkovych and Gerasymenko, 2021). The scarcity of suitable sites for palaeoecological research in the steppe is probably the main underlying reason, since natural lakes are virtually absent and other potential sites such as mires, estuaries, oxbow lakes, lagoons and archaeological sites pose their own challenges in terms of preservation and interpretability of fossil remains. Particularly, and in contrast to the neighbouring northern and western forest-steppe ecotone (see e.g. Shumilovskikh et al., 2018; Feurdean et al., 2021; Lukanina et al., 2022, 2023), high-resolution studies that allow deciphering the mechanisms driving long-term vegetation dynamics are completely lacking for the steppe and the adjacent azonal riparian forests. Further, the usually poorly constrained chronologies of existing records so far largely prevented assigning vegetation shifts to specific climatic events or to archaeological findings as a proxy for past societal dynamics.

One of the few available palaeoecological studies from the Pontic steppe region covering several millennia was published almost thirty years ago (Kremenetski, 1995), and presented an overview of the vegetation history around Kardashynskiy mire in southern Ukraine for the past c. 9000 years. According to the author, the vegetation around Kardashynskiy was a steppic environment with varying abundances of Poaceae, *Artemisia* and Chenopodiaceae. The relatively high and fluctuating pollen percentages of pine (*Pinus*) until c. 1200 years ago were interpreted as local stands growing together with birch (*Betula*) on the sandy terraces of the Dnipro, under rather dry upland conditions (henceforth called 'sandy terraces'). Besides pines and birches, the record shows that several broadleaved trees (*Ulmus*, *Quercus*, *Fraxinus*, *Carpinus betulus* and *Tilia*) grew on the Dnipro floodplain, reaching their maximum spread between 6750 and 4750 cal yr BP (4800–2800 BCE; Kremenetski, 2003). Finally, cultural indicator pollen is scarce and first Cerealia type pollen only appear about 2500 years ago (Kremenetski, 1995), suggesting that arable farming spread only late, during the Iron Age, to the study area.

Here, we present a new palaeoecological record from Kardashynskiy mire, one of the few available natural archives in the region, aimed at closing the existing gap in investigating the drivers of vegetation change in southern Ukraine. Our record, which is located approximately 4 km away from the previous Kardashynskiy record by Kremenetski (1995), provides the following major novelties: (i) more precise and accurate chronology based on 15 radiocarbon dates on terrestrial plant macrofossils, (ii) notably higher temporal resolution, including two high-resolution sections with contiguous 1-cm sampling; and (iii) analysis of proxies for fire occurrence (microscopic charcoal) and grazing (dung

fungal spores), which allow assessing the drivers of vegetation change more comprehensively. In addition to a general overview of vegetation changes over the past c. 8300 years, we specifically address the following research questions: (1) When did the first signs of human land use occur? (2) When did human land use intensify? (3) Can we disentangle climatic, anthropogenic and other forcing (e.g. disturbance, biotic interactions)? Or, in other words, what were the main drivers of Middle and Late Holocene vegetation change in southern Ukraine?

2. Study site

Kardashynskiy mire (46°32'35.1" N, 32°39'6.0", 4 m a.s.l.) lies in southern Ukraine (Kherson Oblast), close to the Black Sea coast (Fig. 1). It is part of the extensive wetland surrounding the estuary of the river Dnipro and looks back on a long history of previous palaeoecological research (Lawrenko and Iswekova, 1932; Artyushenko and Baczurina, 1958; Kremenetski, 1995; Bezusko and Bezusko, 2000). Kremenetski (1995) argued that the mire originated from the infilling of a huge oxbow lake. Soils are peaty at the coring site and mainly chernozems outside the wetland (Wesche et al., 2016). The climate is Dfa (continental with hot summers) according to the Köppen-Geiger Classification, thus without significant changes in precipitation across seasons. The mean annual temperature today (2012–2019 CE) measured at the Kherson weather station is 11.8 °C. The highest mean monthly temperature occurs in August (24.5 °C) and the lowest in January (−1.2 °C). The mean annual precipitation is about 408 mm (Lykhovyd, 2021).

The local vegetation in the wetland is dominated by *Phragmites australis*, *Typha angustifolia* and *Schoenoplectus lacustris*, with interspersed *Salix alba* and *Elaeagnus angustifolia* (own observation). Wetland and riparian vegetation occurs in a radius of approximately 5 km around the coring site. In the vicinity of the mire, salt marshes and saline meadows can be found (Kremenetski, 1995). The natural vegetation around Kardashynskiy mire (i.e. at distances approximately > 5 km from the coring spot) would consist of grass steppe or herb-grass steppe (Bohn et al., 2003). However, apart from a few protected areas the European steppe has nowadays been almost completely destroyed and converted to cropland (Charles, 2010; Wesche et al., 2016).

3. Material and methods

3.1. Coring, lithology and chronology

We took two parallel sediment cores with a modified Streif–Livingstone piston–corer (5 cm diameter) in 2017. In the laboratory, the two cores were correlated according to their lithostratigraphy to compose a 374-cm long master sequence. The lithology was described according to Troels-Smith (1955). We use peat and gyttja formation as proxies for low vs high water table stands, which is particularly important to assess if the increase of macrophytes was connected to diminishing or augmenting water levels (see Results). To find suitable short-lived terrestrial plant macrofossils for radiocarbon dating, we sieved 80 sediment subsamples (thickness: 2 cm; volume: 4–11 cm³) through a 200 μm mesh. We then identified plant remains under a stereomicroscope at 8–100× magnification, using published atlases (e.g. Cappiers et al., 2006; Bojnanský and Fargašová, 2007) as well as the reference collection at the University of Bern. Fifteen macrofossil samples were radiocarbon-dated using accelerator mass spectrometry (AMS) at the laboratory for the analysis of radiocarbon using AMS (LARA) of the University of Bern (Table 1). We calibrated the radiocarbon dates to years before present (cal yr BP) with the IntCal20 calibration curve (Reimer et al., 2020), and modelled the age–depth relationship with the Bayesian approach implemented in the package 'rbacon' (version 2.5.7; Blaauw and Christen, 2011), which runs in R version 4.2.2 (R Core Team, 2022). The following settings were used: 'thick' = 3, 'mem.mean' = 0.3, otherwise default settings. Additionally, we calculated an extended 95% confidence envelope using mixed-effect modelling according to Heegaard et al. (2005), which takes



Fig. 1. Location of the Kardashynskiy mire in southern Ukraine. Overview map showing the location of the study area in Eastern Europe (left). Satellite picture of the Dnipro estuary (Google Earth Pro [7.3.4.8248]), where Kardashynskiy mire and the coring site (red circle) are located (right). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

into account both the age and depth (of sample) uncertainties.

3.2. Palynology and microscopic charcoal analysis

We took 90 samples of 1 cm³ for pollen and microscopic charcoal analysis at sampling intervals ranging from contiguous to 8 cm. The two high-resolution sections consisted of 23 (175–197 cm) and 26 (128–153 cm) contiguous samples, respectively. We delimited the two high-resolution sections to investigate in detail two periods of particularly high environmental and vegetational variability, specifically to assess the causes and consequences of water plant and upland vegetation dynamics (see Results). *Lycopodium* tablets were added prior to sample treatment to estimate pollen concentration (grains cm⁻³) and influx (grains cm⁻² year⁻¹; Stockmarr, 1971). Sediment subsamples were treated chemically (KOH, HCl, HF and acetolysis) and physically (0.5 mm sieving and decanting) following standard procedures (Moore et al., 1991). Pollen, spores and other non-pollen palynomorphs were counted under a light microscope with 400× magnification, using published identification keys and photographic atlases (e.g. Moore et al., 1991; Reille, 1999; Jankovská and Komárek, 2000; van Geel et al., 2003; Beug, 2004) as well as the reference collection of the University of Bern. Pollen type taxonomy follows Moore et al. (1991). In the case of

Chenopodiaceae, we kept the original pollen taxonomic definition according to the keys we used, instead of adopting the new family concept of Amaranthaceae, which includes far more genera, and thus possibly other pollen types. Well preserved Cerealia t. (t. = type) pollen grains were further distinguished into *Avena* t., *Hordeum* t. and *Triticum* t. after Beug (2004), using phase contrast and 1000× magnification. A minimum of 500 terrestrial pollen grains per sample were counted. Pollen tetrads and clumps of pollen of the same taxon (mainly found for Brassicaceae) were counted as one. The pollen, spores and other non-pollen palynomorph curves in the diagrams are based on percentages calculated with respect to the terrestrial pollen sum, which includes trees, shrubs, and herbs. To visualise the data we used the software ‘Tilia’ version 3.0.1 (Grimm, 1991–2020).

Given the size of the wetland and considering the composition of the surface sample (15% *Artemisia*, 18% Chenopodiaceae), we assume that pollen from the steppe is important at the site (Lang et al., 2023). This assessment agrees with calibration studies demonstrating that pollen can be easily transported over more than 5 km, particularly if the local vegetation of the wetland is herbaceous (e.g. Conedera et al., 2006; Zhao et al., 2021). To track human impact, palynology relies on the presence of cultural indicator taxa. In Europe, those cultural indicators were originally identified for the temperate forest biome (Behre, 1981; Lang,

Table 1
Radiocarbon dates from the Kardashynskiy mire sediment record.

Laboratory code	Depth (cm)	Material dated	¹⁴ C-age (yr BP)	Calibrated age, 2σ (cal yr BP)
BE-15952.1.1	15–17	<i>Carex</i> seeds, <i>Lycopus europaeus</i> seed	470 ± 20	499–528
BE-15953.1.1	31–33	<i>Carex</i> seeds	605 ± 20	550–646
BE-16814.1.1	43–45	<i>Carex</i> seeds	1335 ± 35	1177–1303
BE-15954.1.1	51–53	<i>Carex</i> seeds	1555 ± 40	1361–1525
BE-16815.1.1	67–69	<i>Carex</i> seeds	2870 ± 70	2793–3207
BE-15128.1.1	77–79	<i>Carex</i> seeds	3355 ± 35	3484–3688
BE-15129.1.1	81–83	<i>Carex</i> seeds	3490 ± 35	3643–3867
BE-15955.1.1	95–97	<i>Carex</i> seeds	3600 ± 110	3592–4234
BE-16816.1.1	115–117	Charcoal	4490 ± 70	4881–5315
BE-15956.1.1	145–147	<i>Carex</i> seeds	5655 ± 45	6312–6551
BE-15957.1.1	163–165	<i>Carex</i> seeds, Asteraceae seeds, Apiaceae seeds, seeds indet.	5970 ± 90	6563–7153
BE-15958.1.1	199–201	<i>Carex</i> seeds, Chenopodiaceae seeds, Asteraceae seed, seed indet.	6210 ± 50	6979–7254
BE-15130.1.1	231–233	Charcoal, seed indet.	7020 ± 80	7685–7972
BE-15959.1.1	247–249	Charcoal	7280 ± 110	7878–8340
BE-15131.1.1	281–283	cf. <i>Salix</i> twig fragment	7320 ± 90	7974–8329

1994; Deza-Araujo et al., 2020). More recently, this approach was extended to the Mediterranean (Mercuri et al., 2013; Deza-Araujo et al., 2020, 2022). So far, however, no specific work has addressed cultural indicator taxa for the steppe biome. We therefore used Behre's primary and secondary cultural indicator approach to discuss land use (Behre et al., 2023). We are aware that the interpretation of *Cerealia t.* pollen in the steppe region, where wild relatives of cereals might be native (Mosyakin and Fedoronchuk, 1999; Stobbe et al., 2015), is less certain than in other parts of Europe. Additionally, in a large wetland such as the one surrounding Kardashynskiy mire, *Cerealia t.* pollen might potentially also derive from wetland Poaceae such as *Glyceria*, which would however affect the *Hordeum t.* but not *Triticum t.* or *Avena t.* (Beug, 2004). Indeed, *Cerealia t.* pollen trends do not mirror those of Poaceae (see Fig. A1), suggesting that a relevant portion of *Cerealia t.* did not derive from wild grasses. Therefore, we base our land use reconstruction on common patterns of pollen indicative of human impact, not individual pollen types (Deza-Araujo et al., 2020).

Microscopic charcoal particles >10 µm were counted on the pollen slides following Tinner and Hu (2003) and Finsinger and Tinner (2005). Microscopic charcoal concentration (particles cm⁻³) and influx values (particles cm⁻² year⁻¹) were calculated as for pollen. To determine the statistically significant local pollen assemblage zones, optimal partitioning by minimal sum-of-squares (Birks and Gordon, 1985) and the broken-stick model (Bennett, 1996) were used in R v. 4.2.2 (R Core Team, 2022).

3.3. Numerical analyses

Ordination analyses, aimed at identifying underlying ecological gradients in the pollen dataset and tracking changes in vegetation composition over time, were conducted on square root transformed and centered terrestrial pollen percentage data using the program Canoco 5.1 (ter Braak and Šmilauer, 2017). To select the optimal ordination method, we first ran a detrended correspondence analysis (DCA). As DCA axis 1 was rather short (1.5 standard deviation units of turnover), we chose a method based on linear response models, i.e. principal component analysis (PCA).

For the high-resolution section 1 (HR1: 7140–6830 cal yr BP/ 5190–4880 BCE) and 2 (HR2: 6480–5610 cal yr BP/ 4530–3660 BCE), we used redundancy analysis (RDA) to quantify the effect of changes in local water availability and fire occurrence on the vegetation. RDA was chosen as the length of the DCA axis 1 of both high-resolution sections was rather short (both 0.9 standard deviation units of turnover). RDA was performed in the program Canoco 5.1 (ter Braak and Šmilauer, 2017) on square root transformed and centered pollen, fern spore and algae percentage data. As environmental variables, *Nymphaea* influx and microscopic charcoal influx were taken. *Nymphaea* was chosen as a proxy for low local water availability because its occurrence is restricted to shallow waters with a depth of up to 3 m (e.g. Cook, 1990; Paillisson and Marion, 2006). Moreover, it was very abundant during some periods together with other aquatic and wetland plants such as *Potamogeton*, *Sparganium t.*, and *Utricularia* (Fig. 4). Age was used as a covariable, to exclude long-term trends that are simply due to changes in time. To identify leads and lags in the responses of vegetation to changing local water availability and fire occurrence, we conducted cross-correlation analysis (Bahrenberg et al., 1992; Tinner et al., 1999). We used influx of microscopic charcoal and *Nymphaea* pollen as independent variables and pollen percentages of selected taxa as dependent variables to explore potential effects of fire and moisture changes on upland vegetation. We ran this analysis for HR1 (7140–6830 cal yr BP/ 5190–4880 BCE, 23 samples, 14.1 ± 0.4 years/lag) and HR2 (6480–5610 cal yr BP/ 4530–3660 BCE, 26 samples, 35 ± 10 years/lag). Correlation coefficients were calculated at ±5 lags, using SYSTAT 10 and R v. 4.2.2 (R Core Team, 2022).

To estimate biodiversity changes, palynological richness (PRI, Birks and Line, 1992), probability of interspecific encounter (PIE, Hurlbert,

1971), and evenness-detrended palynological richness (DE-PRI, Colombaroli and Tinner, 2013) were calculated using R v. 4.2.2 (R Core Team, 2022). PRI estimates the number of pollen taxa in a standardised sample size, using rarefaction analysis. PIE is an estimate of evenness, ranging between 0 and 1. Low values of PIE indicate that samples are dominated by a few taxa, whereas values close to 1 indicate a high evenness. Finally, DE-PRI intends to minimise the effect of evenness on palynological richness by using a regression between PRI and PIE, and calculating the residuals of pollen richness (Colombaroli and Tinner, 2013). DE-PRI may reveal biases related to uneven conditions and correct for distortions of palynological richness by uneven samples (e.g. as caused by strong pollen producers such as *Pinus*; Senn et al., 2022).

4. Results and interpretation

4.1. Lithology and chronology

The lowermost sections of the core consist of sand (374–332 cm), sandy clay (332–312.5 cm) and sandy clayey gyttja (312.5–298 cm). Above 298 cm, the sediment gets more organic and gradually less sandy. Below 264 cm depth the sequence is nearly palynologically sterile. From 241.5 cm upwards, the main sediment types are peaty gyttja and calcareous gyttja, interrupted by layers of peat, gyttja and a thin section of lake marl (166.5–164.5 cm). The topmost 22 cm of the core consist of decomposed peat (see Table 2 for more details). This finding suggests that the wetland was for most of the time a lake (predominance of gyttja and lake marl), with numerous water table oscillations (peaty sections) and only relatively recently developed into a peatland.

In general, terrestrial plant macrofossils were scarce. All the available radiocarbon dates (Table 1) were included in the age–depth model (Fig. 2). The age–depth model shows that the palaeoecological record presented here (264–0 cm depth) spans the past c. 8300 years. The most remarkable changes in deposition time occurred at c. 150 cm depth, showing a significant slowdown in sediment deposition, and at c. 80 cm depth, when sediment deposition times become highly variable (Fig. 2).

Table 2
Lithology of the Kardashynskiy mire sediment record (NA = not available).

Depth (cm)	Age (cal yr BP)	Sediment description
0–22	–65–490	Decomposed peat
22–52.5	490–1520	Peaty gyttja
52.5–81	1520–3700	Peaty, calcareous gyttja
81–96	3700–4180	Peaty gyttja
96–103	4180–4500	Calcareous gyttja
103–108	4500–4730	Peaty gyttja
108–112	4730–4920	Calcareous gyttja
112–123	4920–5410	Peaty gyttja
123–130.5	5410–5720	Calcareous gyttja
130.5–147	5720–6370	Gyttja
147–154	6370–6500	Calcareous gyttja
154–159	6500–6590	(Peaty) gyttja with molluscs
159–160.5	6590–6610	Calcareous gyttja
160.5–164.5	6610–6680	Peaty gyttja
164.5–166.5	6680–6710	Lake marl
166.5–178	6710–6870	Peat
178–186	6870–6980	Calcareous gyttja (layered)
186–191	6980–7050	Peaty gyttja
191–197	7050–7140	Calcareous gyttja
197–203	7140–7240	Peaty gyttja
203–207.5	7240–7320	Calcareous gyttja
207.5–226	7320–7670	Peaty gyttja (with peat layers)
226–241.5	7670–7930	Gyttja
241.5–262	7930–8220	Sandy, silty gyttja
262–298	8220–NA	Gyttja (with sand)
298–312.5	NA	Sandy, clayey gyttja
312.5–332	NA	Sandy clay
332–374	NA	Sand

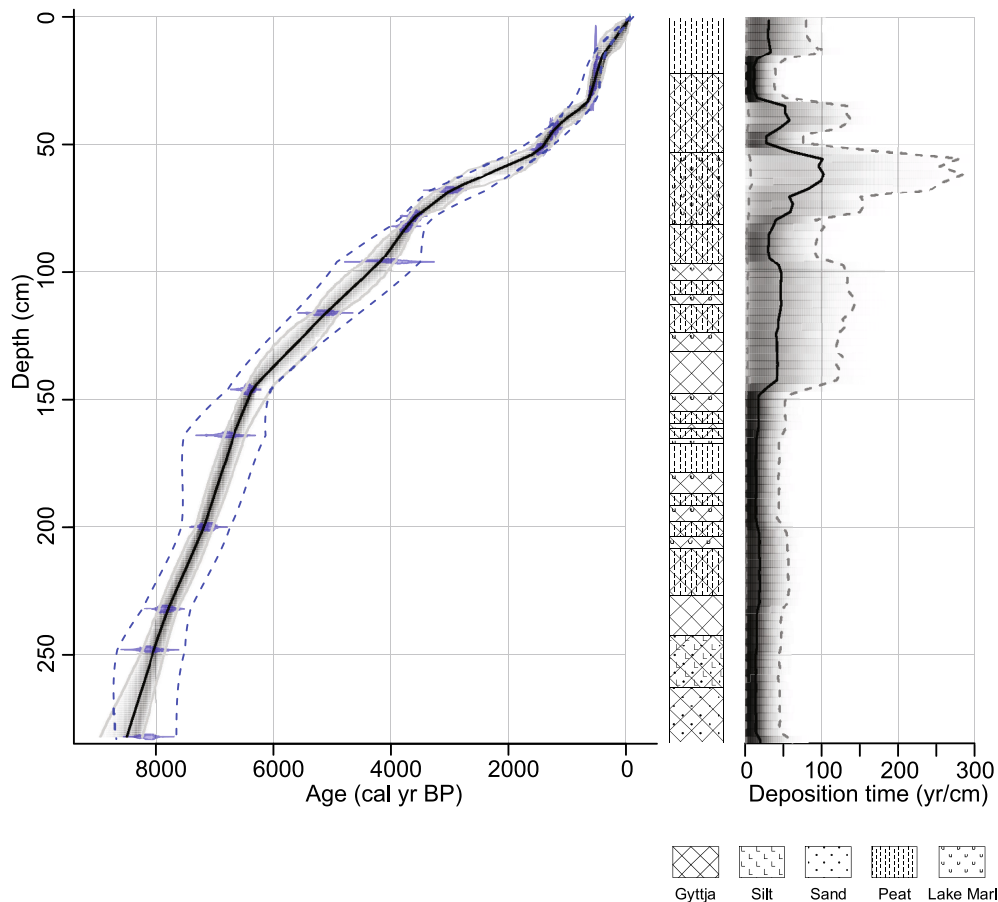


Fig. 2. Age–depth model (left), lithology (middle) and sediment deposition time (right) of the Kardashynskiy mire sedimentary sequence. The age–depth model was fitted using the Bayesian approach in ‘rbacon’ (version 2.5.7, [Blaauw and Christen, 2011](#)). Age–depth model: blue density plots = calibrated radiocarbon dates used to fit the model; solid black line = single best model = mean age–depth model; grey envelope = 95% confidence intervals of the model; blue dashed lines = 95% confidence interval of a mixed effect model taking into account between-object variance (calibration error + sample thickness, [Heegaard et al., 2005](#)). Deposition time: solid black line = mean deposition time; grey-scales = modelled deposition times (the darker, the more likely); dashed grey line = 95% confidence range. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2. Vegetation and fire history

A total number of 132 terrestrial pollen types were identified. This is about twice as many as in the original study of [Kremenetski \(1995\)](#), which may derive from the higher number of samples analysed in our study and higher taxonomic resolution. According to the numerical zonation, the Kardashynskiy pollen record can be divided into seven statistically significant local pollen assemblage zones (LPAZ; KR1 to KR7; [Figs. 3–5](#)). Pollen percentage, concentration, and influx curves have comparable trends ([Fig. A2](#)), indicating that the patterns observed in the percentage pollen data are robust. Below, we describe and interpret the main results of each LPAZ in terms of vegetation, fire, and land use history.

4.2.1. KR1 (8250–7950 cal yr BP/6300–6000 BCE)

The oldest LPAZ has the highest arboreal pollen (AP) percentage of the whole sequence (60%), consisting almost exclusively of *Pinus* ([Fig. 3](#)). Non arboreal pollen (NAP) is dominated by Chenopodiaceae (15%), Cichorioideae (10%), Poaceae (10%) and *Artemisia* (5–10%). Towards the end of this zone, *Botryococcus* and Cyperaceae increase ([Fig. 4](#)). Microscopic charcoal influx and concentration reach their highest values of the whole sequence (104,000 particles $\text{cm}^{-2} \text{yr}^{-1}$ and $1.5 \cdot 10^6$ particles cm^{-3} , respectively).

The high abundances of drought-resistant taxa (Chenopodiaceae, Cichorioideae, Poaceae, and *Artemisia*) suggest the dominance of steppe vegetation, whereas the large amount of *Pinus* pollen points to the

presence of pine stands. Pines, most probably *Pinus sylvestris* (see also [Kremenetski, 2003](#)), were likely growing on the sandy terraces along the Dnipro. Interestingly, no *Pinus stomata* or macrofossils were found, suggesting that the taxon was not growing locally in the wetlands. Apart from a single occurrence of *Polygonum aviculare* t. pollen, there is no palynological evidence of agricultural activity during this zone. The presence of only few macrophytes (e.g. *Sparganium* t.) and algae may indicate high water stands, which is in agreement with lithological evidence of lacustrine conditions (gyttja). Maximum fire activity during this zone might be due to the high abundance of *P. sylvestris*, which resulted in high fuel availability.

4.2.2. KR2 (7950–7000 cal yr BP/6000–5050 BCE)

AP decreases to 40%, mostly because *Pinus* drops to 20–30%. Deciduous broadleaved trees such as *Betula*, *Corylus*, *Ulmus*, *Quercus robur* t. and, to a lesser extent, also *Alnus glutinosa* t., *Salix*, *Fraxinus excelsior* t. and *Tilia* start to expand although still at low percentages. Poaceae (10–35%) and *Artemisia* (10–20%) dominate among the NAP. Chenopodiaceae abundances show abrupt fluctuations between 5 and 40%. Cultural indicators such as *Cerealia* t., *Plantago lanceolata* t., *Plantago major-media* t., *Cannabis sativa* t. and *Rumex acetosa/acetosella* t. are regularly present at low abundances from 7900 cal yr BP (5950 BCE) onwards ([Fig. 3](#)). Spores from the dung fungus *Sporormiella* also occur in this zone, albeit in low numbers ([Fig. 3](#)). *Botryococcus*, *Nymphaea* and *Tetraedron minimum* show several peaks throughout this zone. Microscopic charcoal influx and concentration show gradual decreases: influx

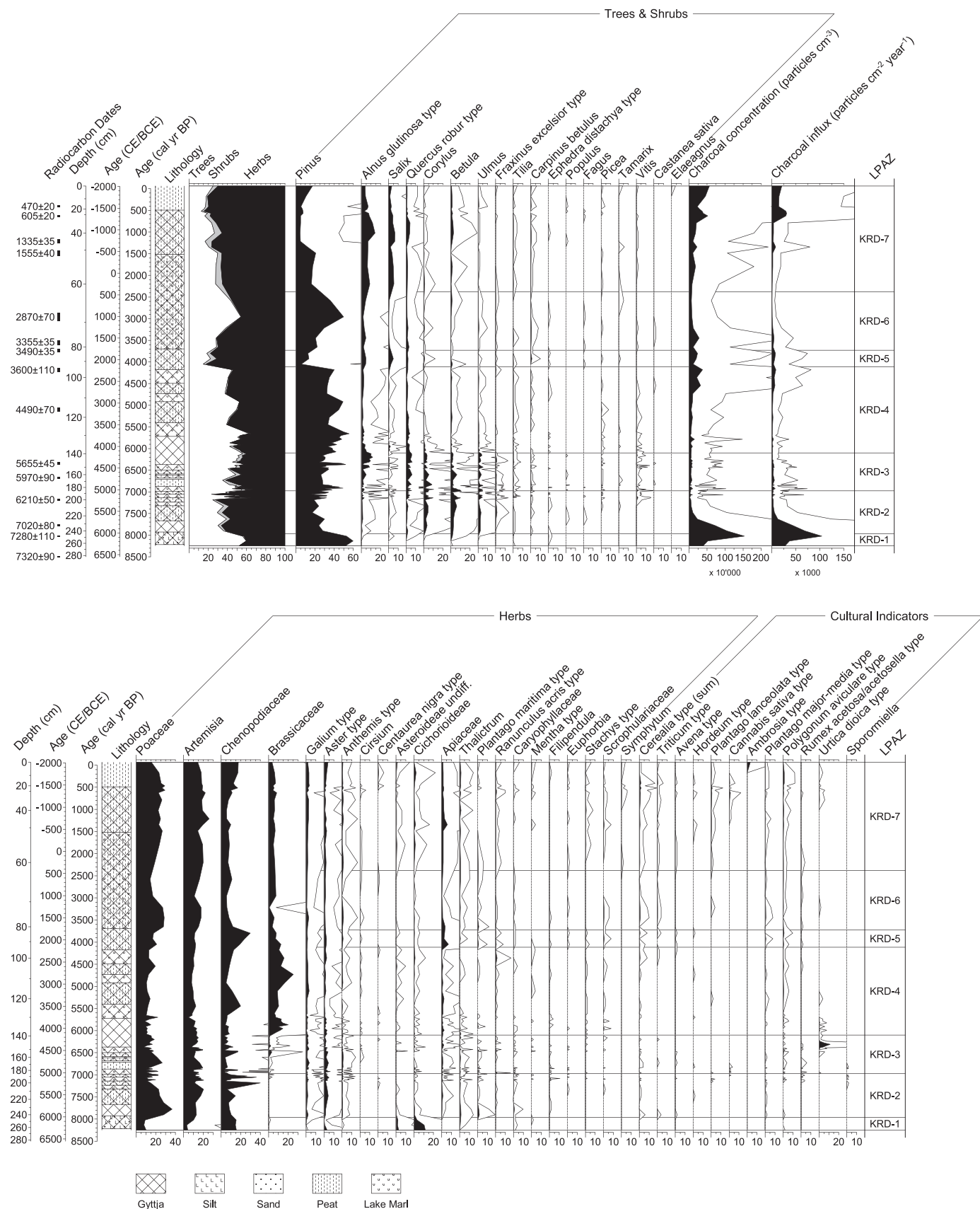


Fig. 3. Pollen percentage diagram of Kardashynskiy mire showing selected trees, shrubs and herbs as well as *Sporormiella* (dung fungal spores) and microscopic charcoal influx and concentration. The values shown for pollen taxa are percentages of the terrestrial pollen sum (*i.e.* sum of trees, shrubs and herbs). Empty curves show 10x exaggerations. LPAZ = local pollen assemblage zone. The depiction of the different sediment types is based on Troels-Smith (1955).

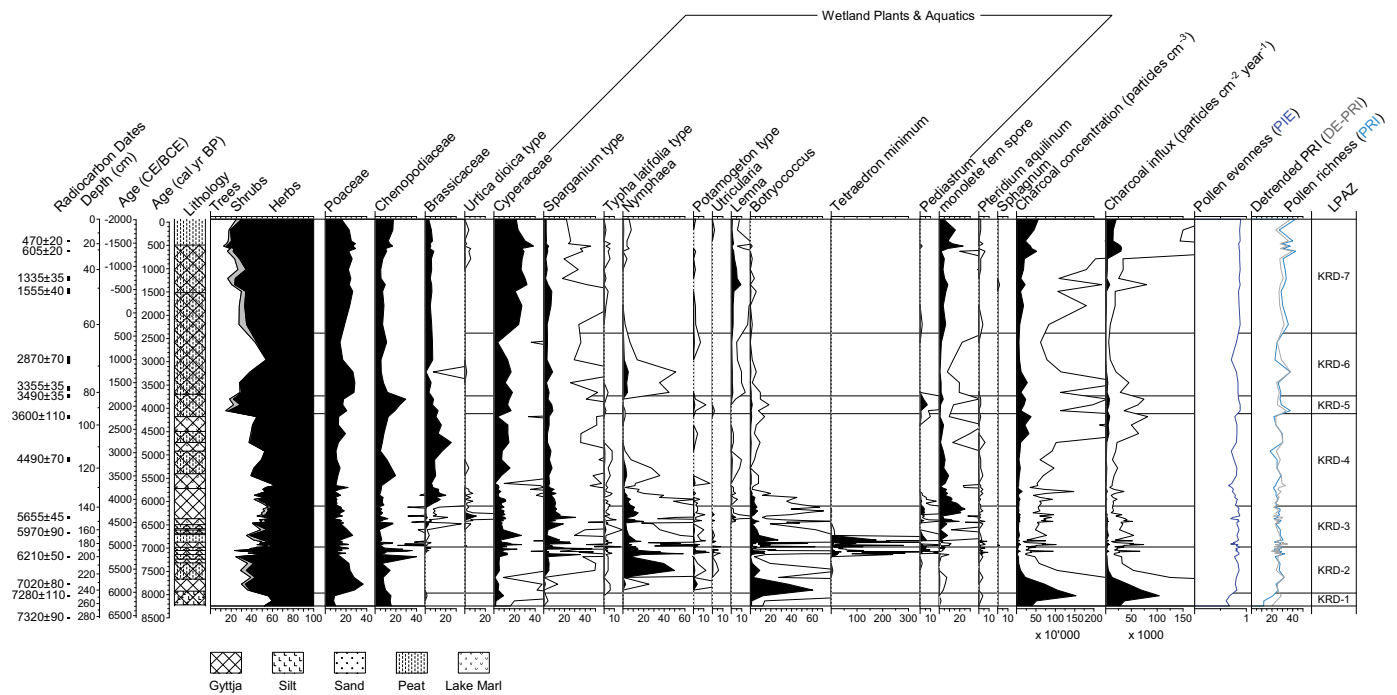


Fig. 4. Percentage pollen diagram of Kardashynskiy mire showing obligate wetland plants and aquatic plants as well as other abundant taxa that could potentially include wetland or aquatic plants in the current setting. Additionally, fern spores, microscopic charcoal concentration and microscopic charcoal influx, as well as the probability of interspecific encounter (PIE, dark blue), palynological richness (PRI, light blue) and evenness-detrended palynological richness (DE-PRI, grey) are shown. The values shown for pollen taxa, spores and algae are percentages of the terrestrial pollen sum (*i.e.* sum of trees, shrubs and herbs). Empty curves show 10x exaggerations. LPAZ = local pollen assemblage zone. The depiction of the different sediment types is based on Troels-Smith (1955). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

drops markedly from 69,000 particles $\text{cm}^{-2} \text{yr}^{-1}$ at 7900 cal yr BP (5950 BCE) to 3000 particles $\text{cm}^{-2} \text{yr}^{-1}$ at 7300 cal yr BP (5350 BCE).

The changes observed in the pollen assemblages suggest that steppe vegetation expanded while pine stands collapsed and deciduous broadleaved trees spread. Chenopodiaceae peaks suggest that drier variants of steppe were more widespread (*e.g.* El-Moslimany, 1990). The mass expansion of macrophytes (*e.g.* *Nymphaea*) and algae might point to water table lowering, an interpretation which is in very good agreement with the lithology documenting a first appearance of peaty, shallow water conditions from c. 7700 cal yr BP (Table 2). The marked decrease in fire activity throughout the zone coincided with the decrease in pines and the expansion of temperate deciduous broadleaved tree stands along the riverbanks.

4.2.3. KRD-3 (7000–6100 cal yr BP/5050–4150 BCE)

The increase in *Pinus* (25–50%) drives the rise in AP to c. 50%. However, the most remarkable feature of this zone is the overall high abundance of deciduous broadleaved trees and shrubs such as *Alnus glutinosa* t., *Quercus robur* t., *Corylus*, *Betula*, *Ulmus*, *Fraxinus excelsior* t., *Tilia*, and *Vitis* (the latter likely growing as a liana in the riparian forest, Figs. 3, 5). *Castanea sativa* pollen occurs for the first time (Fig. 3). Poaceae, *Artemisia*, and Chenopodiaceae dominate the NAP. Around 6300 cal yr BP (4350 BCE), *Urtica dioica* t. shows a peak of >10%. *Cerealia* t., *Polygonum aviculare* t. and *Rumex acetosa/acetosella* t. regularly occur although in low abundances. Some grains of *Plantago major-media* t. and *Cannabis sativa* t. appear between c. 6950 cal yr BP (5000 BCE) and 6600 cal yr BP (4650 BCE). *Tetradion minimum* shows a large peak at c. 6850 cal yr BP (4900 BCE). *Nymphaea*, *Sparganium* t., Cyperaceae and *Botryococcus* oscillate, reaching low values at around 6500 cal yr BP (4550 BCE). Monolete fern spores increase markedly towards the end of the zone. Microscopic charcoal influx and concentration fluctuate at low values to further decrease towards the end of the zone (influx: 1000–7000 particles $\text{cm}^{-2} \text{yr}^{-1}$).

Taken together, the pollen assemblages suggest a reduction of steppe vegetation, a partial recovery of pine stands and a moderate expansion of temperate deciduous broadleaved tree stands in gallery forests, along rivers and estuaries. Pollen records of crops and weeds suggest that locally, human impact was slight but persistent. The *Urtica dioica* t. peak, however, was likely caused by natural disturbances rather than by human impact, because it does not co-occur with any primary human indicator. The pollen might come from natural occurrence of species of *Urtica* either growing in riparian forests or in reed communities in floodplains (Behre, 1981; Wolters et al., 2005; Tinner et al., 2009). Aquatic plants (*e.g.* *Nymphaea*) show large fluctuations, but overall declined markedly, suggesting that the lake-level underwent several substantial changes. Fire activity stayed comparably low throughout the zone.

4.2.4. KRD-4 (6100–4100 cal yr BP/4150–2150 BCE)

AP remains around 50% but deciduous broadleaved trees and shrubs such as *Alnus glutinosa* t., *Quercus robur* t., *Ulmus*, *Betula*, *Fraxinus excelsior* t. and *Corylus* decline markedly around 6100 cal yr BP (4150 BCE, Figs. 3, 5b, A2). Simultaneously, Brassicaceae show a major increase, while Poaceae, *Artemisia* and Chenopodiaceae are still abundant. Some cultural indicators such as *Plantago major-media* t. and *Polygonum aviculare* t. are present throughout the zone. From 4450 cal yr BP (2500 BCE) onwards, *Cerealia* t. (more specifically *Triticum* t.) increases and becomes nearly continuous. Most wetland plants and algae (*Nymphaea*, *Botryococcus*, *Pediastrum*, *Potamogeton* t., *Sparganium* t.) decrease markedly between 6100 cal yr BP (4150 BCE) and 5000 cal yr BP (3050 BCE, Figs. 4, A2). In contrast, Cyperaceae show a slight increase. Microscopic charcoal concentration and influx increase, starting around 4600 cal yr BP (2650 BCE); *e.g.* influx increases from 1000 to 8000 particles $\text{cm}^{-2} \text{yr}^{-1}$.

The sudden decline of deciduous broadleaved tree and shrub pollen suggests a strong decline of riparian forests, possibly due to changes in

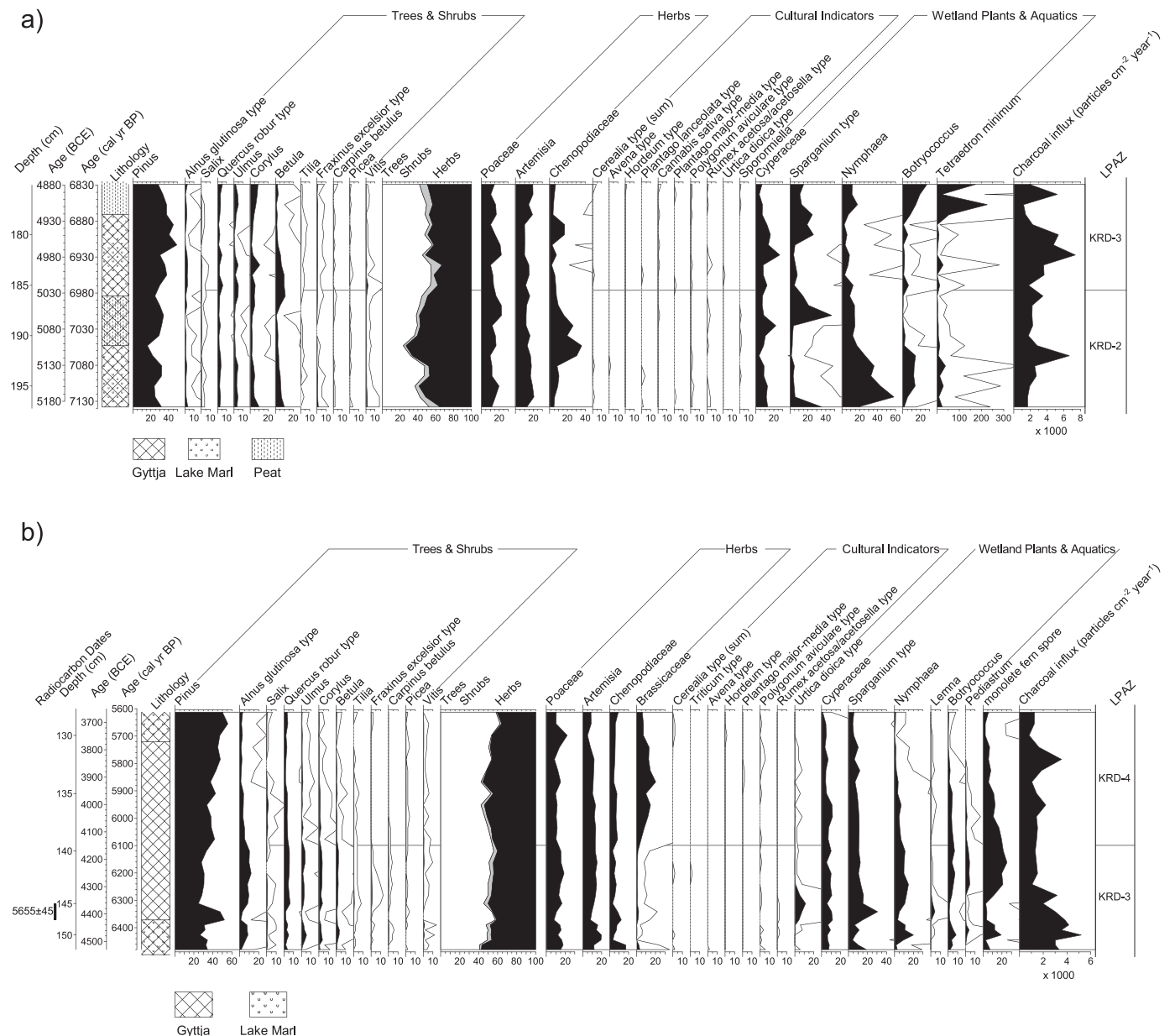


Fig. 5. High-resolution pollen, spore and algae percentage, and microscopic charcoal influx diagrams of Kardashynskiy mire for selected taxa from a) HR1 (7140–6830 cal yr BP; 5190–4880 BCE) and b) HR2 (6480–5610 cal yr BP; 4530–3660 BCE). The values shown for pollen taxa, spores and algae are percentages of the terrestrial pollen sum (*i.e.* sum of trees, shrubs and herbs). Empty curves show 10x exaggerations. LPAZ = local pollen assemblage zone. The depiction of the different sediment types is based on Troels-Smith (1955).

local water availability. The mass expansion of Brassicaceae at around 6100 cal yr BP (4150 BCE) may have occurred in wetlands close to the lake. At that time macrophytes (*e.g.* *Nymphaea*) and algae were still abundant but started to decline. A drying up of the site can be excluded given that lake sediments (gyttja) were deposited until c. 5400 cal yr BP, when shallow lake conditions re-established (peaty gyttja, Table 2), causing a minor re-expansion of *Nymphaea* (Fig. 4). After 4900 cal yr BP (2950 BCE) lake levels probably rose again (calcareous gyttja, Table 2) until c. 4200 cal yr BP (2250 BCE), interrupted by a transient lowering c. 4750–4500 cal yr BP (peaty gyttja, 2800–2550 BCE). Arable and pastoral land use increased to moderate levels during the Bronze Age around 4450 cal yr BP (2500 BCE), synchronously with fire activity.

4.2.5. KRD-5 (4100–3750 cal yr BP/2150–1800 BCE)

AP suddenly drops from around 40 to 20% mostly because of the collapse of *Pinus* (from 40% to 10%). Chenopodiaceae percentages

almost triple, reaching a maximum of 30% around 3800 cal yr BP (1850 BCE). Pollen of wetland trees and shrubs such as *Salix* and *Alnus glutinosa* t. peaks, while Poaceae, *Artemisia* and Brassicaceae are still abundant. *Cerealia* t., *Plantago major-media* t. and *Polygonum aviculare* t. show in general fluctuating but moderately high values. Cyperaceae and *Sparganium* t. are abundant, and *Pediastrum* and *Potamogeton* t. show minor peaks. Microscopic charcoal concentration and influx stay elevated.

Maxima in several primary and secondary cultural indicators alongside high fire activity probably indicates land use intensification during the Bronze Age. Lake levels likely dropped, as suggested by the occurrence of peaty, shallow lake conditions (Table 2), causing minor increases of shore macrophytes such as *Potamogeton*.

4.2.6. KRD-6 (3750–2400 cal yr BP/1800–450 BCE)

Pinus recovers and reaches c. 50% around 2950 cal yr BP (1000 BCE), before declining again. *Castanea sativa* is present in two samples.

Poaceae, the main herbs, show first an increase and then decline again from c. 3100 cal yr BP (1150 BCE) onwards. *Artemisia*, Chenopodiaceae and, to a lesser extent, Brassicaceae are abundant. Cerealia t. pollen, mainly *Triticum* t., and *Plantago lanceolata* t. show their highest values so far between 3500 and 3200 cal yr BP (1550 and 1250 BCE, Fig. 3). *Plantago major-media* t. and *Polygonum aviculare* t. are also relatively abundant. *Nymphaea* shows a little upsurge until 3100 cal yr BP (1150 BCE). Cyperaceae and *Sparganium* t. are abundant. Microscopic charcoal concentration and influx drop to the lowest levels observed over the whole sequence (influx < 1000 particles cm⁻² yr⁻¹).

High NAP percentages together with mainly pine pollen suggest the prevalence of steppe vegetation with pine stands in the region. Fire activity decreased together with Bronze Age arable farming around 3100 cal yr BP (1150 BCE; Fig. 3). Peaty deposits point to rather low lake levels throughout this zone, supporting last expansions of aquatic plants such as *Nymphaea* until c. 3000 cal yr BP (1050 BCE).

4.2.7. KRD-7 (2400 cal yr BP–present/450 BCE–present)

During the past c. 2400 years, AP decreases to 20–30% and *Pinus* drops to only 5%. Meanwhile, *Alnus glutinosa* t. and *Salix* increase. Poaceae, *Artemisia* and Chenopodiaceae dominate NAP with still notable abundances of Brassicaceae. Cerealia t. and *Plantago lanceolata* t. occur continuously. *Cannabis sativa* t. starts to occur regularly from 1200 cal yr BP (750 CE) onwards and peaks at c. 650 cal yr BP (1300 CE). *Ambrosia* t. and *Elaeagnus* are found in the surface sample (Fig. 3). Both plants were introduced to Ukraine more than 100 years ago and are now invasive. *Ambrosia artemisiifolia* was accidentally introduced with seeds from North America (Afonin et al., 2018) and *Elaeagnus angustifolia* was originally planted in shelterbelts (Sudnik-Wójcikowska et al., 2009). Cyperaceae increase markedly, whereas *Sparganium* t. declines slightly. Around 1350 cal yr BP (600 CE), *Lemna* features as a minor peak. Microscopic charcoal influx and concentrations show a huge increase starting around 650 cal yr BP (1300 CE).

Pine stands or parklands on the sandy terraces of the Dnipro declined and riparian forest stands recovered. The recent slight increase of pines is likely due to afforestation that started in the middle of the 19th century CE (Bujanov, 2014). The increase in Cyperaceae likely resulted from the gradual conversion of the lake into a mire. This process was completed by c. 500 cal yr BP (1450 CE; peat, Table 2). During the past c. 800 years, fire activity and land use increased massively (Fig. 3).

4.3. Numerical analyses: Ordinations, cross-correlations and biodiversity estimates

PCA axis 1 explains 29% of the total variance in the pollen dataset and may represent a land use gradient, with Cerealia t., *Triticum* t., *Plantago lanceolata* t. and *Polygonum aviculare* t. having high loads along the axis 1 and trees and shrubs such as *Pinus*, *Ulmus*, *Corylus*, *Fraxinus excelsior* t. and *Betula* having low axis 1 loads (Fig. 6). PCA axis 2 explains 22% of the total variance. Axis 2 basically mirrors *Pinus* and might at least for the first half of the sequence be related to climate and/or edaphic conditions, particularly moisture availability, whereas the second half might be co-determined by human impact (see 4.2).

For HR1 (7140–6830 cal yr BP/5190–4880 BCE), the RDA shows that *Nymphaea* influx and microscopic charcoal influx explain 18.3% ($P = 0.008$) and 14.5% ($P = 0.028$) of the variation in the data respectively (simple effects). Together, they explain 32.2% of the variation. Therefore, for this high-resolution section, water availability seemed to have played a prominent role in driving vegetation dynamics (Fig. 7a). Specifically, *Nymphaea* influx is highly positively correlated with the algae *Botryococcus* and with *Artemisia*, *Ulmus* and *Ostrya* t., but negatively with *Pinus*. Microscopic charcoal influx is positively correlated with herbs such as *Aster* t. and Fabaceae, suggesting that those steppe taxa might have benefited from fires, while wetland organisms such as *Utricularia*, *Tetraedron minimum* and *Salix* are negatively correlated.

Cross-correlation analyses show marked correlations between

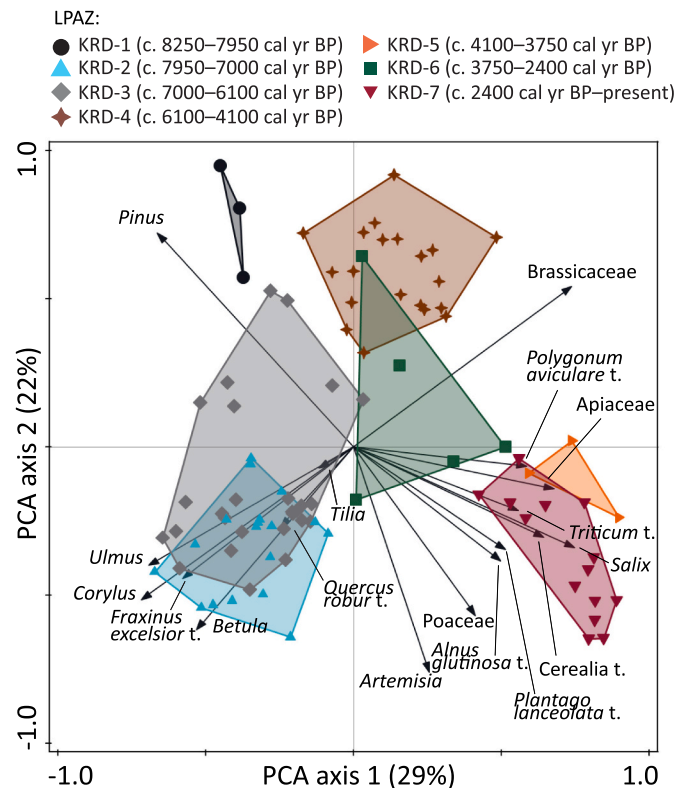


Fig. 6. PCA biplot showing species and sample scores of the Kardashynsky mire pollen record. Axis scores in the plot are standardised. The 15 most important taxa are shown and additionally also the two tree taxa *Quercus robur* t. and *Tilia*. In this figure, Cerealia t. does not include *Triticum* t., which is displayed separately. The sample groups are based on the seven statistically significant pollen zones (LPAZ; KRD-1 until KRD-7).

Nymphaea influx (as a wetland proxy) and pollen percentages (as an upland vegetation proxy) during HR1 (7140–6830 cal yr BP/5190–4880 BCE). Specifically, *Nymphaea* influx and *Pinus* percentages show significant negative correlations peaking at lags 0 and 1 (Fig. 8a). Conversely, the typically steppe genus *Artemisia* reaches highest significant positive correlations at lag 0. Chenopodiaceae, another taxon abundant in steppes, are also positively correlated with *Nymphaea* reaching a correlation peak at lag 4 (i.e. after c. 52 years). A decrease in *Nymphaea* influx can be caused by either a drying up of the site, making the water table too shallow for the species to grow (i.e. < 0.5 m) or by an increase in the water table so that it gets too deep for *Nymphaea* to grow (i.e. > 3 m, Cook, 1990). Our findings suggest significant impact of moisture availability on upland vegetation, with drought disturbance likely causing rapid declines of *Pinus sylvestris* and expansions of steppic herbs such as *Artemisia* and Chenopodiaceae. Cross correlations for charcoal (as fire proxy) vs pollen (as vegetation proxy) are less pronounced. For instance, *Artemisia* and *Ulmus* percentages are weakly negatively correlated with charcoal influx at lags 1, respectively 2 (i.e. after c. 14 years, 28 years respectively), likely showing that fire-disturbance induced only subtle declines of *Artemisia* in the steppe and *Ulmus* in the floodplain.

For HR2 (6480–5610 cal yr BP/4530–3660 BCE), the RDA shows that 16% ($P = 0.002$) of the variation in the dataset is explained by *Nymphaea* influx but only 4.8% ($P = 0.294$) by microscopic charcoal influx (simple effects). Together, they explain 28.6% of the variation. This result indicates that water availability was also the main driver of vegetation change during HR2 (Fig. 7b). As in HR1, *Nymphaea* influx is again positively correlated with *Artemisia* as well as with several broadleaved tree taxa (e.g. *Ostrya* t., *Ulmus*, *Carpinus betulus*, *Quercus robur* t.) and *Botryococcus*, suggesting that those taxa reacted similarly to

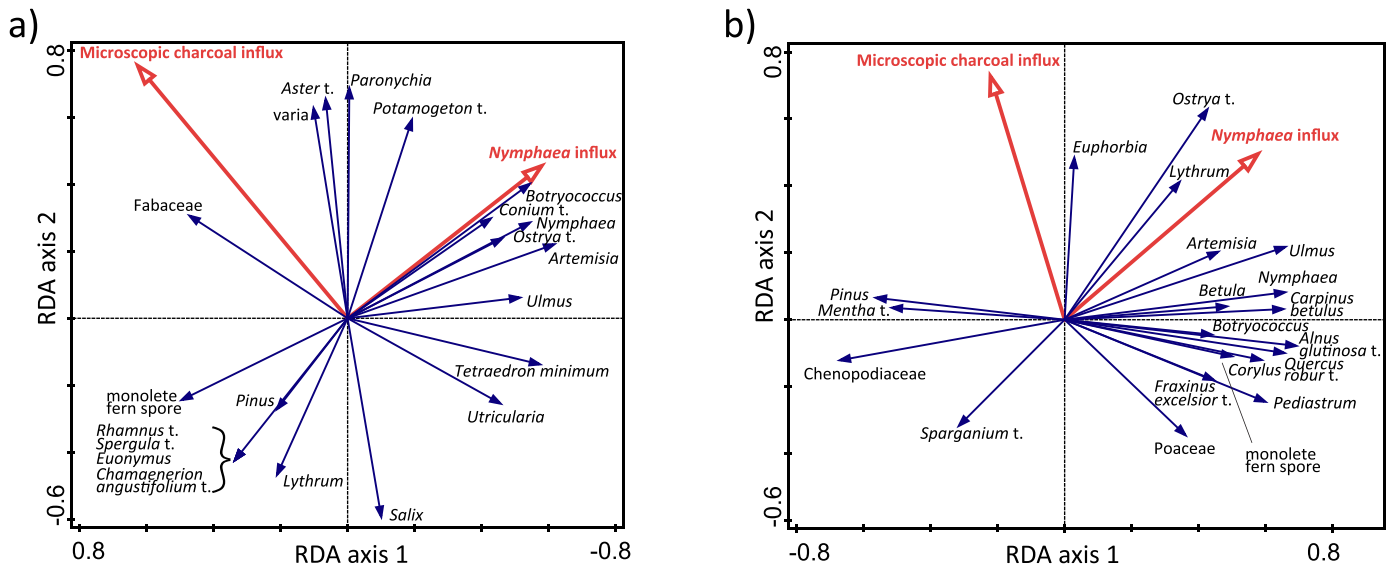


Fig. 7. Redundancy analysis (RDA) for (a) HR1 (7140–6830 cal yr BP; 5190–4880 BCE) and (b) HR2 (6480–5610 cal yr BP; 4530–3660 BCE). Response variables are the pollen taxa, fern spores and algae (square-root transformed percentages), while the environmental variables are *Nymphaea* influx (pollen grains $\text{cm}^{-2} \text{year}^{-1}$) and microscopic charcoal influx (particles $\text{cm}^{-2} \text{year}^{-1}$). Only the 20 best fitting taxa are shown and in HR1 additionally also *Pinus*. *Nymphaea* influx and microscopic charcoal influx separately explain 18.3% ($P = 0.008$) and 14.5% ($P = 0.028$) of the variation in HR1, and 16.0% ($P = 0.002$) and 4.8% ($P = 0.294$) in HR2, respectively (simple effects).

local changes in water availability. *Pinus* percentages are again negatively correlated with *Nymphaea* influx, showing that the RDA results for HR1 can be generally reproduced in HR2.

The cross-correlation analysis of HR2 (6480–5610 cal yr BP/4530–3660 BCE) again shows a marked significant negative correlation peaking at lag 0 between *Nymphaea* influx and *Pinus* percentages, while *Artemisia* is positively correlated at lag 0 (Fig. 8b). During HR2 the vegetation responses to moisture availability changes are more pronounced than during HR1. Indeed, significant positive correlation peaks at lag 0 occur also for *Quercus robur* t., *Alnus glutinosa* t., *Ulmus*, *Betula* the sum of all broadleaved trees, *Corylus* and the sum of all shrubs (which is here largely dominated by *Corylus*). In contrast, Brassicaceae reach a significant negative correlation peak at lags -1 and 0 . Altogether this suggests that moisture availability changes caused similar shifts to those recorded during HR1, with *Artemisia* benefitting at the expense of *Pinus* when moisture availability declined and resulted in lowering lake levels. Broadleaved deciduous trees may have indirectly benefitted from declines of dominant *Pinus* (see Discussion). Brassicaceae were likely growing locally and were therefore directly affected by water level changes. Charcoal influx is weakly negatively correlated with *Pinus* percentages at lag 5 and with *Artemisia* percentages at lags -1 and 0 . In contrast to HR1, it seems as if fire had a slightly beneficial effect on *Artemisia* during HR2.

Palynological richness (PRI) and detrended palynological richness (DE-PRI) show a minor increase towards the present, which is however largely overridden by strong fluctuations throughout the sequence (Fig. 4). The uneven dominance of *Pinus* has no effect on overall species richness/diversity, however, palynological evenness (PIE) is negatively correlated with pine pollen percentages. In summary, the indices suggest that even though taxon composition changed over the past c. 8300 years, overall diversity did not change much.

5. Discussion

5.1. Vegetation and fire responses to natural environmental variability prior to 7900 cal yr BP

Although the course and timeline of the Black Sea marine transgression have been under debate for several decades there is still

considerable disagreement between researchers (see e.g. Yanko-Hombach et al., 2014; Yanchilina et al., 2017; Aksu and Hiscott, 2022). Recent evidence dates the post-glacial sea-level rise, which led to the initial and gradual marine inflow into the Neoeuxine Lake (today's Black Sea), to c. 9500 cal yr BP (Ankindinova et al., 2019; Huang et al., 2021), although brackish water might have spilled outward into the Marmara Sea even earlier (Aksu and Hiscott, 2022). Later, about 8200 years ago, a transient rapid cooling event and a subsequent alteration in precipitation regimes have been observed widely (Alley et al., 1997; von Grafenstein et al., 1998; Seppä and Birks, 2001; Heiri et al., 2004; Rohling and Pälike, 2005; Göktürk et al., 2011). The sea-level rise associated with the Black Sea marine transgression and alterations in precipitation regimes likely raised the freshwater table and led to the emergence of wetlands (e.g. oxbow lakes) around the Dnipro estuary where Kardashynskiy mire is located. At the beginning of our sequence, c. 8300 years ago, the prevailing vegetation was steppic, with pine stands on the sandy terraces along the Dnipro. Highly flammable fuel loads accumulating in the pine stands could explain why the highest values of biomass burning of our entire record have been reconstructed for this period. *Pinus sylvestris* can resist surface fires and even promote the spread of these fires by accumulating thick layers of flammable and slowly decomposing litter on the soil (Feurdean et al., 2017). The pollen data suggest that riparian and wetland vegetation was barely developed during this early period (e.g. low abundances of *Alnus* and *Salix*). Around 8000 cal yr BP (6050 BCE), mixed stands with *Ulmus*, *Corylus*, deciduous *Quercus*, *Alnus* and *Betula* established in the region (Fig. 3), probably in gallery forests. Roughly around the same time, an increase in *Quercus* also occurred at Kamyana Mohyla, 220 km east of Kardashynskiy in the Pontic steppe (Gobet et al., 2017). The spread of mixed temperate tree stands at Kardashynskiy was seemingly synchronous with the initial expansion of wetland vegetation, which suggests a vegetation response to changing hydrologic conditions. The absence of pollen indicative of land use like *Cerealia* t., *Plantago lanceolata* t. or *Cannabis sativa* t. (Figs. 3, 9) suggests that humans did not have a discernible impact on vegetation at Kardashynskiy before 7900 cal yr BP (5950 BCE).

5.2. Earliest agriculture already around 7900 cal yr BP (5950 BCE)?

Earliest pollen evidence of agricultural activities found at

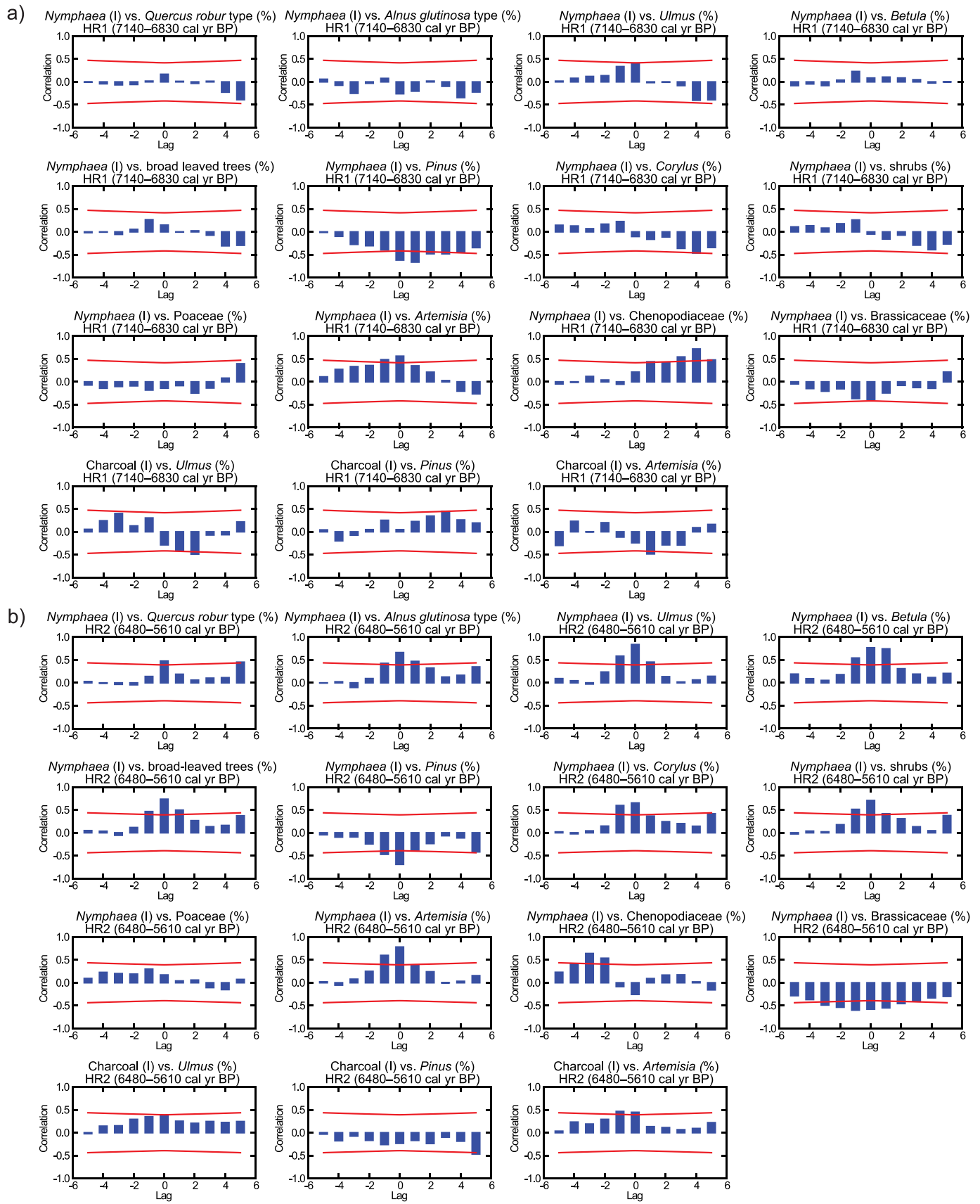


Fig. 8. Cross correlation plots between influx of *Nymphaea* pollen or charcoal and percentages of selected taxa for (a) HR1 (7140–6830 cal yr BP; 5190–4880 BCE, 1 lag = 14.1 ± 0.4 years) and (b) HR2 (6480–5610 cal yr BP; 4530–3660 BCE, 1 lag = 35 ± 10 years). The red lines mark the significance level. I = influx, % = percentage. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

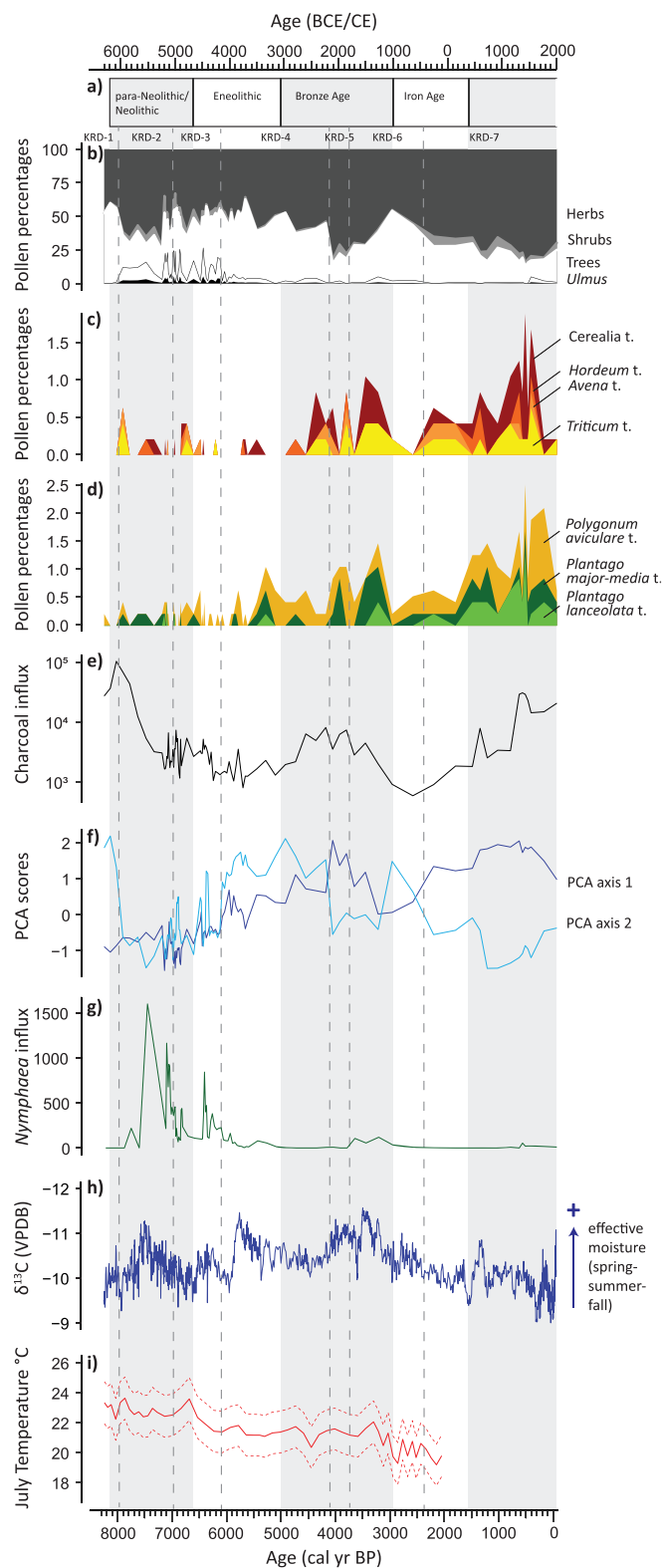


Fig. 9. Summary figure with a) selected Ukrainian archaeological epochs (Gobet et al., 2017; Kotova, 2018); b) percentage pollen diagram showing trees, shrubs and herbs as well as *Ulmus*. The black line indicates a 5x exaggeration of the *Ulmus* curve; c) pollen percentages of the primary cultural indicators *Cerealia* t. (red), *Hordeum* t. (dark orange), *Avena* t. (bright orange) and *Triticum* t. (yellow); d) pollen percentages of the adventive secondary cultural indicators (according to Behre et al., 2023) *Polygonum aviculare* t. (ochre), *Plantago major-media* t. (dark green) and *Plantago lanceolata* t. (bright green); e) microscopic charcoal influx (particles cm⁻² year⁻¹); f) sample scores of PCA axis 1 (dark blue) and 2 (light blue); g) *Nymphaea* influx (pollen grains cm⁻² year⁻¹); h) δ¹³C record, relative to the VPDB (Vienna PeeDee Belemnite) standard, from Sofular cave in northern Türkiye as a proxy for hydroclimate variability (Fleitmann et al., 2009). δ¹³C is interpreted to reflect fluctuations in effective moisture (more negative values mean more spring–summer–fall precipitation, Göktürk et al., 2011); i) July air temperature reconstruction at sea level calculated using the chironomid-inferred temperature anomalies from Lake Brazi, in the southern Carpathians of Romania (Tóth et al., 2015). For better visibility, every second archaeological epoch is shaded in grey throughout the diagram. The grey dashed lines represent the pollen zone boundaries. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Kardashynskiy dates to 7900 cal yr BP (5950 BCE). In central and northern Europe, single occurrences of *Cerealia* t. are usually considered indicative of agricultural activity if found together with pollen of *Plantago lanceolata* t., *Plantago major-media* t. or other adventive plants (Behre, 1981; Lang, 1994; Deza-Araujo et al., 2020; Behre et al., 2023). This may however not apply to the steppe region, where some of those cultural indicators could be native. So far, no direct archaeological evidence of a food-producing economy has been reported from Kardashynskiy for this period, not least probably also because of the lack of systematically excavated archaeological sites. Indirect evidence of early agricultural activities (e.g. pottery) attributed to the first half of the 6th millennium BCE has been found in the region of Kardashynskiy (Telegin, 1968; Kotova and Pashkevich, 2003; Kotova et al., 2021) although new radiocarbon dates from the site Chapaevka point to a younger age (Kiosak et al., 2023). Based on the available evidence and even if tentative, our palynological evidence of Neolithic arable farming should not be dismissed and highlights the need of further studies to elucidate this issue.

From 7900 cal yr BP (5950 BCE) until the beginning of the Bronze Age at c. 5000 cal yr BP (3050 BCE), regular but discontinuous occurrence of cultural indicators suggest that land use including arable and pastoral farming – if present at all locally – remained at rather low levels. Currently, imprints of cultivated plant grains on ceramics are known only for the Late Neolithic and Eneolithic sites (5000–4000 BCE) located in the neighbouring steppe area of the Dnipro valley between Zaporizhzhia and Dnipro (Kotova and Pashkevich, 2003; Kotova, 2008). Early farmers were probably very vulnerable to changes in their environment, and it took several attempts to make farming sustainable in southern Ukraine.

5.3. High-resolution insights into vegetation dynamics between 7200 and 5600 cal yr BP (5250 and 3650 BCE)

Continuous high-resolution time series can reveal ecological dynamics in response to disturbance that are not accessible through studies with average resolution (Birks, 1997; Tinner et al., 1999; Paquette and Gajewski, 2013; Rey et al., 2013). Our two continuous pollen sections (HR1, HR2) suggest that between 7140 and 6830 cal yr BP (5190–4880 BCE) as well as between 6480 and 5610 cal yr BP (4530–3660 BCE) drought disturbance as inferred from macrophyte abundances (e.g. *Nymphaea*) likely induced repeated reductions of *Pinus* stands and

expansions of steppe vegetation (e.g. *Artemisia*, Figs. 5, 7, 8). While during the first period 7140–6830 cal yr BP (HR1) broadleaved deciduous trees or shrubs such as *Ulmus* and *Corylus* did not respond synchronously to water-table oscillations and/or moisture changes (Fig. 8a), they spread during the second period when water levels were supposedly low (Fig. 8b). For this second period we assume that broadleaved tree stands expanded during dry periods with lower water table on deep and fertile soils along the river. Later, around 6100 cal yr BP (4150 BCE), the extent of riparian forests decreased again when the water table rose, as inferred from the decline of *Nymphaea* and other aquatic plants as well as gyttja formation. The decline of broadleaved trees and *Nymphaea* was also noticed by Kremenetski (1995, 2003). However, Kremenetski dated it notably later, around 4750 cal yr BP (2800 BCE; Kremenetski, 2003). We propose two possible explanations for this discrepancy: (i) large chronological issues related to bulk dating in Kremenetski (1995), and (ii) spatially variable pollen representation of sparse and relatively small forest stands (the coring spots of the two studies differ by about 4 km).

Unfortunately, to our knowledge, no continuous, decadal-scale moisture reconstruction is available for southern Ukraine and the adjacent steppe areas to test our interpretation on vegetation dynamics in response to past drought and flood disturbance. However, in regard to the general course of climate, some Central and Western Mediterranean records suggest rather dry conditions prior to 7000–6000 cal yr BP (5050–4050 BCE) and moisture peaking at 7000–6000 cal yr BP (Reed et al., 2001; Carrión, 2002; Tinner et al., 2009), while some Eastern Mediterranean records suggest the contrary, with rather moist conditions prevailing between 8500 cal yr BP (6550 BCE) and 6100 cal yr BP (4150 BCE), which were then followed by a trend to drier conditions (Göktürk et al., 2011; Finné et al., 2019). Whereas we try to capture short-term disturbance events, those moisture reconstructions represent conditions over large temporal scales, are rather far away from our study area and span thousands of kilometres, which might explain the discrepancies. However, when considering solely the $\delta^{13}\text{C}$ record from Sofular cave on the southern Black Sea coast, a major increase in effective moisture (spring–summer–fall) occurred around 5900 cal yr BP (3950 BCE; Fleitmann et al., 2009; Göktürk et al., 2011). Taking chronological uncertainties into account, this increase in effective moisture might be contemporaneous with the major change in vegetation at Kardashynskiy around 6100 cal yr BP (4150 BCE; Fig. 9), supporting our hypothesis that an increase in the water table caused the decline of the broadleaved trees.

Other factors than water table oscillations that might cause vegetation changes such as temperature, fire (human induced or natural) and land use cannot sufficiently explain the patterns observed. Even though there was a general cooling trend after the Holocene Thermal Maximum (c. 10,000–5000 cal yr BP) in Europe and the Northern Hemisphere (Lang et al., 2023), it cannot account for the decline of all broadleaved trees, including e.g. *Betula*, a boreal and thus cold-adapted tree. Furthermore, based on our analysis, fire does not appear as a main driver of environmental change at Kardashynskiy either (see cross-correlation results). Lastly, palynological indicators of land use are virtually absent for this period. In agreement, archaeological evidence suggests a major decrease in population density in the Ukrainian steppe at 4200–3800 BCE (6150–5750 cal yr BP; Kotova and Makhortkyh, 2010; Kotova, 2013; Kotova et al., 2017a, 2017b). However, huge sedentary agricultural settlements, the so-called mega-settlements of the Cucuteni-Trypillian culture, were thriving only c. 300 km northwards of our site in today's forest-steppe ecotone, e.g. at Nebelivka (Albert et al., 2020; Kiosak et al., 2021), suggesting that environmental conditions including water supply were favourable for this Neolithic culture.

Taken together, the Dnipro estuary was and still is a highly dynamic setting and local, short-term processes in the mire as well as drought and flood spells in the river basin as well as the source area of the river likely played an important role in shaping the local vegetation but cannot be captured by long-term climate reconstructions from elsewhere. Our

continuous high-resolution evidence from HR1 and HR2 underscores for the first time the relevance of water-table oscillations and the associated drought and/or flood disturbance for vegetation dynamics. The transient expansions and declines of pine stands and *Artemisia* suggest that moisture changes also affected upland vegetation on the sandy terraces and in the adjacent steppe. The decline of broadleaved trees such as *Ulmus*, *Quercus* and *Corylus* may have resulted from both, water table changes and/or human impact, however, more archaeological and highly resolved palaeoclimatic evidence is needed to better assess such vegetation shifts.

5.4. Land use and climate impacts during the Bronze Age

The linkage between pollen indicative of arable farming (e.g. *Cerealia* t., *Triticum* t.) and microscopic charcoal (Figs. 3, 9) suggests that fire activity between 4600 cal yr BP (2650 BCE) and 3300 cal yr BP (1350 BCE) was related to land use practices. Moreover, the intensification of land use inferred from pollen matches very well the archaeological evidence. The beginning of the Bronze Age was marked by the spread of the 'Yamna' (Pit Grave) cultural community in the Lower Dnipro (c. 5250–4550 cal yr BP; 3300–2600 BCE). Despite being perceived as mobile herder groups, the Yamna also practiced arable farming at some sites (Pashkevych, 2012). While the Yamna culture around the Dnipro estuary was characterised by moderate agricultural activities according to our data, the later Catacomb culture (4550–4250 cal yr BP; 2600–2300 BCE) shows a strong increase in land use (Fig. 9). Regionally, evidence of arable farming in the form of a bag of spikelets from *Triticum dicoccum* and *T. monococcum* attributed to the Catacomb culture has been found on Crimea (Pashkevich, 2000; Endo et al., 2022).

Around 4100 cal yr BP (2150 BCE) pine collapsed and *Chenopodiaceae* and *Poaceae* expanded massively, inducing a major vegetation shift which might have been caused by increased dryness. This hypothesis is supported by the lithology, showing a transition from calcareous to peaty gyttja, which suggests a shift from lake to shallow lake or peatland conditions, as well as the expansion of *Pediastrum* and *Botryococcus*. Chronologically this period falls within the '4.2 ka event'. This climatic event has been widely reported across the Northern Hemisphere, although it does not leave a clear imprint in many records and its spatial and temporal extent is a matter of debate (e.g. Göktürk et al., 2011; Railsback et al., 2018; Ön et al., 2021 and references therein). In our study area, soil evidence from Crimea (Cordova and Lehman, 2005) and the Southern Bug (Lisetskii et al., 2016) suggests an arid phase lasting for several centuries around 4200 cal yr BP, which is in best agreement with the original description of the '4.2 ka event' as a time of increased aridity (Weiss et al., 1993). However, 4250 cal yr BP (2300 BCE) was also the onset of the Babyne culture, an economy mostly based on herding, with arable farming playing a secondary role (Lytyvynenko, 2018), lasting until c. 3650 cal yr BP (1700 BCE). Therefore, the *Pinus* decline may have been further reinforced by agricultural practices of the Babyne culture, as indicated by the presence of crops and weeds (e.g. *Triticum* t., *Avena* t., *Plantago major-media* t., *Polygonum aviculare* t., Fig. 3).

Between 3500 and 3200 cal yr BP (1550 and 1250 BCE), Bronze Age farming reached its highest development (e.g. *Cerealia* t., *Triticum* t., *Plantago lanceolata* t., *P. major-media* t., Fig. 9) during the time of the Sabatynivka Culture (3550–3150 cal yr BP; 1600–1200 BCE). The Sabatynivka Culture inhabited large, long-term settlements with stone, clay and wooden architecture, and people were mostly herders but also practiced arable farming. These are the most numerous archaeological sites so far found in the steppe region of the Dnipro (Gerškovič, 1999). For instance, the Novokyivka site, located 50 km away from Kardashynskiy, has provided much evidence of crop farming (Endo et al., 2022). In the final period of the Bronze Age, human impact decreased and pine stands recovered around Kardashynskiy, when the Bilozerka Culture (3150–2950 cal yr BP; 1200–1000 BCE) settled in the area. An approximately tenfold decrease in the number of settlements found in

the southern part of the steppe zone, the degradation of the construction industry, the reduction in bronze casting production and the revival of the flint industry indicate that the Bilozerka economy suffered serious crises (Makhortykh, 2012).

5.5. Vegetation changes from the Iron Age to the present

The high abundance of pine stands during the early Iron Age, starting around 2950 cal yr BP (1000 BCE), together with low agricultural activities and low fire activity suggests that the nomadic to semi-nomadic Cimmerians, which inhabited the steppe during this time, did not have a huge impact on vegetation around Kardashynskiy (Makhortykh, 2005). The final population decline of pine stands occurred around 2800–2400 cal yr BP (850–450 BCE) and roughly coincided with cold events reported for this period (e.g. van Geel et al., 1996; Haas et al., 1998; Maise, 1998). These cooling events may have affected agriculture, as shown by rather low pollen abundances of crops (Fig. 9). Herodotus from Halicarnassus described the Black Sea steppe and mentions forests ‘*Hylaea*’ east of the Borysthenes (=Dnipro) in the mid-5th century BCE. He reported arable farmland and lush pastures for grazing cattle (Historia IV, see also Paroń, 2021), which is in agreement with the presence of tree stands and open land as indicated by the pollen data.

After 2400 cal yr BP (450 BCE), human impact, as inferred from the increase of indicators of arable farming (e.g. *Cerealia* t., *Avena* t., *Triticum* t., *Plantago lanceolata* t., Fig. 9), probably enhanced the further decline of pine forests and led to its final demise after the Early Middle Ages at c. 700 CE. Indeed, land use surpassed Bronze Age and Iron Age levels during the past c. 800 years. The association of land use and fire proxies shows that most fires were still of human origin (Fig. 9). Palynological richness also reached its highest values during the past c. 800 years (Fig. 4). Although the Late Holocene upward trend is less pronounced than at other sites in Southern and Eastern Europe (e.g. Colombaroli and Tinner, 2013; Schwörer et al., 2021), it likely reveals beneficial effects of historical land use on diversity. Less pronounced diversity increases during the past four millennia might result from only marginal increases in habitat diversity (which is in turn associated with an increase in species diversity). Indeed, the landscape at Kardashynskiy was always dominated by grassland for the past c. 8300 years which strongly contrasts with most other European records, where the landscape was forested prior to the introduction of agriculture (Lang, 1994; Lang et al., 2023). Furthermore, in the steppe most biodiversity comes from herbs, which are often badly resolved in pollen taxonomy and might lead to large fluctuations that blur the underlying pattern.

The drastic drop in cultural indicators during the past c. 400 years might reflect cultural crises related to the wars between the regional empires such as the Ottoman, the Russian and others. Alternatively, it could be a taphonomic artefact associated with a substantial reduction of the pollen catchment caused by the complete disappearance of an open water body at the coring location, as evidenced by the sedimentological change from peaty gyttja to decomposed peat and the modern conditions comprising peat exploitation and peatland drainage.

Today, most of the Pontic steppe has been converted to cropland and very few relict enclaves of this biodiversity-rich ecosystem persist outside nature reserves (Wesche et al., 2016). The Ukrainian steppes were almost completely tilled and destroyed during the Soviet era. Despite large areas becoming fallow land following the collapse of the Soviet Union and the establishment of secondary steppe, only about 3% of the natural and semi-natural steppes of Ukraine remain nowadays (Korotchenko and Peregrym, 2012). Ongoing climate change poses further threat to the remnants of this once extensive biome (Liu et al., 2021).

6. Conclusions

Our reinvestigation of Kardashynskiy mire provides the first vegetation history record for the steppe region of southern Ukraine with two

contiguous high-resolution pollen sections and a robust chronology. Furthermore, our focus on human and natural disturbance, including proxies for arable farming, grazing, fire history and drought impacts is novel for the region. The results show a complex interplay between local wetland vegetation and regional steppe. Steppe communities dominated around Kardashynskiy mire for the past c. 8300 years, but their composition showed considerable variability over time. Owing to the two high-resolution sections, we could show that drought disturbance likely induced repeated reductions of pine stands and expansions of steppe vegetation. Earliest agriculture might have started around 7900 cal yr BP (5950 BCE), but only increased significantly from the Bronze Age onwards. Ultimately, human impact likely led to the demise of the pine stands growing on the sandy terraces of the Dnipro. Overall, both climate and humans seem to have contributed significantly to define the extant landscape. In order to make more reliable inferences about land use, cultural indicators should however be calibrated for the steppe region. Well dated, pre-Neolithic pollen studies from the steppe are still needed, to resolve whether or not the cultural indicators usually used for central and northern Europe are truly adventive and not native to the Pontic steppe. High-resolution multi-proxy studies (especially including climate reconstructions) and interdisciplinary studies are urgently needed to properly disentangle climate from human impact.

Author contributions

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Erika Gobet: palynological and macrofossil analysis, supervision, writing – review and editing.

Dmytro Kiosak: funding acquisition, writing – review and editing.

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Sergey Makhortykh: funding acquisition, writing – review and editing.

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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 pollen and charcoal datasets are available from the Alpine Palynological database (ALPADABA) via Neotoma (charcoal: <https://doi.org/10.21233/7PPW-2860>, pollen: <https://doi.org/10.21233/Y97S-ZR89>).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2023.105019>.

References

- Afonin, A.N., Luneva, N.N., Fedorova, Y.A., Kletchkovskiy, Y.E., Chebanovskaya, A.F., 2018. History of introduction and distribution of common ragweed (*Ambrosia artemisiifolia* L.) in the European part of the Russian Federation and in the Ukraine. *EPO Bull.* 48, 266–273. <https://doi.org/10.1111/epp.12484>.
- Aksu, A.E., Hiscott, R.N., 2022. Persistent Holocene outflow from the Black Sea to the eastern Mediterranean Sea still contradicts the Noah's Flood Hypothesis: a review of 1997–2021 evidence and a regional paleoceanographic synthesis for the latest Pleistocene–Holocene. *Earth Sci. Rev.* 227, 103960 <https://doi.org/10.1016/j.earscirev.2022.103960>.
- Albert, B., Innes, J., Kremenskiy, K., Millard, A.R., Gaydarska, B., Nebbia, M., Chapman, J., 2020. What was the ecological impact of a *Trypilia* megasite occupation? Multi-proxy palaeo-environmental investigations at Nebelivka, Ukraine. *Veg. Hist. Archaeobotany* 29, 15–34. <https://doi.org/10.1007/s00334-019-00730-9>.
- Alley, R.B., Mayewski, P.A., Sowers, T., Stuiver, M., Taylor, K.C., Clark, P.U., 1997. Holocene climatic instability: a prominent, widespread event 8200 yr ago. *Geology* 25, 483–486.
- Ankindinova, O., Hiscott, R.N., Aksu, A.E., Grimes, V., 2019. High-resolution Sr-isotopic evolution of Black Sea water during the Holocene: implications for reconnection with the global ocean. *Mar. Geol.* 407, 213–228. <https://doi.org/10.1016/j.margeo.2018.11.004>.
- Artushenko, A.T., Baczurina, A.F., 1958. Novi dannii po stratygrafii ta sporo-pylkovym doslidzhenniam Kardashynskogo torfovyscha [New data on the stratigraphy and spore and pollen investigation of the Kardashinka peat bog]. *Ukrainiskiy botanichnyi zhurnal* 15, 60–69.
- Bahrenberg, G., Giese, E., Nipper, J., 1992. *Statistische Methoden in der Geographie: Band 2. Multivariate Statistik*, Teubner, Stuttgart.
- Behre, K.-E., 1981. The interpretation of anthropogenic indicators in pollen diagrams. *Pollen Spores* 23, 225–245.
- Behre, K.-E., van der Knaap, W.O., Lang, G., Morales-Molino, C., Tinner, W., 2023. Anthropogenic changes to the vegetation. In: Lang, G., Ammann, B., Behre, K.-E., Tinner, W. (Eds.), *Quaternary Vegetation Dynamics of Europe*. Haupt Verlag, Bern, pp. 363–408.
- Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. *New Phytol.* 132, 155–170. <https://doi.org/10.1111/j.1469-8137.1996.tb04521.x>.
- Beug, H.-J., 2004. *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete*. Verlag Dr. Friedrich Pfeil, München.
- Bezusko, L.G., 2010. New palynological characteristics of the Holocene deposits of the section Troizkoye (Mykolayiv region, Ukraine). *Ukrain. Bot. J.* 67, 560–576.
- Bezusko, L.G., Bezusko, A.G., 2000. Do pytanii pro poshyrennia lisiv u Nyzhniomy Podniproviu v pizniomu holotseni (za palinologichnymy dannymi) [To the question of forest spreading on the territory of low Pridniprovia in the Late Holocene (on the palynological data)]. *Naukovi zapysky NaUKMA. Biologiya ta ekologiya* 18, 3–11.
- Birks, H.J.B., 1997. Reconstructing environmental impacts of fire from the Holocene sedimentary record. In: Clark, J.S., Cachier, H., Goldammer, J.G., Stocks, B. (Eds.), *Sediment Records of Biomass Burning and Global Change, NATO ASI Series*, vol. 51. Springer, Berlin, pp. 295–311.
- Birks, H.J.B., Gordon, A.D., 1985. *Numerical Methods in Quaternary Pollen Analysis*. Academic Press, London.
- Birks, H.J.B., Line, J.M., 1992. The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. *The Holocene* 2, 1–10.
- Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Anal.* 6, 457–474. <https://doi.org/10.1214/11-BA618>.
- Bohn, U., Gollub, G., Hettwer, C., Neuhäuslová, Z., Raus, T., Schlüter, H., Weber, H., 2003. *Map of the Natural Vegetation of Europe*. Scale 1:2 500 000. Münster, Landwirtschaftsverlag.
- Bojniński, V., Fargašová, A., 2007. *Atlas of Seeds and Fruits of Central and East-European Flora: The Carpathian Mountains Region*. Springer, Dordrecht.
- Bujanov, P.M., 2014. Ecological problems of sandy area afforestation in the south of Ukraine. *Ecol. Neospherol.* 25, 92–100. <https://doi.org/10.15421/031409>.
- Cappers, R.T.J., Bekker, R.M., Jans, J.E.A., 2006. *Digital Seed Atlas of the Netherlands*. Barkhuis Publishing, Groningen.
- Carrion, J.S., 2002. Patterns and processes of Late Quaternary environmental change in a montane region of southwestern Europe. *Quatern. Sci. Rev.* 21, 2047–2066.
- Charles, D., 2010. Renewing the Post-Soviet Steppe. *Science* 328, 1225. <https://doi.org/10.1126/science.328.5983.1225>.
- Colombaroli, D., Tinner, W., 2013. Determining the long-term changes in biodiversity and provisioning services along a transect from Central Europe to the Mediterranean. *The Holocene* 23, 1625–1634. <https://doi.org/10.1177/0959683613496290>.
- Conedera, M., Tinner, W., Cramer, S., Torriani, D., Herold, A., 2006. Taxon-related pollen source areas for lake basins in the southern Alps: an empirical approach. *Veg. Hist. Archaeobotany* 15, 263–272. <https://doi.org/10.1007/s00334-006-0056-8>.
- Cook, C.D.K., 1990. *Aquatic Plant Book*. SPD Academic Publishing, The Hague.
- Cordova, C.E., Lehman, P.H., 2005. Holocene environmental change in southwestern Crimea (Ukraine) in pollen and soil records. *The Holocene* 15, 263–277. <https://doi.org/10.1191/0959683605hl791rp>.
- Deza-Araujo, M., Morales-Molino, C., Tinner, W., Henne, P.D., Heitz, C., Pezzatti, G.B., Hafner, A., Conedera, M., 2020. A critical assessment of human-impact indices based on anthropogenic pollen indicators. *Quat. Sci. Rev.* 236 <https://doi.org/10.1016/j.quascirev.2020.106291>.
- Deza-Araujo, M., Morales-Molino, C., Conedera, M., Henne, P.D., Krebs, P., Hinz, M., Heitz, C., Hafner, A., Tinner, W., 2022. A new indicator approach to reconstruct agricultural land use in Europe from sedimentary pollen assemblages. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 599 <https://doi.org/10.1016/j.palaeo.2022.111051>.
- El-Moslimany, A.P., 1990. Ecological significance of common nonaraboreal pollen: examples from drylands of the Middle East. *Rev. Palaeobot. Palynol.* 64, 343–350.
- Endo, E., Nasu, H., Haskevych, D., Gershkovych, Y., Videiko, M., Yanevich, O., 2022. Re-identification of plant impressions on prehistoric pottery from Ukraine. *J. Archaeol. Sci. Rep.* 42, 103364 <https://doi.org/10.1016/j.jasrep.2022.103364>.
- Feurdean, A., Florescu, G., Vannièrè, B., Tanțău, I., O'Hara, R.B., Pfeiffer, M., Hutchinson, S.M., Galka, M., Moskal-del Hoyo, M., Hickler, T., 2017. Fire has been an important driver of forest dynamics in the Carpathian Mountains during the Holocene. *For. Ecol. Manage.* 389, 15–26. <https://doi.org/10.1016/j.foreco.2016.11.046>.
- Feurdean, A., Grindean, R., Florescu, G., Tantău, I., Niedermeyer, E.M., Diaconu, A.C., Hutchinson, S.M., Nielsen, A.B., Sava, T., Panait, A., Braun, M., Hickler, T., 2021. The transformation of the forest steppe in the lower Danube Plain of southeastern Europe: 6000 years of vegetation and land use dynamics. *Biogeosciences* 18, 1081–1103. <https://doi.org/10.5194/bg-18-1081-2021>.
- Finné, M., Woodbridge, J., Labuhn, I., Roberts, C.N., 2019. Holocene hydro-climatic variability in the Mediterranean: a synthetic multi-proxy reconstruction. *The Holocene* 29, 847–863. <https://doi.org/10.1177/0959683619826634>.
- Finsinger, W., Tinner, W., 2005. Minimum count sums for charcoal-concentration estimates in pollen slides: accuracy and potential errors. *The Holocene* 15, 293–297.
- Fleitmann, D., Cheng, H., Badertscher, S., Edwards, R.L., Mudelsee, M., Gökürk, O.M., Fankhauser, A., Pickering, R., Raible, C.C., Matter, A., Kramers, J., Tüysüz, O., 2009. Timing and climatic impact of Greenland interstadials recorded in stalagmites from northern Turkey. *Geophys. Res. Lett.* 36 <https://doi.org/10.1029/2009GL040050>.
- Gassner, S., Gobet, E., Schwörer, C., van Leeuwen, J., Vogel, H., Giagkoulis, T., Makri, S., Grosjean, M., Panajiotidis, S., Hafner, A., Tinner, W., 2020. 20,000 years of interactions between climate, vegetation and land use in Northern Greece. *Veg. Hist. Archaeobotany* 29, 75–90. <https://doi.org/10.1007/s00334-019-00734-5>.
- Gershkovych, Y.P., Gerasyenko, N.P., 2021. Agriculture in the steppe on the left bank of the Dniro in the middle of the IInd millennium BC. In: *Archaeology and Early History of Ukraine*, 39, pp. 318–329.
- Gerškovič, J.P., 1999. *Studien zur spätbronzezeitlichen Sabatinovka-Kultur am unteren Dnepr und an der Westküste des Azov'schen Meeres*. Verlag Marie Leidorf GmbH.
- Gobet, E., Schwörer, C., van Leeuwen, J.F.N., Wahab, S.A., Nielsen, E.H., Kotova, N., Makhortykh, S., Kiosak, D., Tinner, W., 2017. Vegetation shifts at the monumental Ukrainian site of Kamyana Mohyla during the Neolithisation period. In: *Makhortykh, S., de Capitani, A. (Eds.), Archaeology and Palaeoecology of the Ukrainian Steppe*, pp. 51–60. Kyiv.
- Gökürk, O.M., Fleitmann, D., Badertscher, S., Cheng, H., Edwards, R.L., Leuenberger, M., Fankhauser, A., Tüysüz, O., Kramers, J., 2011. Climate on the southern Black Sea coast during the Holocene: implications from the Sofular Cave record. *Quat. Sci. Rev.* 30, 2433–2445. <https://doi.org/10.1016/j.quascirev.2011.05.007>.
- Govedarica, B., Manzura, I., 2020. Die Bolgrad-Aldeni-Kultur im nordwestlichen Schwarzmeergebiet: zur Frage einer balkanischen Steppenkolonisation in der Mitte des 5. Jt. v. Chr. In: *Bodi, G., Govedarica, B., Hansen, S., Rubel, A., Ursu, C.-E. (Eds.), Die Cucuteni-Kultur und ihre südlichen Nachbarn: Forschungsgeschichte - Kulturbeziehungen - offene Fragen*. Verlag Karl A. Romstorfer, Suceava, pp. 113–129.
- Grimm, E.C., 1991–2020. *Tilia*. Springfield Illinois State Museum, Research and Collection Center, Springfield, MO.
- Haas, J.N., Richoz, I., Tinner, W., Wick, L., 1998. Synchronous holocene climatic oscillations recorded on the Swiss Plateau and at timberline in the Alps. *The Holocene* 8, 301–309. <https://doi.org/10.1191/095968398675491173>.
- Heegaard, E., Birks, H.J.B., Telford, R.J., 2005. Relationships between calibrated ages and depth in stratigraphical sequences: an estimation procedure by mixed-effect regression. *The Holocene* 15, 612–618. <https://doi.org/10.1191/0959683605hl836rr>.

- Heiri, O., Tinner, W., Lotter, A.F., 2004. Evidence for cooler European summers during periods of changing meltwater flux to the North Atlantic. *PNAS* 101, 15285–15288. <https://doi.org/10.1073/pnas.0406594101>.
- Hofmanová, Z., Kreutzer, S., Hellenthal, G., Sell, C., Diekmann, Y., Díez-Del-Molino, D., van Dorp, L., López, S., Kousathanas, A., Link, V., Kirsanow, K., Cassidy, L.M., Martiniano, R., Strobel, M., Scheu, A., Kotsakis, K., Halstead, P., Triantaphyllou, S., Kyparissi-Apostolika, N., Urem-Kotsou, D., Ziota, C., Adaktylou, F., Gopalan, S., Bobo, D.M., Winkelbach, L., Blöcher, J., Unterländer, M., Leuenberger, C., Çilingiroğlu, Ç., Horejs, B., Gerritsen, F., Shennan, S.J., Bradley, D.G., Currat, M., Veeramah, K.R., Wegmann, D., Thomas, M.G., Papageorgiou, C., Burger, J., 2016. Early farmers from across Europe directly descended from Neolithic Aegeans. *PNAS* 113, 6886–6891. <https://doi.org/10.1073/pnas.1523951113>.
- Huang, Y., Zheng, Y., Heng, P., Giosan, L., Coolen, M.J.L., 2021. Black Sea paleosalinity evolution since the last deglaciation reconstructed from alkenone-inferred Isochrysidale diversity. *Earth Planet. Sci. Lett.* 564, 116881 <https://doi.org/10.1016/j.epsl.2021.116881>.
- Hurlbert, S.H., 1971. The nonconcept of species diversity : a critique and alternative parameters. *Ecology* 52, 577–586.
- Jankovská, V., Komárek, J., 2000. Indicative value of *Pediastrum* and other coccal green algae in Palaeoecology. *Folia Geobot.* 35, 59–82. <https://doi.org/10.1007/BF02803087>.
- Kiosak, D., Kotova, N., Tinner, W., Szidat, S., Nielsen, E.H., Brugger, S.O., de Capitani, A., Gobet, E., Makhortkyh, S., 2021. The last hunter-gatherers and early farmers of the middle Southern Buh river valley (central Ukraine) in VIII-V mill. BC. *Radiocarbon* 63, 121–137. <https://doi.org/10.1017/RDC.2020.120>.
- Kiosak, D., Kotova, N., Demchenko, O., Bardeckiy, A., Werra, D.H., 2023. Verifying the chronology of Ukrainian Neolithic. *Præhistorische Zeitschrift*. <https://doi.org/10.1515/pz-2022-2058>.
- Korotchenko, I., Peregrym, M., 2012. Ukrainian steppes in the past, at present and in the future. In: Werger, M.J.A., van Staaldunin, M.A. (Eds.), *Eurasian Steppes. Ecological Problems and Livelihoods in a Changing World*. Springer, pp. 173–196.
- Kotova, N.S., 2003. Neolithization in Ukraine. In: *BAR International Series* 1109, Oxford.
- Kotova, N.S., 2008. Early Eneolithic in the Pontic Steppes. In: *BAR International Series* 1735, Oxford.
- Kotova, N., 2013. Dereivka Culture and Monuments of the Low Michajlovka Type. Kharkiv.
- Kotova, N., 2018. Revisiting the Neolithic chronology of the Dnieper steppe region with consideration of a reservoir effect for human skeletal material. *Sprawozdania Archeologiczne* 70, 47–66. <https://doi.org/10.23858/SA70.2018.003>.
- Kotova, N., Makhortkyh, S., 2010. Human adaptation to past climate changes in the northern Pontic steppe. *Quat. Int.* 220, 88–94. <https://doi.org/10.1016/j.quaint.2009.09.026>.
- Kotova, N.S., Pashkevich, G.A., 2003. The catalog of imprints of cultivated plants on ceramics of the Neolithic cultures of Ukraine. In: *Neolithisation of Ukraine. BAR International Series* 1109, Oxford, pp. 142–148.
- Kotova, N., Anthony, D., Brown, D., Degermendzhy, S., Crabtree, P., 2017a. Excavation at the Razdolnoe site on the Kalmius River in 2010. In: Makhortkyh, S., de Capitani, A. (Eds.), *Archaeology and Palaeoecology of the Ukrainian Steppe*, pp. 90–114. Kyiv.
- Kotova, N., Tuboltsev, O., Kiosak, D., Spitsyna, L., Makhortkyh, S., Tinner, W., Nielsen, E. H., Dzhoz, V., 2017b. Preliminary results of excavations at the multilayer Kamyana Mohyla 1 site. In: Makhortkyh, S., de Capitani, A. (Eds.), *Archaeology and Palaeoecology of the Ukrainian Steppe*, pp. 28–50. Kyiv.
- Kotova, N., Demchenko, O., Kiosak, D., 2021. Innovations of the beginning of the sixth millennium BC in the Northern Pontic Steppe. *Open Archaeol.* 7, 1529–1549. <https://doi.org/10.1515/opar-2020-0185>.
- Kozłowski, J.K., 2005. The importance of the Aegean Basin for the Neolithization of South-Eastern Europe. *J. Israel Prehist. Soc.* 409–424.
- Kremenetski, C.V., 1995. Holocene vegetation and climate history of southwestern Ukraine. *Rev. Palaeobot. Palynol.* 85, 289–301. [https://doi.org/10.1016/0034-6667\(94\)00123-2](https://doi.org/10.1016/0034-6667(94)00123-2).
- Kremenetski, K.V., 2003. Steppe and forest-steppe belt of Eurasia: Holocene environmental history. In: Scarre, C., Kemp, D.A., Boyle, K. (Eds.), *Prehistoric Steppe Adaptation and the Horse*. McDonald Institute of Archaeological Research, pp. 11–27.
- Kremenetski, C.V., Chichagova, O.A., Shishlina, N.I., 1999. Palaeoecological evidence for Holocene vegetation, climate and land-use change in the low Don basin and Kalmuk area, southern Russia. *Veg. Hist. Archaeobotany* 8, 233–246. <https://doi.org/10.1007/s003340200020>.
- Lang, G., 1994. *Quartäre Vegetationsgeschichte Europas: Methoden und Ergebnisse*. Gustav Fischer Verlag, Jena.
- Lang, G., Ammann, B., Behre, K.-E., Tinner, W. (Eds.), 2023. *Quaternary Vegetation Dynamics of Europe*, 1st ed. Haupt Verlag, Bern. <https://boris.unibe.ch/185253/>
- Lawrenko, E.M., Iswekova, Z.T., 1932. Do vyvchennia landschafitiv i stratygrafii Kardashynskogo bolota v mezhakh nyzu Dnipro [To the investigation of landscapes and stratigraphy of Kardashynskiy mire on the Lower Dnieper]. *Chetvertynnyi period* 2, 3–14.
- Lemmen, C., Gronenborn, D., Wirtz, K.W., 2011. A simulation of the Neolithic transition in Western Eurasia. *J. Archaeol. Sci.* 38, 3459–3470. <https://doi.org/10.1016/j.jas.2011.08.008>.
- Lisetskii, F.N., Matsibora, A.V., Pichura, V.I., 2016. Geodatabase of buried soils for reconstruction of palaeoecologic conditions in the steppe zone of East European Plain. *Res. J. Pharm., Biol. Chem. Sci.* 7, 1637–1643.
- Liu, X., Feng, S., Liu, H., Ji, J., 2021. Patterns and determinants of woody encroachment in the eastern Eurasian steppe. *Land Degrad. Dev.* 32, 3536–3549. <https://doi.org/10.1002/ldr.3938>.
- Lukanina, E., Shumilovskikh, L., Novenko, E., 2022. Vegetation and fire history of the East-European forest-steppe over the last 14,800 years: a case study from Zamostye, Kursk region, Russia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 605, 111218 <https://doi.org/10.1016/j.palaeo.2022.111218>.
- Lukanina, E., Lyubichev, M., Schneeweiss, J., Schultze, E., Myzgin, K., Shumilovskikh, L., 2023. Did Holocene climate drive subsistence economies in the East-European forest-steppe? Case study Omelchenki, Kharkiv region, Ukraine. *Quatern. Sci. Rev.* 305, 108004 <https://doi.org/10.1016/j.quascirev.2023.108004>.
- Lykhovyd, P., 2021. Study of climate impact on vegetation cover in Kherson Oblast (Ukraine) using normalized difference and enhanced vegetation indices. *J. Ecol. Eng.* 22, 126–135. <https://doi.org/10.12911/22998993/137078>.
- Lytvynenko, R.A., 2018. The Dnieper River region as a crossroad of Babyne cultures area. *Arheologia* 14, 20–30.
- Maise, C., 1998. *Archäoklimatologie - Vom Einfluss nacheiszeitlicher Klimavariabilitäten in der Ur- und Frühgeschichte. Jahrbuch der Schweizerischen Gesellschaft für Ur- und Frühgeschichte* 81, 197–235.
- Makhortkyh, S.V., 2005. The Cimmerians in the North Pontic Region. Shlyakh, Kyiv.
- Makhortkyh, S.V., 2012. Final Bronze – Early Iron Age transition in the North Black Sea region. In: *Russian Archaeological Yearbook*, 2, pp. 276–286.
- Matishov, G.G., Novenko, E.Y., Dyuzhova, K.V., 2013. Palynological indication of anthropogenic changes in the Azov region vegetation based on the bottom sediments of the Sea of Azov. *Dokl. Earth Sci.* 450, 672–675. <https://doi.org/10.1134/S1028334X13060184>.
- Mercuri, A.M., Bandini Mazzanti, M., Florenzano, A., Montecchi, M.C., Rattighieri, E., Torri, P., 2013. Anthropogenic pollen indicators (API) from archaeological sites as local evidence of human-induced environments in the Italian Peninsula. *Ann. Bot.* 3, 143–153. <https://doi.org/10.4462/annbotm-10316>.
- Moore, P.D., Webb, J.A., Collinson, M.E., 1991. *Pollen Analysis*, 2nd ed. Blackwell Science, Oxford.
- Mosyakin, S.L., Fedoronchuk, M.M., 1999. *Vascular Plants of Ukraine: A Nomenclatural Checklist*. M. G. Kholodny Institute of Botany, Kiev.
- Motuzaitė-Matuzevičiūtė, G., Telizhenko, S., 2016. The first farmers of Ukraine: an archaeobotanical investigation and AMS dating of wheat grains from the Ratniv-2 site. *Archaeol. Lituanica* 17, 100–111. <https://doi.org/10.15388/archlit.2016.17.10685>.
- Motuzaitė-Matuzevičiūtė, G., Hunt, H.V., Jones, M.K., 2009. Multiple sources for Neolithic European agriculture: Geographical origins of early domesticates in Moldova and Ukraine. In: Dolukhanov, P.M., Sarson, G.R., Shukurov, A.M. (Eds.), *The East European Plain on the Eve of Agriculture*. Archaeopress, Oxford, UK, pp. 53–64.
- Nikitin, A.G., Ivanova, S., Culleton, B.J., Potekhina, I., Reich, D.E., n.d. New radiocarbon and stable isotope data from the Usovate culture site of Mayaki in Ukraine (October 3, 2022). Available at SSRN: <https://ssrn.com/abstract=4236123> or <https://doi.org/10.2139/ssrn.4236123>.
- Ön, Z.B., Greaves, A.M., Akçer-Ön, S., Özeren, M.S., 2021. A Bayesian test for the 4.2 ka BP abrupt climatic change event in southeast Europe and southwest Asia using structural time series analysis of paleoclimate data. *Clim. Change* 165, 1–19. <https://doi.org/10.1007/s10584-021-03010-6>.
- Paillisson, J.-M., Marion, L., 2006. Can small water level fluctuations affect the biomass of *Nymphaea alba* in large lakes? *Aquat. Bot.* 84, 259–266. <https://doi.org/10.1016/j.aquabot.2005.10.004>.
- Paquette, N., Gajewski, K., 2013. Climatic change causes abrupt changes in forest composition, inferred from a high-resolution pollen record, southwestern Quebec, Canada. *Quatern. Sci. Rev.* 75, 169–180. <https://doi.org/10.1016/j.quascirev.2013.06.007>.
- Paroň, A., 2021. Black Sea-Caspian steppe: natural conditions. In: *The Pechenegs: Nomads in the Political and Cultural Landscape of Medieval Europe*. <https://doi.org/10.1163/9789004441095>. Brill.
- Pashkevich, G.A., 2000. Zemledelie v stepi i lesostepi Vostochnoy Evropy v neolite-bronzovom veke (paleoetnobotanicheskiye vostoitelstva) [Agriculture in the Steppe and Forest Steppe zones of Eastern Europe in the Neolithic und Bronze Age (Palaeo-Ethnic and Botanic Evidence)]. *Stratum plus* 2, 404–418.
- Pashkevich, G., 2003. Palaeoethnobotanical evidence of agriculture in the steppe and the forest-steppe of East Europe in the Late Neolithic and Bronze Age. In: Levine, M., Renfrew, C., Boyle, K. (Eds.), *Prehistoric Steppe Adaptation and the Horse*. McDonald Institute for Archaeological Research, Cambridge, pp. 287–297.
- Pashkevych, G., 2012. Environment and economic activities of Neolithic and Bronze age populations of the Northern Pontic area. *Quat. Int.* 261, 176–182. <https://doi.org/10.1016/j.quaint.2011.01.024>.
- R Core Team, 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Railsback, L.B., Liang, F., Brook, G.A., Voarintsoa, N.R.G., Sletten, H.R., Marais, E., Hardt, B., Cheng, H., Edwards, R.L., 2018. The timing, two-pulsed nature, and variable climatic expression of the 4.2 ka event: a review and new high-resolution stalagmite data from Namibia. *Quatern. Sci. Rev.* 186, 78–90. <https://doi.org/10.1016/j.quascirev.2018.02.015>.
- Reed, J.M., Stevenson, A.C., Juggins, S., 2001. A multi-proxy record of Holocene climatic change in southwestern Spain: the Laguna de Medina, Cádiz. *The Holocene* 11, 707–719. <https://doi.org/10.1191/09596830195735>.
- Reille, M., 1999. *Pollen et spores d'Europe et d'Afrique du Nord*, 2nd ed. Laboratoire de Botanique 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-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., Talamo, S., 2020. The IntCal20 northern hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon* 62, 725–757. <https://doi.org/10.1017/RDC.2020.41>.
- Rey, F., Schwörer, C., Gobet, E., Colombaroli, D., van Leeuwen, J.F.N., Schleiss, S., Tinner, W., 2013. Climatic and human impacts on mountain vegetation at Launensee (Bernese Alps, Switzerland) during the last 14,000 years. *The Holocene* 23, 1415–1427. <https://doi.org/10.1177/0959683613489585>.
- Roberts, C.N., Woodbridge, J., Palmisano, A., Bevan, A., Fyfe, R., Shennan, S., 2019. Mediterranean landscape change during the Holocene: synthesis, comparison and regional trends in population, land cover and climate. *The Holocene* 29, 923–937. <https://doi.org/10.1177/0959683619826697>.
- Rohling, E.J., Pälike, H., 2005. Centennial-scale climate cooling with a sudden cold event around 8200 years ago. *Nature* 434, 975–979.
- Salavert, A., Gouriveau, E., Messenger, E., Lebreton, V., Kiosak, D., 2021. Multi-proxy archaeobotanical analysis from Mesolithic and Early Neolithic sites in south-west Ukraine. *Environ. Archaeol.* 26, 349–362. <https://doi.org/10.1080/14614103.2020.1746879>.
- Schwörer, C., Gobet, E., van Leeuwen, J.F.N., Bögli, S., Imboden, R., van der Knaap, W. O., Kotova, N., Makhortykh, S., Tinner, W., 2021. Holocene vegetation, fire and land use dynamics at Lake Svitvaz, an agriculturally marginal site in northwestern Ukraine. *Veg. Hist. Archaeobotany* 31, 155–170. <https://doi.org/10.1007/s00334-021-00844-z>.
- Senn, C., Tinner, W., Felde, V.A., Gobet, E., van Leeuwen, J.F.N., Morales-Molino, C., 2022. Modern pollen – vegetation – plant diversity relationships across large environmental gradients in northern Greece. *The Holocene* 32, 159–173. <https://doi.org/10.1177/09596836211060494>.
- Seppä, H., Birks, H.J.B., 2001. July mean temperature and annual precipitation trends during the Holocene in the Fennoscandian tree-line area: Pollen-based climate reconstructions. *The Holocene* 11, 527–539. <https://doi.org/10.1191/095968301680223486>.
- Shumilovskikh, L.S., Novenko, E., Giesecke, T., 2018. Long-term dynamics of the East European forest-steppe ecotone. *J. Veg. Sci.* 29, 416–426. <https://doi.org/10.1111/jvs.12585>.
- Stobbe, A., Gummior, M., Röpke, A., Schneider, H., 2015. Palynological and sedimentological evidence from the Trans-Ural steppe (Russia) and its palaeoecological implications for the sudden emergence of Bronze Age sedentarism. *Veg. Hist. Archaeobotany* 24, 393–412. <https://doi.org/10.1007/s00334-014-0500-0>.
- Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. *Pollen Spores* 13, 615–621.
- Sudnik-Wójcikowska, B., Moysiyanenko, I., Slim, P.A., Moraczewski, I.R., 2009. Impact of the invasive species *Elaeagnus angustifolia* L. on vegetation in pontic desert steppe zone (southern Ukraine). *Pol. J. Ecol.* 57, 269–281.
- Telegin, D., 1968. Dnipro-donetska kultura. Do istorii naseleння eposi neolitu ranniogo metalu pivdnia Shidnoi Evropi. *Naukova Dumka, Kyiv*.
- ter Braak, C.J.F., Šmilauer, P., 2017. *Canoco. Version 5.1. Biometris, Wageningen*.
- Tinner, W., Hu, F.S., 2003. Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. *The Holocene* 13, 499–505. <https://doi.org/10.1191/0959683603hl615rp>.
- Tinner, W., Hubschmid, P., Wehrli, M., Ammann, B., Conedera, M., 1999. Long-term forest fire ecology and dynamics in southern Switzerland. *J. Ecol.* 87, 273–289.
- Tinner, W., van Leeuwen, J.F.N., Colombaroli, D., Vescovi, E., van der Knaap, W.O., Henne, P.D., Pasta, S., D'Angelo, S., La Mantia, T., 2009. Holocene environmental and climatic changes at Gorgo Basso, a coastal lake in southern Sicily, Italy. *Quatern. Sci. Rev.* 28, 1498–1510. <https://doi.org/10.1016/j.quascirev.2009.02.001>.
- Tóth, M., Magyari, E.K., Buczkó, K., Braun, M., Panagiotopoulos, K., Heiri, O., 2015. Chironomid-inferred Holocene temperature changes in the South Carpathians (Romania). *The Holocene* 25, 569–582. <https://doi.org/10.1177/0959683614565953>.
- Troels-Smith, J., 1955. Characterization of unconsolidated sediments. *Danmarks Geologiske Undersøgelse IV. Række* 3, 1–73. <https://doi.org/10.34194/raekke4.v3.6989>.
- van Geel, B., Buurman, J., Waterbolk, H.T., 1996. Archaeological and palaeoecological indications of an abrupt climate change in the Netherlands, and evidence for climatological teleconnections around 2650 BP. *J. Quat. Sci.* 11, 451–460. [https://doi.org/10.1002/\(SICI\)1099-1417\(199611/12\)11:6<451::AID-JQS275>3.0.CO;2-9](https://doi.org/10.1002/(SICI)1099-1417(199611/12)11:6<451::AID-JQS275>3.0.CO;2-9).
- van Geel, B., Buurman, J., Brinkkemper, O., Schelvis, J., Aptroot, A., van Reenen, G., Hakbijl, T., 2003. Environmental reconstruction of a Roman Period settlement site in Uitgeest (the Netherlands), with special reference to coprophilous fungi. *J. Archaeol. Sci.* 30, 873–883. [https://doi.org/10.1016/S0305-4403\(02\)00265-0](https://doi.org/10.1016/S0305-4403(02)00265-0).
- von Grafenstein, U., Erlenkeuser, H., Müller, J., Jouzel, J., Johnsen, S., 1998. The cold event 8200 years ago documented in oxygen isotope records of precipitation in Europe and Greenland. *Climate Dynam.* 14, 73–81. <https://doi.org/10.1007/s003820050210>.
- Weiss, H., Courty, M.A., Wetterstrom, W., Guichard, F., Senior, L., Meadow, R., Curnow, A., 1993. The genesis and collapse of third millennium north Mesopotamian civilization. *Science* 261, 995–1004. <https://doi.org/10.1126/science.261.5124.995>.
- Wesche, K., Ambarli, D., Kamp, J., Török, P., Treiber, J., Dengler, J., 2016. The Palaeartic steppe biome: a new synthesis. *Biodivers. Conserv.* 25, 2197–2231. <https://doi.org/10.1007/s10531-016-1214-7>.
- Wolters, S., Bittmann, F., Kummer, V., 2005. The first subfossil records of *Urtica kioviensis* Rogow. and their consequences for palaeoecological interpretations. *Veg. Hist. Archaeobotany* 14, 518–527. <https://doi.org/10.1007/s00334-005-0084-9>.
- Yanchilina, A.G., Ryan, W.B.F., McManus, J.F., Dimitrov, P., Dimitrov, D., Slavova, K., Filipova-Marinova, M., 2017. Compilation of geophysical, geochronological, and geochemical evidence indicates a rapid Mediterranean-derived submergence of the Black Sea's shelf and subsequent substantial salinification in the early Holocene. *Mar. Geol.* 383, 14–34. <https://doi.org/10.1016/j.margeo.2016.11.001>.
- Yanko-Hombach, V., Mudie, P.J., Kadurin, S., Larchenkov, E., 2014. Holocene marine transgression in the Black Sea: New evidence from the northwestern Black Sea shelf. *Quat. Int.* 345, 100–118. <https://doi.org/10.1016/j.quaint.2013.07.027>.
- Zhao, Y., Miao, Y., Fang, Y., Li, Y., Lei, Y., Chen, X., Dong, W., An, C., 2021. Investigation of factors affecting surface pollen assemblages in the Balikun Basin, central Asia: implications for palaeoenvironmental reconstructions. *Ecol. Indic.* 123, 107332. <https://doi.org/10.1016/j.ecolind.2020.107332>.