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Late Quaternary Paleoecology and Environmental History of the Hortobágy, an Alkaline Steppe in Central Europe

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Abstract: Hungary's first national park was created in 1973 in the Hortobágy area to protect Europe's largest contiguous steppe area and its flora and fauna. The Hortobágy National Park—the Puszta was inscribed on the UNESCO World Heritage List as a cultural landscape in 1999. The park's outstanding importance is due to the predominantly non-arboreal steppe vegetation, home to a unique bird fauna, and alkaline and chernozem soils with a complex, mosaic-like spatial structure. In addition, the landscape of Hortobágy has a pastoral history stretching back thousands of years. Several hypotheses have been put forward that suggest that the alkaline soils and the habitats that cover them were formed as a result of human activities related to river regulation that began in the second half of the 19th century. However, paleoecological and paleobiological studies over the last 30–40 years have pointed to the natural origin of the alkaline steppes, dating back to the end of the Ice Age. For thousands of years, human activities, in particular, grazing by domestic animals, hardly influenced the natural evolution of the area. The drainage of marshy and flooded areas began in the 19th century, as well as the introduction of more and more intensive agriculture, had a significant impact on the landscape. This paper aims to describe the past natural development of this special alkaline steppe ecosystem, with particular reference to the impacts of past and present human activities, including conservation measures.

Keywords: undisturbed core sequence; Holocene and Pleistocene paleobotanical data; salty environment; alkalinization; Hortobágy National Park; Carpathian Basin

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1. Introduction

One of the most important cornerstones of the management system of an IUCN cate-gory II national park is the identification of its "original" vegetation, where original means its natural flora and fauna prior to significant changes caused by humans at the landscape level, such as cutting down and fragmenting continuous forests and turning natural grasslands to arable land. The first and still largest national park in Hungary was established 50 years ago in the eastern part of the country in the Great Hungarian Plain. Most of the park area is dominated by different kinds of alkaline soils covered by mosaics of grassland–wetland vegetation complexes (Video S1). According to the prevailing academic views at that time, there were two major human activities that significantly changed the original character of the flat landscape of the Hortobágy region. The first one was supposed to be, like in other lowland areas of Europe, the cutting down of forests to create pastures for grazing domestic animals, mostly cattle and sheep. In the first and still only monograph on Hortobágy National Park [1], the secondary character of the alkaline grassland–wetland mosaics was assumed to be a starting point for the future management of the grassland–wetland mosaics of the park. The potential vegetation map published in this monograph by Jakucs [2] suggested the dominance of hard and softwood gallery forests enclosing ancient alkaline grassland patches during the Early Neolithic period in the Hortobágy region. However, according to a recent critical source analysis, the presence of continuous forests in the Hortobágy region was assumed on the basis of a misinterpretation of a royal charter issued in the mid-15th century [3].

The second significant human intervention that was supposed to play an important role in the significant extension of alkaline areas was the landscape-scale change in the water regime of Hortobágy caused by major river regulation and drainage works started in the mid-19th century. This assumption is contradicted by descriptions of naturalists, such as Kitaibel [4] and Townson [5], indicating the presence of alkaline soils and vegetation in large areas before the start of hydroregulations in the Hortobágy region. These observations are also supported by the relevant map sheets and their description of the first military mapping survey of Hungary [6], undertaken in the second half of the 18th century. In addition, the presence of endemic plant species in the Hortobágy National Park, which occur exclusively in alkaline habitats, also indicates the much earlier appearance of such vegetation in the region. The most obvious representative of these species is *Plantago schwarzenbergiana* (Figure 1), which inhabits alkaline habitats in Hungary, Romania, and Ukraine and is abundant in the southwestern part of the Hortobágy National Park, called Kunkápolnás marsh, the study area of the present paper (Figure 2).

Figure 1. *Plantago schwarzenbergiana* in alkaline grassland (photo: Balázs Lesku).

The CORINE Land Cover GIS database of the European Union (2018, 100 m resolution) indicates the dominance of natural grasslands in Hortobágy National Park (Figure 2), and even with a relatively low resolution, places covered by the typical alkaline plant-less or single-plant association *Camphorosmetum annue* are distinguished as “sparsely vegetated areas”.

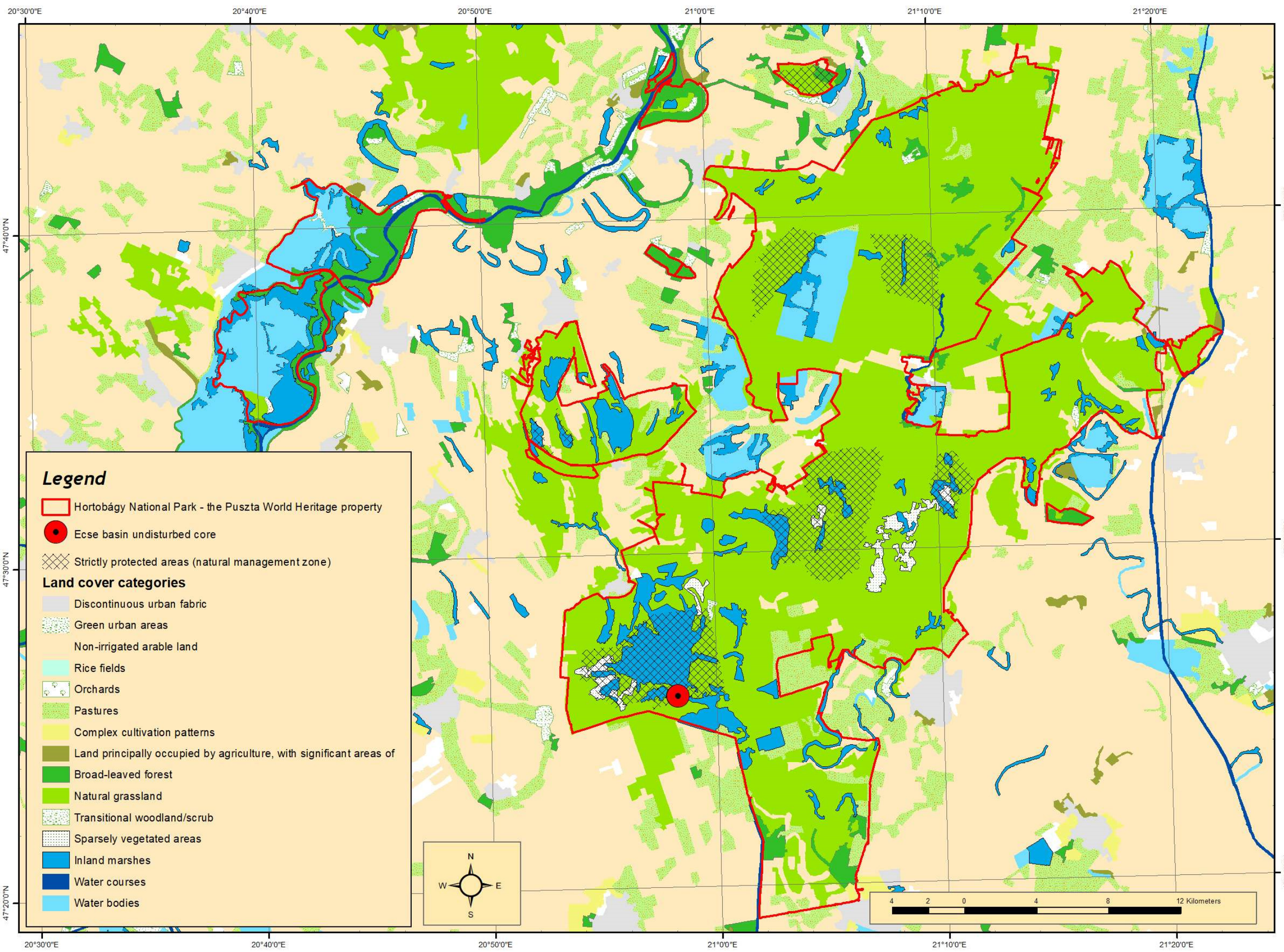

Figure 2. CORINE Land Cover map of the Hortobágy National Park—the Puszta World Heritage property (2018).

Archaeological data can also contribute to understanding the development of a landscape. However, the number of archaeological sites actually found within the boundaries of the Hortobágy landscape is rather low, most probably because the area was suitable for arable cultivation only in small, loess-covered patches [7], and the continuous vegetation cover, maintained by grazing land use over several millennia, prevented archaeological remains from being brought to the surface. In addition, there is no summary study systematically processing the basic data from the few archaeological sites actually located within the Hortobágy landscape. Paleolithic, Mesolithic material has not been found in the Hortobágy area, and the oldest Neolithic culture is the Alföld Linear Pottery [8] culture (5330–4940 BC: [9]), but its appearance is related mainly to the neighboring Tisza Valley [10,11]. Likewise, the known Late Neolithic archaeological sites are predominantly associated with the Tisza River valley and Pleistocene, loess-covered residual surfaces [12,13]. The most surveyed archaeological level is the Late Copper Age/Early Bronze Age—Pit Grave (Yamnaja) culture, which left visible traces on the surface in the form of burial mounds (kurgans) [14–17]. Several waves of this culture have been modeled in the Carpathian Basin [18], and data have been reported from radiocarbon analysis of kurgans in the wider region between 3300 and 2600 BC [19–21]. In fact, this can be considered the first productive farming culture to appear in the whole Hortobágy region [22]. Unfortunately, archaeological data from the later periods to the Hungarian Conquest (9–10th centuries AD) are scattered [23,24], and most of them are not actually located in the Hortobágy landscape but rather in the surrounding, cultivated areas. The absence of data on Iron Age cultures related to the large pastoral peoples of Eastern Europe (Mezőcsát culture, Scythians) is striking, as the data available so far [25,26] suggest that Hortobágy could have been an ideal habitat for these cultures. Small medieval villages (destroyed during the Ottoman conquest) are also prominent and easily recognizable archaeological objects [27–31], as they were located on or close to the surface.

According to an alternative view, the process of alkalinization dates back much further in natural landscape evolution, and the contemporary measures regulating the water regime could only extend the coverage of already-existing alkaline areas of primary, natural origin. First of all, the geological, hydrogeological, geomorphological, and climatic basis of the alkalinization process had to be clarified, which required the collection and analysis of all the data and information regarding the origin of sodium salts; the chemical processes and climatic characteristics responsible for their accumulation in the close to surface soil levels; and the role of the unique geomorphology in the development of the grassland–wetland mosaic landscape of the Hortobágy region [32]. Geological and paleontological evidence suggests that salt accumulation may have been caused by specific climatic and environmental conditions [33].

Although one of the most important questions about the historicity of salt accumulation near the surface and accumulating in soils is whether the environment adapted to excess sodium developed before or after hydroregulation; travelers' descriptions and sporadic research data from the second half of the 19th century before river regulation [3,34,35] indicate that salt accumulation in soils and a biota adapted to the saline environment had already developed in the northern part of the Transdanubian region before the hydroregulation measures [3,36–41]. One of the major problems in understanding the historical aspect of alkalinization in the Carpathian Basin is that the source of alkalinization has not been correctly identified by researchers. In addition, theoretical considerations based on these foundations have completely excluded the possibility of alkalinization during the glacial periods, stating that the environmental conditions in the Hungarian Lowlands were not favorable for the process [42]; hence, the presence of glacial alkaline deposits and signs of prehistoric alkalization were not assumed and searched for in the Great Hungarian Plain until 1988, when a multi-proxy paleoecological study of an undisturbed core series from the eastern margin of the Hortobágy, which was obtained via multiproxy paleoecology, succeeded in identifying an alkaline paleosol horizon dated between 30–40,000 years beneath the glacial loess deposits [43]. Subsequent analyses revealed the presence of minerals typical of alkaline soils, such as gypsum, polyaluminates, and amorphous silica gel, supporting the assumptions established in the field [44]. These data provided consistent evidence that conditions favorable to alkalization may have developed during the last glacial cycle, dated to MIS 3, as part of intense, brief interstadial warming: the Dansgaard–Oeschger cycle [45]. Cores taken from Bronze Age burial mounds have also revealed the presence of buried chernozem and alkaline soils in the study area in the Early Holocene [46].

Since previous data and studies generally included only a part of the salt landscape's development over time [47], we searched for a region for sampling where the whole sequence of changes and the complete evolution of the salt landscape could be captured. This place was found in the Kunkápolnás Marshland area, in the territory of Kunmadaras Town.

2. Materials and Methods

Alkaline habitats cover an area of ca. 10,000 km^2 in several parts of the Great Hungarian Plain, including the Danube–Tisza and the Körös–Maros Interfluves. The area of Hortobágy is the largest coherent occurrence of these habitat types in Europe, covering an area of ca. 2300 km^2 (Figure 3). The first national park in the Carpathian Basin was established here in 1973 and was followed by several international designations, such as the UNESCO Biosphere Reserve, the Ramsar Convention, and the Natura 2000 network of the European Union. In 1999, the Hortobágy National Park—the Puszta was inscribed on the World Heritage List of UNESCO as a cultural landscape, as it maintains intact and visible traces of its traditional land use forms over several thousand years and illustrates the harmonious interaction between people and nature.

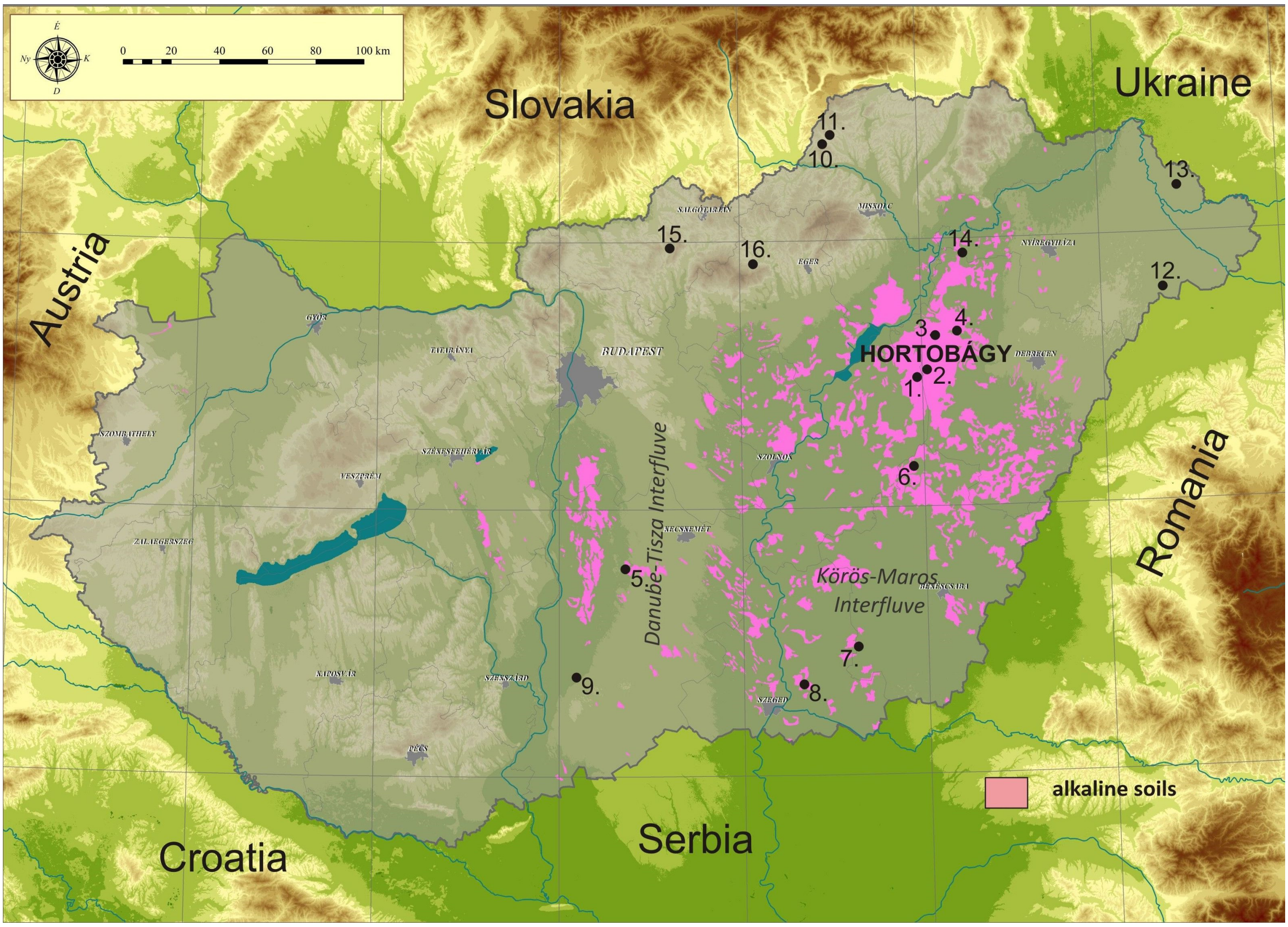

Figure 3. Distribution of salt accumulation areas in Hungary. Location of undisturbed core points in Hungary: 1 = Kunkápolnás marsh, Kunmadaras; 2 = Halas Basin, Hortobágy; 3 = Pap-ere, Hortobágy; 4 = Fecske meadow, Balmazújváros; 5 = Lake Kolon, Izsák [48]; 6 = Lake Kiri, Ecsegfalva [49]; 7 = Lake Fehér, Kardoskút [50]; 8 = Pana-hát, Maroslele [51]; 9 = Hajós [52]; 10 = Kis–Mohos, Kelemér [53]; 11 = Nagy–Mohos, Kelemér [54]; 12 = Bátorliget fen, Bátorliget [55]; 13 = Nyírjes fen, Csaroda [56]; 14 = Sarló-hát, Tiszadob [54]; 15 = Nádas Lake, Nagybárkány [56]; 16 = Nyírjes Lake, Sirok [57].

In the northern part of the Trans-Tisza region, in the center of the salt build-up region, species-rich halophilous vegetation developed both in dry and marshy areas [58]. Levels of salt accumulation were detectable in the higher, drier, predominantly grassy levels of the earth pyramid layers of a Yamnaja culture burial mound and in the deepest areas (meadows) of the studied region (Figure 4). Since the target area of sampling was a bombing range until August 1991, and Hungary was under Soviet military occupation (1956–1991), no correct map of the area could be made, which is why a digital elevation model of the drilling site was prepared at first (Figure 5).

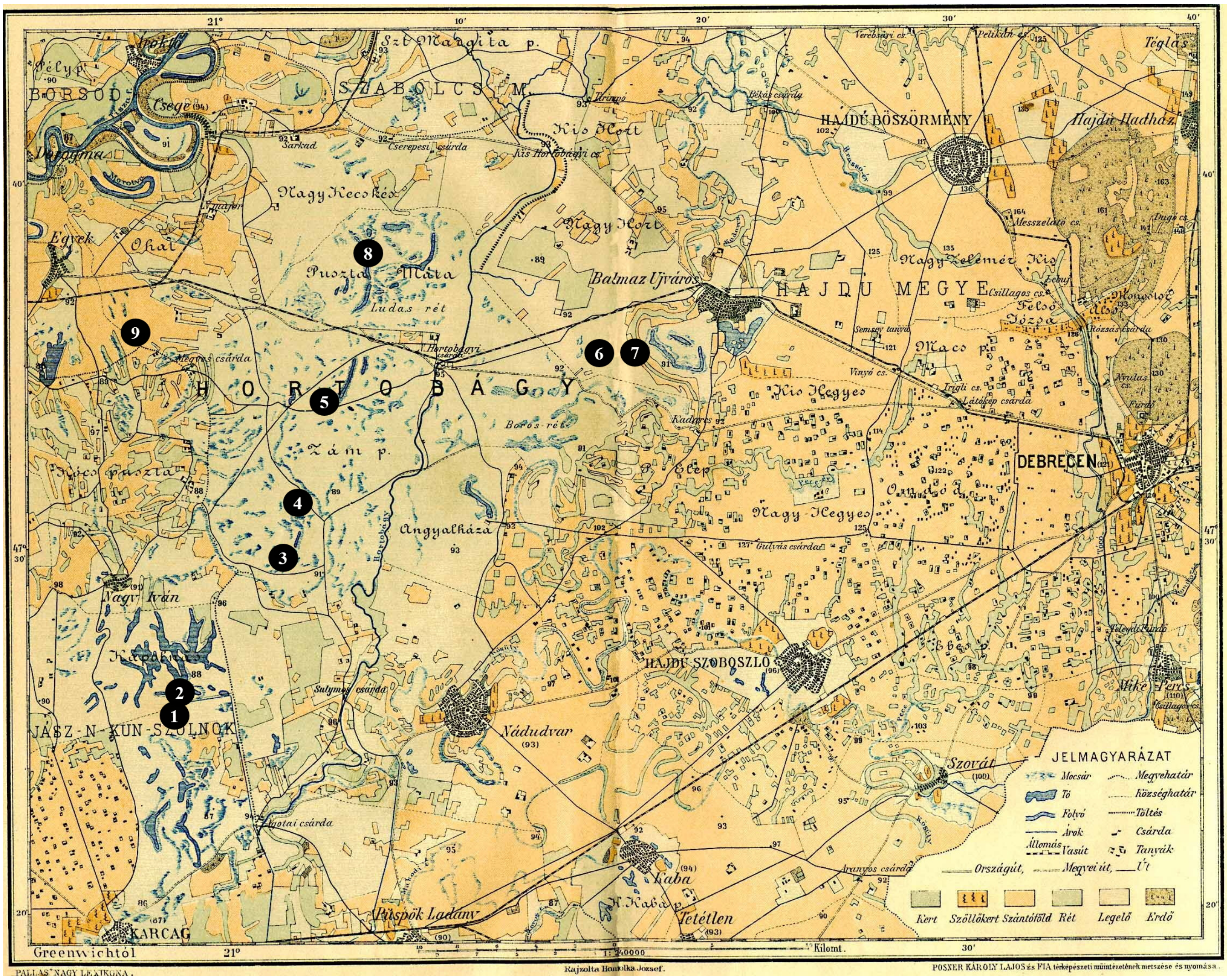

Figure 4. Map of the wider Hortobágy region and surroundings [59] prepared before the major river regulations and creation of fishponds with undisturbed core points. 1. Ecse mound near Kunmadaras (Yamnaja culture burial hill); 2 Kunkápolnás marsh near Kunmadaras with the analyzed paleochannel (Róna basin); 3. Halas Basin (paleochannel); 4. Faluvég mound (Yamnaja culture burial hill); 5. Kungyörgy Lake (paleochannel); 6. Szálka mound (Yamnaja culture burial hill); 7 = Fecske meadow (paleochannel); 8. = Pap-ere (paleochannel); 9. Csípő mound (Yamnaja culture burial hill). Legend items of land cover/use categories: Mocsár = Marsh; Tó = Lake; Folyó = River; Kert = Garden; Szőllőkert = Vineyard; Szántóföld: Arable land; Rét = Meadow; Legelő = Pasture; Erdő = Forest.

The undisturbed core-drilling site was located at the edge of the Kunkápolnás marsh complex and in the middle of a backfilled embankment across one of the paleochannels of the swamp. The embankment was constructed in 1958, and the surrounding area was used as a bombing range and had human-disturbed surfaces, in particular, thousands of bomb craters. However, the embankment protected the underlying stratigraphic sequence, so we could use the most complete data set possible from the sedimentary assemblage accumulated up to the beginning of the Neolithic for our paleoecological study. We also used our drone images to map the morphological evolution of the area and to show the development of the vegetation. The drone images were taken at an average altitude of 500 m with a DJI Mavic 2 Pro drone and a Hasselblad L1D-20c camera. The sampling sites correspond to abandoned and infilled paleochannels fringing the open vegetation of alkaline grasslands (Figure 6).

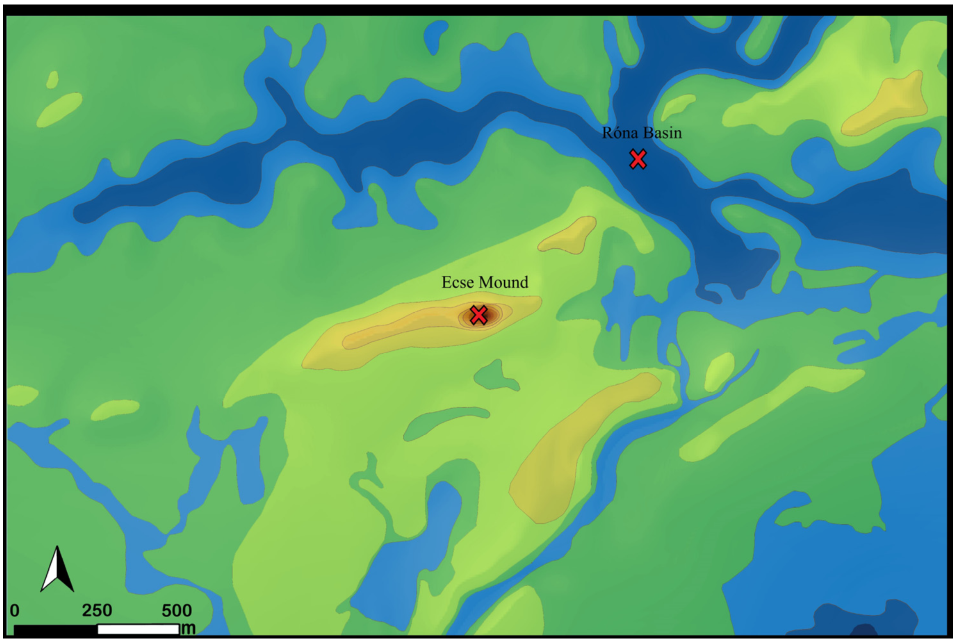

Figure 5. Digital surface model of the southern part of the Kunkápolnás marsh system. x, undisturbed core points. Coordinates and altitudes above Baltic sea level—Róna basin: 47.429540° N, 20.969391° E, 87.2 m; Ecse mound: 47.425279° N, 20.963044° E, 94.5 m.

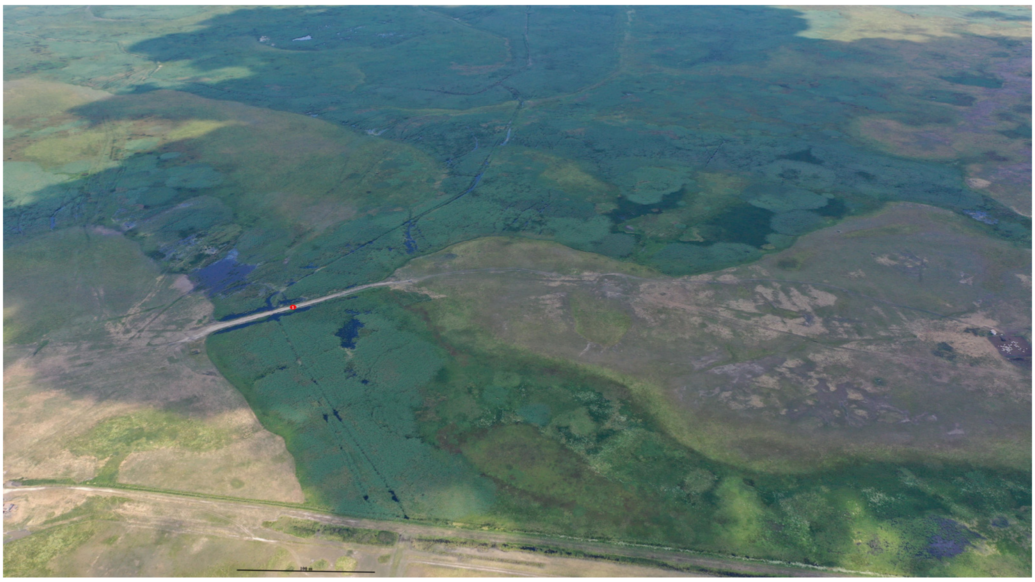

Figure 6. Drone image of the southern part of the Kunkápolnás marsh system (bird's eye view from the south) (drone photo: Attila Szilágyi). •, undisturbed core point (Róna basin).

Samples were taken in winter to avoid possible pollen contamination, and they were subjected to sedimentological, geochemical, palynological, malacological, and plant macrofossil and 14C chronological analyses. The independent chronology established suggests that paleoenvironmental changes can be dated back to 50,000 cal BP years.

In the Hortobágy region, undisturbed sediment sequences were sampled from 9 different sites (Figure 4), including the 10 m long core of the Kunmadaras–Kunkápolnás marsh (marked as no. 1 in Figure 3 and no. 2 in Figure 4) using a special double-walled core head with a diameter of 10 cm. The main lithostratigraphic characteristics of the sediment sequence were determined and analyzed. For the description of the cores, the internationally accepted system and symbols developed by Troels-Smith for unconsolidated sediments were used [60]. For the description of the sediment sequence and the development of the figures, a protocol was followed [61].

The organic matter (OM, LOI500), inorganic matter (IM, LOIres), and carbonate (CC, LOI900) contents of the samples were determined based on the loss on ignition method [62]. The core was sampled at 2 cm sampling intervals, providing a total of 501 samples. The bulk samples were subjected to magnetic susceptibility testing [63]. The magnetic susceptibility of the samples was measured at 2 kHz using a Bartington MS2 magnetic susceptibility meter with an MS2E high-resolution sensor [64,65]. Each sample was measured three times, and the average values of magnetic susceptibility were calculated and reported. Each sample was measured three times, and the average values of magnetic susceptibility were calculated and reported. Grain size data from pretreated sediment core samples were obtained at 2 cm (501 samples) intervals for 42 grain-size classes via laser diffraction using the OMEC Easysizer20 laser grain size analyzer [66].

The concentrations of selected major and trace elements were determined using flame and graphite furnace atomic absorption spectroscopy. Radiocarbon dates of the sequences were obtained using AMS (accelerator mass spectrometry) analysis. The radiocarbon ages of twenty-one samples were analyzed at the Nuclear Research Center of the Hungarian Academy of Sciences (Debrecen, Hungary) and the Direct Radiocarbon Laboratory (DirectAMS, Seattle, WA, USA). Sample preparation and measurement protocols are described in detail by Hertelendi et al. [67] and Molnár et al. [68]. Prior to graphitization, samples were pretreated with weak acid (2% HCl) to remove surface impurities and carbonate coatings. Raw dates were calibrated using the Intcal20 calibration curve [69], using the atmospheric data of Stuiver et al. [70]. The original dates (14C) are indicated as uncal BP, while the calibrated dates are indicated as cal BC and cal BP. Age–depth modeling and the estimation of the sedimentation rate (accrate.depth) were conducted using rbacon 2.5.8 [71] in RStudio [72] Build 461 and the IntCal20 calibration curve [73].

The cores were also subsampled at 2 cm/4 cm intervals for pollen analysis. Samples of 1 cm^3 were obtained using a volumetric sampler and processed for pollen analysis [74]. Some pollen samples were analyzed using the Zólyomi–Erdtman $ZnCl_2$ method, which is the most commonly used method in Hungary [75], as this method provides better results than others for oxbow lake sediments [76]. A known amount of exotic pollen was added to each sample to determine the concentration of identified pollen grains [77]. To ensure a statistically manageable sample size, at least 300 grains per sample were counted (excluding exotics) [78]. Charcoal abundance was determined using the point count method [79]. Tablets with known Lycopodium spore content (from Lund University, Lund, Sweden) were added to each sample to calculate pollen concentrations and accumulation rates. Pollen types were identified and modified according to Moore et al. [80], Beug [81], and Kozáková and Pokorny [82], supplemented by examinations of photographs by Reille [83–85] and reference material held in the Hungarian Geological Institute in Budapest. The analysis of local pollen zones and the statistical interpretations were carried out with the Psimpoll software package (version 4.26) created by Keith David Benneth [86,87]. For macrobotanical studies, QLCMA analyses [88,89] were used. For the quarter-malacological analyses, the methods, assessments, and recent distribution data of Ložek [90], Sparks [91], Alexandrowicz [92,93], Krolopp [94–96], and Welter-Schultes [97] were applied, and the samples were pooled at 16 cm intervals to achieve a minimum of 100 per sample. The overall study procedure was based on the approach of Birks and Birks [98]. The sedimentological, geochemical, pollen, macrobotanical, and quarter-malacological material, as well as the geochronological results, were used to reconstruct local and regional evolutionary events over the last 50,000 years.

It must also be acknowledged that watersheds in floodplains subject to recurrent flooding receive large amounts of so-called "alien" pollen from distant areas, which greatly distorts the final pollen spectrum [99,100]. Consequently, these paleochannels are far from being ideal pollen traps. The extent of "pollen pollution" is highly dependent on the depth and extent of flooding and the vegetation of the flooded area, which can distort the reconstruction of local and regional vegetation. To control and limit the potential bias as much as possible, our work used the analysis of plant macrofossils that provide information on vegetation that has been destroyed and preserved in situ. In this way, elements of the previously in situ flora could be separated from potential regional and extra-regional elements. Paleovegetation can be reconstructed from pollen data using several approaches. For our purposes, the key goal was to assess the extent to which the surrounding landscape and region are occupied by forest–steppe or steppe, as opposed to a closed forest [54]. In our work, the so-called biomization method [101] was used, complemented by an indicator taxa approach to infer the potential local presence of steppe [54,102].

According to the biomization approach [101], steppe indicator pollen taxa are predominantly composed of herbaceous taxa typical of steppe grasslands. Although their occurrence was used as further evidence for the local presence of open stands, such conclusions should be drawn with caution. Many steppe indicator taxa (herbs) are insect or self-pollinated species and produce relatively small amounts of pollen (e.g., *Allium*, *Astragalus*, *Euphoria*, *Verbascum*) and, thus, are under-represented in the pollen spectra. Other steppe indicators are wind-pollinated and produce abundant pollen (e.g., *Artemisia*, *Gramineae*, *Chenopodiaceae*) and are, therefore, over-represented. Based on the work of Beug [81], Kozáková and Pokorný [82], and Magyari et al. [54], the following steppe indicator pollen taxa were identified in the core sequence of the analyzed paleochannels: *Ajuga*, *Allium*, *Compositae* (including *Artemisia*, *Aster*-type species, and representatives of the subfamily *Cichorioideae*), *Caryophyllaceae* (including undetermined and *Dianthus*-type species), *Chenopodiaceae* (*Atriplex*, *Kochia*), *Euphorbia*, *Gramineae*, *Helianthemum*, *Inula*, *Matricaria*-type species (including *Achillea*, *Anthemis*, *Matricaria*), *Plantago lanceolata*, *Plantago major*/*P. media*, *Thalictrum*, *Astragalus*, *Trifolium pratense*-type species, *Trifolium repens*-type species, and *Verbascum*. The ultimate aim of our work was to provide a reliable reconstruction of the vegetation development of Hortobágy based on the study of local catchment basins [47,51].

Recently, attempts have been made to extend the pollen results of oxbow lakes located in the distant floodplain of the Tisza (ca. 60 km) to the Hortobágy area [54]. These distance inferences are rather ambiguous, partly because of the taphonomic problems mentioned above and partly because the present floodplain of the Tisza is much younger (15–18,000 years) and has a morphological and geological evolution that is quite different from that of Hortobágy [33].

3. Results

3.1. Geochronological Results

According to the calibration of radiocarbon ages, the age of the bedrock sand dates back to 50,000 cal BP years (Figure 7). The age of the top of the profile at 10 cm has also been slightly modified thanks to the new calibration from 403 $\pm$ 17 uncal BP years to 35,696 $\pm$ 297 uncal BP (850 cm). Thus, the Kunkápolnás 1000 cm section captures the paleoecological changes from approximately 400 years to 50,000 years in the 21 radiocarbon data (Table 1). We focused mainly on the geochronological delineation of the LGM, MIS 2, and MIS 3 development in the eastern Carpathian Basin and did not specifically address the Late Glacial/Post-Glacial transition, which is the main issue of this paper. The 100 cm (10 m) long core sequence taken near Kunkápolnás (Figure 7) provides us with information about the paleoenvironmental and paleovegetational changes in the study area during the past 50,000 years (Figures 7 and 8).

The results obtained show that the paleochannel studied was characterized by a relatively steady and slow accumulation of clayey silt (As2Ag2), reflecting natural flood cycles over the last 50 years. Evidence of changes in sedimentation, associated with an increase in organic and clay content, is limited to the upper part of the past 5–6000 years. This suggests that relatively uniform sedimentological processes have prevailed over most of the evolution of the channel, which is advantageous from a paleoecological point of view, as the fluctuations and differences observed in the pollen and macrobotanical spectra reflect changes independent of changing geological processes (changing erosion base, selective pollen accumulation, and retention). Sedimentation rates showed relatively uniformly low values at the minimum, maximum, and mean (Figure 8), but some faster rates were also identified. The acceleration of sedimentation rates during the glacial period is associated with the acceleration of loess accumulation phases observed in the Carpathian Basin (Figure 8) [103]. The increase in clay and organic matter content recorded in the upper part of the sequence may indicate anthropogenic disturbances in the basin environment, which may be attributed to the emergence of food-producing cultures [104], as this level appears to coincide with the appearance of Late Bronze Age–Early Bronze Age pit grave culture representatives in the study area [46]. Representatives of this culture are characterized by extensive animal husbandry and the construction of earth burial mounds (kurgans). One of these mounds is located 650 m southwest of the studied core of Kunkápolnás, and others associated with this culture have also been identified scattered within a radius of about 1 km from other investigated profiles in the Hortobágy area.

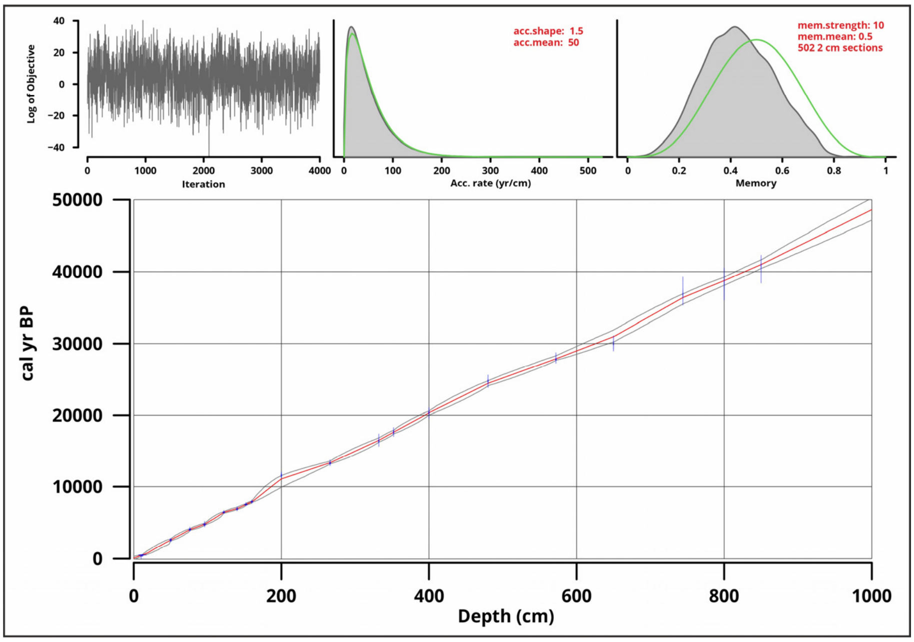

Figure 7. Age–depth modeling and an estimation of the sedimentation rate (accrate.depth) were conducted using rbacon 2.5.8 [71] in RStudio [72] and the IntCal20 calibration curve [69,73]. Red line: linear interpolation of dated points; Vertical lines: dated samples.

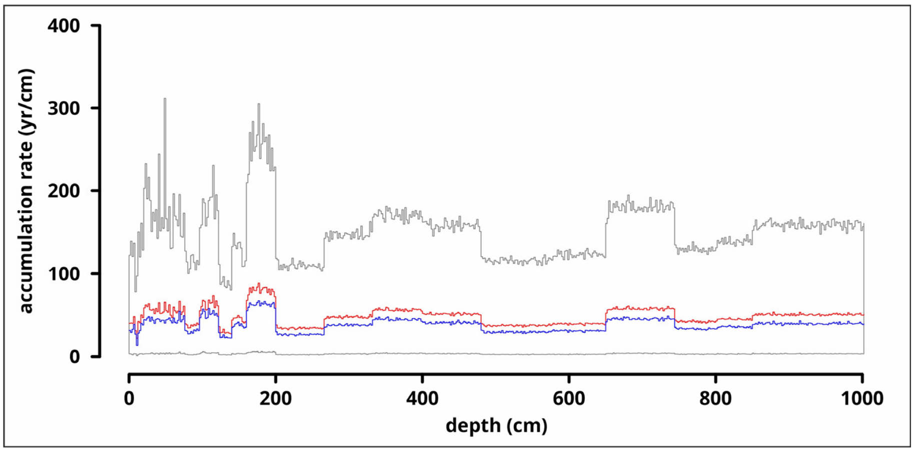

Figure 8. Sedimentation rate (accrate.depth) made in RStudio [72] with rbacon [71] based on the results of age–depth modeling. Red line: mean accumulation rates; Blue and grey lines: 95% confidence intervals.

Table 1. Twenty-one radiocarbon (AMS) data from undisturbed core sequence of the Kunkápolnás marsh in Hortobágy.

Cm	Type of Organic Material	Code	Uncal BP	+/−	Cal BP Interval	Cal BC/AD Interval
10	*Planorbis* shell	DeA–130891	403	17	339–506	1444–1611 AD
12	*Planorbis* shell	D–AMS21141	444	21	461–524	1426–1469 AD
50	*Planorbis* shell	D–AMS21152	2524	23	2496–2736	547–787 BC
76	*Planorbis* shell	DeA–130902	3732	20	3987–4151	2038–2202 BC
96	*Lymnaea* shell	D–AMS2113	4232	29	4649–4857	2700–2908 BC
122	*Unio* shell	DeA–130913	5696	22	6406–6552	4457–4603 BC
140	*Unio* shell	D–AMS21112	6065	26	6799–7146	4850–5197 BC
152	*Unio* shell	D–AMS21123	6698	30	7504–7655	5555–5701 BC
160	*Bithynia* shell	D–AMS21104	7067	29	7836–7965	5887–6016 BC
200	*Unio shell*	DeA–130914	10,055	33	11,357–11,803	9404–9854 BC
266	*Pisidium* shell	D–AMS21095	11,417	52	13,174–13,411	11,225–11,462 BC
332	*Pisidium* shell	D–AMS21086	13,598	70	16,197–16,654	14,208–14,705 BC
352	*Cochlicopa* shell	D–AMS21077	14,474	58	17,412–17,878	15,463–15,929 BC
400	*Succinella* shell	D–AMS21068	16,847	78	20,151–20,535	18,203–18,521 BC
480	*Trochulus hispidus*	DeA–130965	20,529	72	24,366–24,986	22,417–23,037 BC
572	*Succinella* shell	D–AMS21049	23,725	85	27,694–28,008	25,745–26,059 BC
650	*Pinus microharcoal*	DeA–131026	25,661	121	29,681–30,189	27,732–28,240 BC
744	*Helicopsis* shell	D–AMS210510	32,535	175	36,364–37,325	34,415–35,376 BC
800	*Succinella* shell	DeA–130977	33,433	232	37,455–39,161	35,506–37,212 BC
850	*Trochulus* shell	DeA–130988	35,696	297	40,158–41,323	38,209–39,374 BC

3.2. Sedimentological Results

Between 50,000 and 25,000 years (1000–500 cm), the sand content indicates fluvial sedimentation (Figure 9). The bedrock was dominated by the medium sand fraction (Figure 9), the layer was slightly cross-bedded in the undisturbed core layer, and fluvial *Valvata piscinalis* shells were also found. It can be concluded that the analyzed bed of the Kunkápolnás marsh system (Róna basin) was formed by the development of a riverbed. During the first 25,000 years, carbonated river sediment rich in sand and poor in finer-grained fractions accumulated in the gradually disconnected, 50,000-year-old riverbed (Figure 9). The development of the river sediment is completely distinct from the sediments accumulated in the Tisza riverbed in terms of grain composition (Figures 9 and 10) and geochemical parameters (Figure 11), which are characteristic of the Sajó and Hernád Rivers [105]. From about 25/27 thousand years onward, the nature of sedimentation has fundamentally changed (Figures 9–11), and sediment with a finer grain size composition has accumulated in the section. The changes in sediment composition (Figures 9–11) indicate that the fluvial sedimentary phase has ended and that the cutoff meander phase dominated the bed formed for most of the years during MIS 3. It is likely that sandy sediment accumulated in the basin, which developed in the cutoff riverbed only during major floods, and that it was the floodplain loess-like sediment that accumulated on the bank along the developed riverbed that was washed into the basin of the oxbow lake. However, it should be noted that at this time extensive soil formation took place in the region, and this has led to the formation of fossil saline soils [43–45,106].

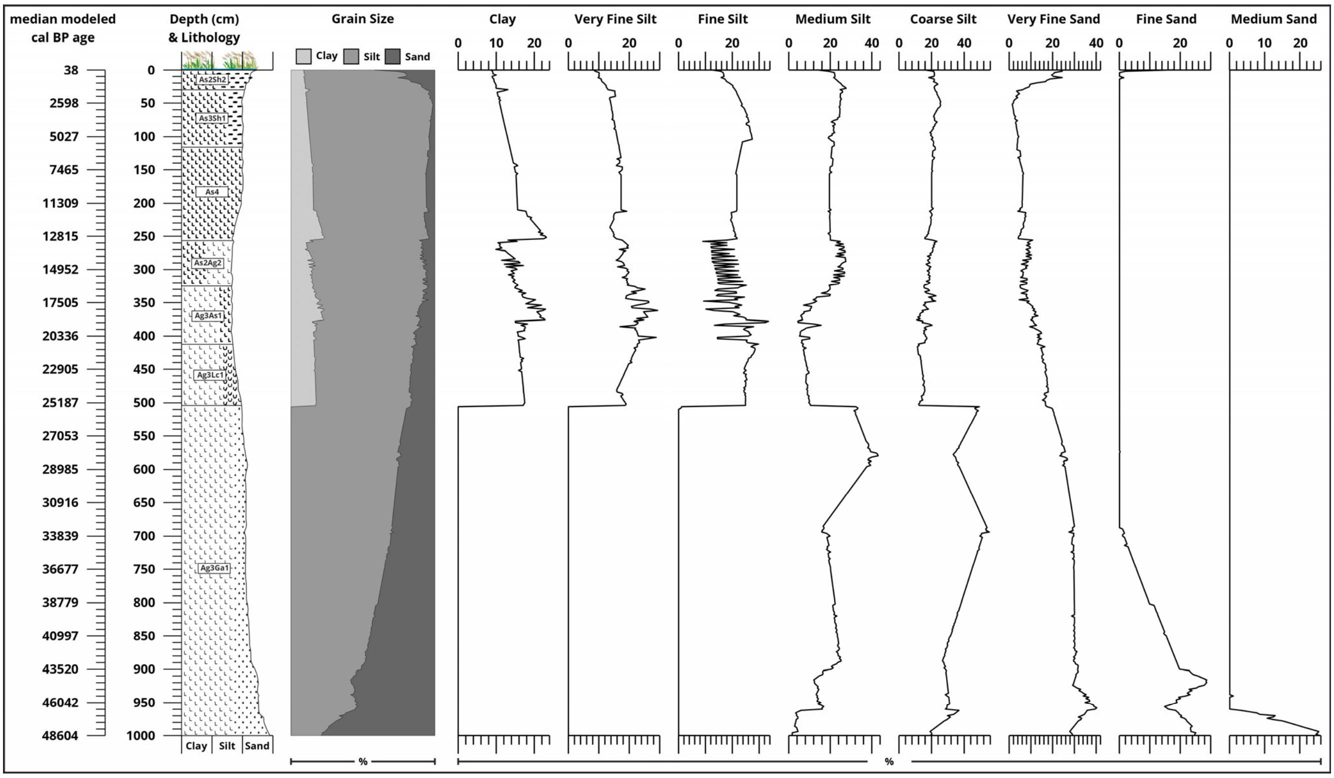

Figure 9. Results of the grain size analysis: clay (<0.004 mm), silt (0.004–0.062 mm), and sand (0.062–0.5 mm) fractions in a percentage diagram and line diagrams of clay (<0.004 mm), very fine silt (0.004–0.008 mm), fine silt (0.008–0.016 mm), medium silt (0.016–0.031 mm), coarse silt (0.031–0.062 mm), very fine sand (0.062–0.125 mm), fine sand (0.125–0.25 mm), and medium sand (0.25–0.5 mm) fractions.

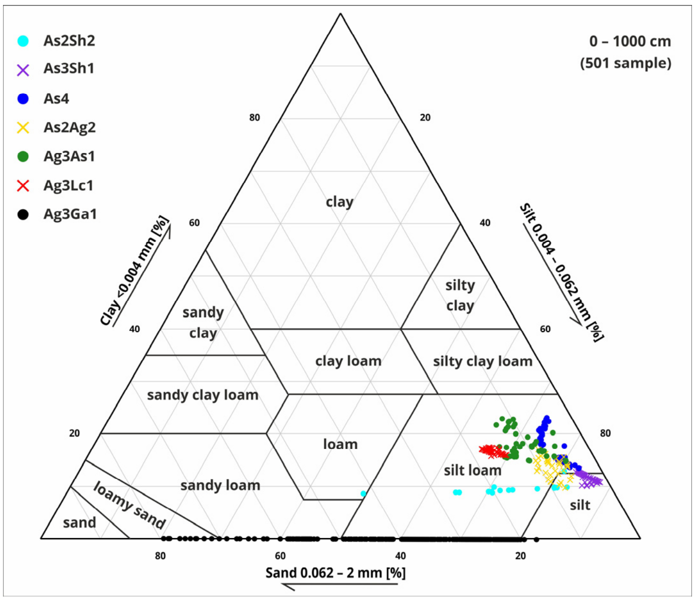

Figure 10. Ternary diagram of clay, silt, and sand grain sizes with Troels-Smith [60] sediment types based on the grain size analysis.

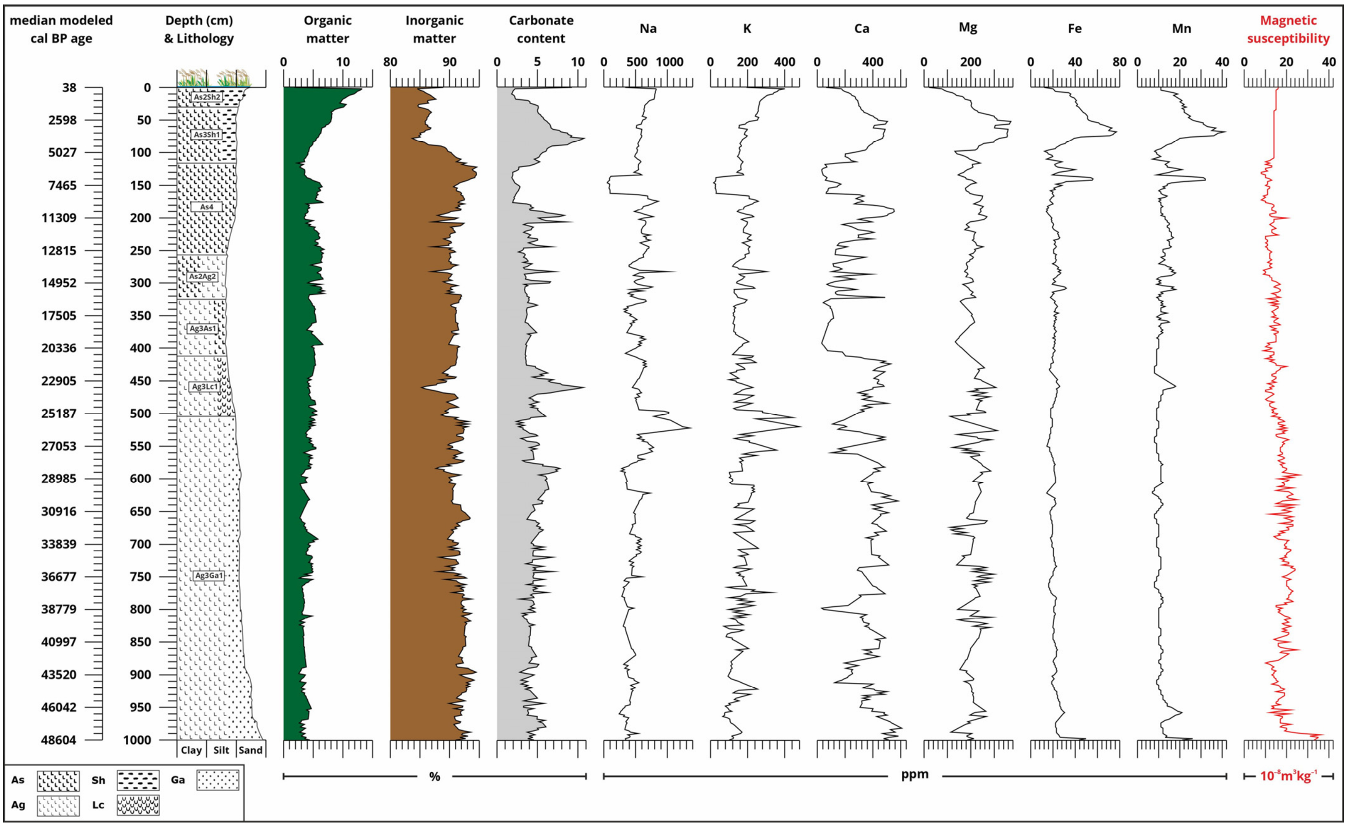

Figure 11. Combined figure of (from **left** to **right**) the modeled median cal BP dates from the radiocarbon analysis; lithology profile based on grain size with Troels-Smith [60] sediment classification and depth (cm); results of the loss on ignition [62] with organic matter (OM), inorganic matter (IM), and carbonate content (CC); results of the geochemical [107]; and magnetic susceptibility analysis [64].

Given continuous military activity, the area was excluded from the comprehensive geological mapping of the Hungarian Lowlands [108–112], so our undisturbed core drilling analyses can only suggest that a saline soil level could have developed in the vicinity of the riverbed, which was transformed into a sediment basin. The material of the eolic sedimentation [44,45,112–114] that developed in the region could have accumulated in the basin of the oxbow lake until 12,800/13,000 cal BP when the eolic sedimentation in the Carpathian Basin came to an end, meaning that, at the end of the Ice Age, polygenetic alluviation took place in the oxbow lake, which evolved over 27/25 thousand years ago. This heterogenetic sedimentation is reflected in the highly heterogeneous grain composition, from the clay to the fine sand fraction, and also in the rhythmic changes of the water-soluble element (Ca, Mg, Na, and K) content (Figures 9–11). The rhythmic changes were completed in the Late Glacial period of the Ice Age, and we can expect steadily increasing clay, fine rock flour, and organic matter content during the Holocene.

The increase in organic matter and clay content became more pronounced from about 5000/5200 cal BP, when livestock-keeping communities colonized the area (Pit Grave culture = Yamnaja = Kurgan culture). In this period, given the human-induced soil erosion around the basin, a sharp increase in organic matter and clay content can be detected in the sediment column of the Róna basin. Today, the riverbed is characterized by an alkaline, marshy environment.

3.3. Results of the Pollen Analysis

The entire pollen sequence, both at the end of the Ice Age and during the Holocene, is dominated by herbaceous taxa, above all, grasses (*Poaceae*), wormwood (*Artemisia*), and goosefoot species (*Chenopodiaceae*) (Figure 12) but also by *Achillea* taxa. The cumulative proportion of arboreal species (Arbor Pollen) exceeded 60% only in two glacial levels (43–46,000 and 25–28,000 years). Both glacial forest levels were dominated by the subgenus Pinus (Figure 12), as shown by anthracological analyses of charred trees recovered from fossil soils [115], and both glacial levels were associated with fossil soil formation [106] when the proportion of vegetation cover, especially coniferous trees, increased in the region.

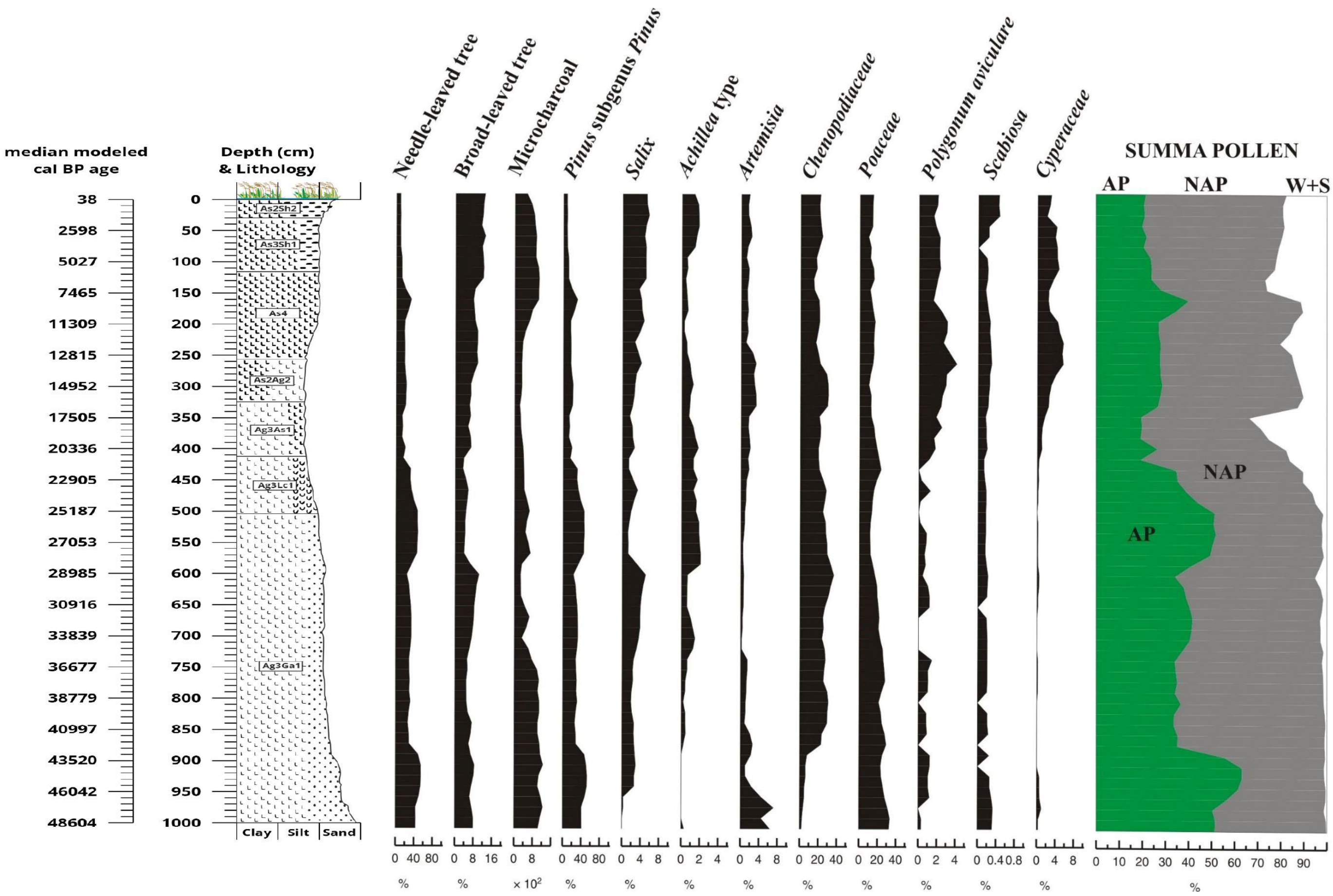

Figure 12. Pollen diagram of Kunkápolnás for the undisturbed core sequence (selected taxa and summarized group).

A characteristic feature of the pollen section is that the alluvial–fluvial influence may have been present from 50,000 years until the end of the Ice Age (12,800 years). This suggests [99,100] that the pollen composition may have reflected a more regional relationship during the glacial period, irrespective of the diameter of the studied basin [116]. However, the basin must have acted as a local pollen trap over the last 12,800 years. Yet, the Holocene pollen assemblage was dominated by herbaceous taxa, with an overall proportion of more than 40–45% in all samples. The share of broad-leaved tree pollen varied between 8 and 16% in total, and the most characteristic broad-leaved taxon in the section was the eurytopic willow (*Salix*), a softwood gallery forest element (Figure 12).

Analysis of the pollen sequence and studies from the Eurasian forest–steppe–steppe environment [117–119] suggest that steppe, or maximum boreal forest–steppe vegetation [54] might have stabilized in the study area during the glacial period. Although the presence of marshy vegetation became more abundant (Figure 12) in the Holocene, herbaceous species continued to dominate, and a predominantly temperate steppe cover developed and persisted to the present day in the study area. Fluctuations in the pollen composition indicate cooler and milder climatic phases in the sequence [120–128]. The cooling phases can be synchronized with the increased dominance of grasses (*Poaceae*) and, in general, non-arboreal pollen [126,129,130], and in parallel with this trend, a decrease in arboreal pollen could be detected (Figure 12). Glacial warmings are indicated by the increasing dominance of coniferous pollen. The Holocene period is reflected in a marked increase in broad-leaved pollen and charcoal abundance (Figure 12). Given the changes in the pollen composition, the vegetation of the Hortobágy area has similarities with that of the Eurasian forest–steppe belt [131].

As the basin is of fluvial origin, the pollen composition may have been influenced by fluvial inflow [99,100], and one has to consider the pollen input by the late glacial flooding of the Tisza river [132] into the already marsh-dominated former riverbed [54]; our findings are based primarily on the AP/NAP pollen ratio. The relevant literature [54,133,134] clearly shows that, during the warming periods, including the Holocene, when AP occurs at 50–60%, forest–steppe vegetation stabilized in the study area. Although the pollen composition can be described to be consistent with Eurasian forest–steppe, the current climate analysis of the Carpathian Basin [135] suggests the development of a basin effect (rain shadowing) caused by the surrounding mountain range rather than by the influence of the Eurasian continental climate zone.

3.4. Macrobotanical Results

Although Jakab has provided a detailed analysis of the pollen and macrobotanical data of the Kunkápolnás core sequence [32], it is reasonable to present his findings in this paper as well to complete the geochronological and sedimentological results.

From the core sequence, 2516 macrobotanical remains were recovered, the distribution of which is shown in Figure 13. Minimal plant remains were found in the bed of the section, corresponding to riverine infilling between 50,000 and 17,500 years (1000–350 cm). The plant remains at this level were dominated by *Juncus* roots; indeterminate monocots; and other indeterminate plant fragments that could easily have leached from the river bank into the Late Glacial river system and accumulated with the leached sediment in the abandoned, infilling riverbed at the study site. The bed was characterized by low vegetation cover with highly fluctuating water levels. Among the macrofossils, roots of a sedge species (*Juncus* sp.) were found in the largest quantities.

At 17,500 years, after the Last Glacial Maximum (LGM), in addition to the taxa that occupied the riverbed and formed the oxbow lake, oogonites (gyrogonites) of the *Chara* tax—above all, *Nitella* cf. *gracilis* and *Chara vulgaris*—appeared in significant numbers. As a result, we can reconstruct the formation of a mesotrophic oxbow lake [136], poor in phosphate and organic matter, from 17,500 years ago and persisting until the beginning of the Holocene (12,000–11,500 years ago). In Northern Europe, this *Chara* lake stage is generally typical of the beginning of the Holocene; however, in the case of the sedimentary deposits in the Carpathian Basin dating back to the end of the Ice Age, such as Kolon-tó near Izsák (Hungary) [61], this stage had already developed in the final part of the Ice Age. In the Chara lake stage, around 15,000 years ago, terrestrial taxa, including those indicating a dry or periodically dry alkaline environment (*Trifolium repens* and *Elatine triandra* seeds), appeared (Figure 13). The presence of elements indicating salinity suggests that alkalinization may have occurred as early as the end of the glacial period in the study area. Habitats typical of the alkaline environment may have developed along this mesotrophic oxbow lake—at the boundary between the loess grassland indicated by *Trifolium repens* seeds—and waterside mudflats, where groundwater fluctuations were (and still are) the most intense [137].

During the transition period between the end of the Ice Age and the beginning of the Holocene (between 12,800 and 11,300 cal BP), the studied floodplain was silted up, and seasonal cyclical groundwater level fluctuations may have been amplified, which appears to be demonstrated by the presence of *Elatine hungarica* seeds in the samples, indicating marked alkalinization, as this species can stay in an anabiotic stage for several years and spread during favorable periods because of shallow water cover. However, no taxa indicating deeper or permanent water cover were found in the samples. The water level could have been very low, a few centimeters at most, and the bed would have seasonally dried up. The constant presence of *Typha* species indicates a gradually warming climate. The vegetation of the marsh was poor, with the occurrence of the common water plantain (*Alisma plantago-aquatica*), a few sand cinquefoil (*Potentilla supina*), and water fern (*Salvinia natans*). Mollusk and ostracod shells were negligible. Of the mosses, *Amblystegium serpens* was found in very small numbers, often living on woody debris, but at this site, it is more likely to live on the decaying stems of some aquatic plant (e.g., *Schoenoplectus lacustris*).

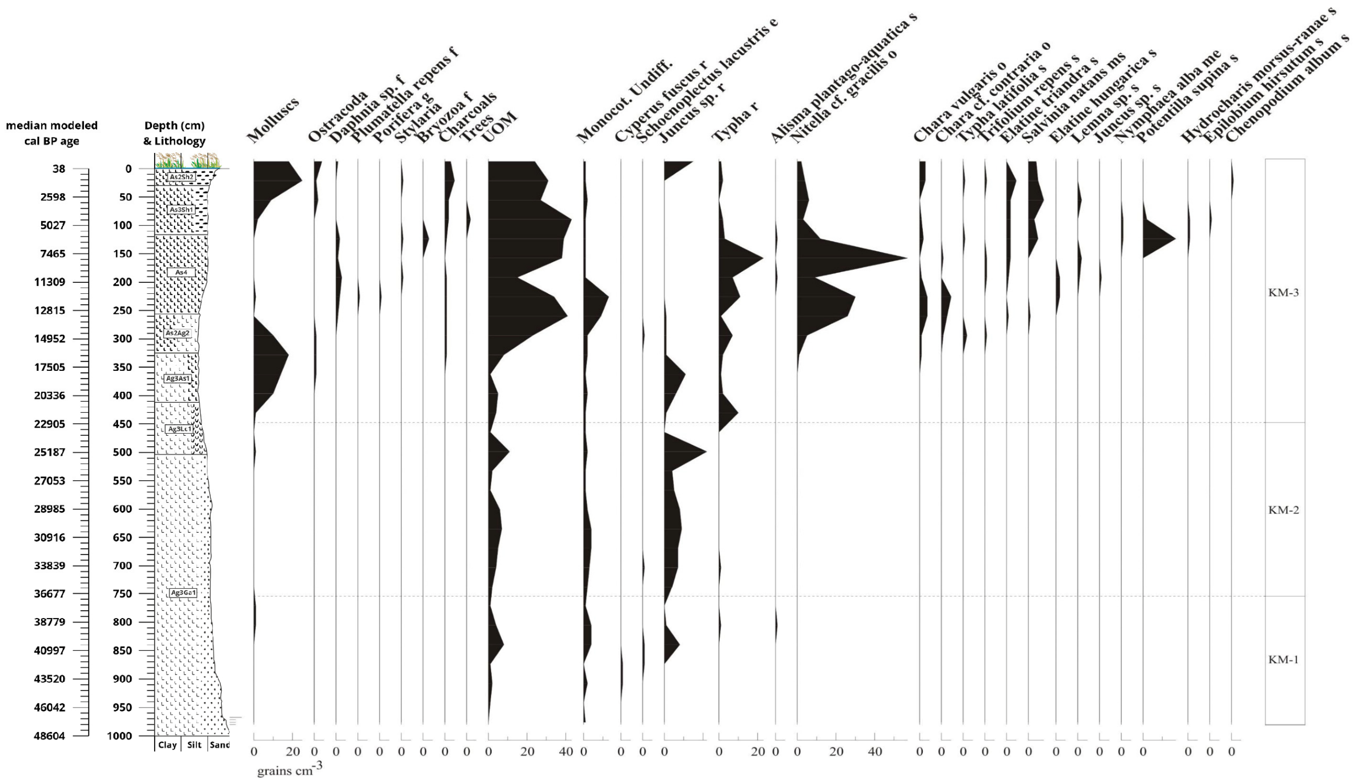

Figure 13. Fauna and macrobotanical remains diagram of Kunkápolnás for the Róna basin (Kunmadaras Town, Jász–Nagykun–Szolnok County) undisturbed core sequence (UOM = unidentified organic matter).

Later in the Holocene (7500–5000 cal BP years), higher water levels are indicated by the appearance of the white waterlily (*Nymphaea alba*), common frogbit (*Hydrocharis morsus-ranae*), water fern (*Salvinia natans*), and duckweed species (*Lemna* sp.). Occasionally, the spiny naiad (*Najas marina*), typical of carbonate-rich waters, also appears, as well as the common bladderwort (*Utricularia vulgaris*) and water crowfoot species (*Batrachium* sp.). In open water, the presence of bryozoans and sponges, which are necessary for their colonization, is also indicative of denser vegetation. Cladocerans and ostracods also appeared in open water, with the most typical species being *Daphnia pulex*, *Cerodaphnia* sp., and *Simocephalus vetulus*. *Juncus* has been replaced by *Typha* in the riparian zone, while the common water plantain was found to be abundant in the marshy vegetation, along with the presence of mint species (*Mentha* sp.) and the fine-leaved water dropwort (*Oenanthe aquatica*). It can be assumed that the marsh may have been periodically filled with water and that typical Holocene aquatic riparian zonation developed without any productive human influence.

At 5000 cal BP years, the same indicator elements appeared, but in a different proportion than before. Mudflat communities spread, and the number of mollusk and ostracod shells increased, while the abundance of carophytes decreased. The amount of fly ash is the highest in this section, indicating more intensive land use. This change is fully associated with the appearance of Pit Grave culture communities, as indicated by the nearby Ecse mound (kurgan). In parallel with the emergence of pastoral communities of the Pit Grave culture, human communities that engaged in productive farming (livestock keeping) also appeared in the landscape of Hortobágy. Species indicative of seasonally drying mudflats are permanently present in the samples, such as the Hungarian waterwort (*Elatine hungarica*), the three-stamen waterwort (*E. triandra*), the sand cinquefoil (*Potentilla supina*), the dwarf clubrush (*Schoenoplectus supinus*), and the white clover (*Trifolium repens*). This community is very typical of regularly drying up or only periodically refilled beds. The occurrence of saltbush species (*Atriplex hastata/saggitata*) also indicates the development of silty, possibly alkaline, soils.

3.5. Malacological Results

Samples were taken and processed at 8 cm but were evaluated and aggregated at 16 cm to reach a statistical minimum of 100 individuals per sample [96]. More than 7800 specimens of 27 molluscan taxa were retrieved from the sequence. Up to the LGM level, i.e., up to 23,000 years, the malacological material (Figure 14) is dominated by taxa preferring flowing water (rheophilous group), and then, in the transitional period of the Ice Age and the Holocene, by aquatic Mollusca that require more water cover but are less sensitive to water quality and belong to the catholic group according to Sparks [91]. Direct fluvial recharge probably occurred in the area for up to 23,000 years, after which, the proportion of elements indicating permanent water cover became dominant; i.e., fluvial recharge became more distant [106], but the area may have received significant additional water through rhythmic flooding after the development of the LGM level. At the same time, the slum group, which also tolerated intermittent water cover, also appeared in the sequence (Figure 14), but only in the second half of the Holocene, during the last 5000 years, when it became dominant within the malacofauna, suggesting a tripartite subdivision of the aquatic fauna composition within the sequence. The bedrock of the sequence indicates riverine recharge between 50,000 and 23,000 years ago, after which, pond species with permanent water cover (*Bithynia tentaculata*, *Anisus vorticulus*, *Gyraulus albus*) dominated, but the members of the slum group also appeared, reflecting cyclical water-level fluctuations.

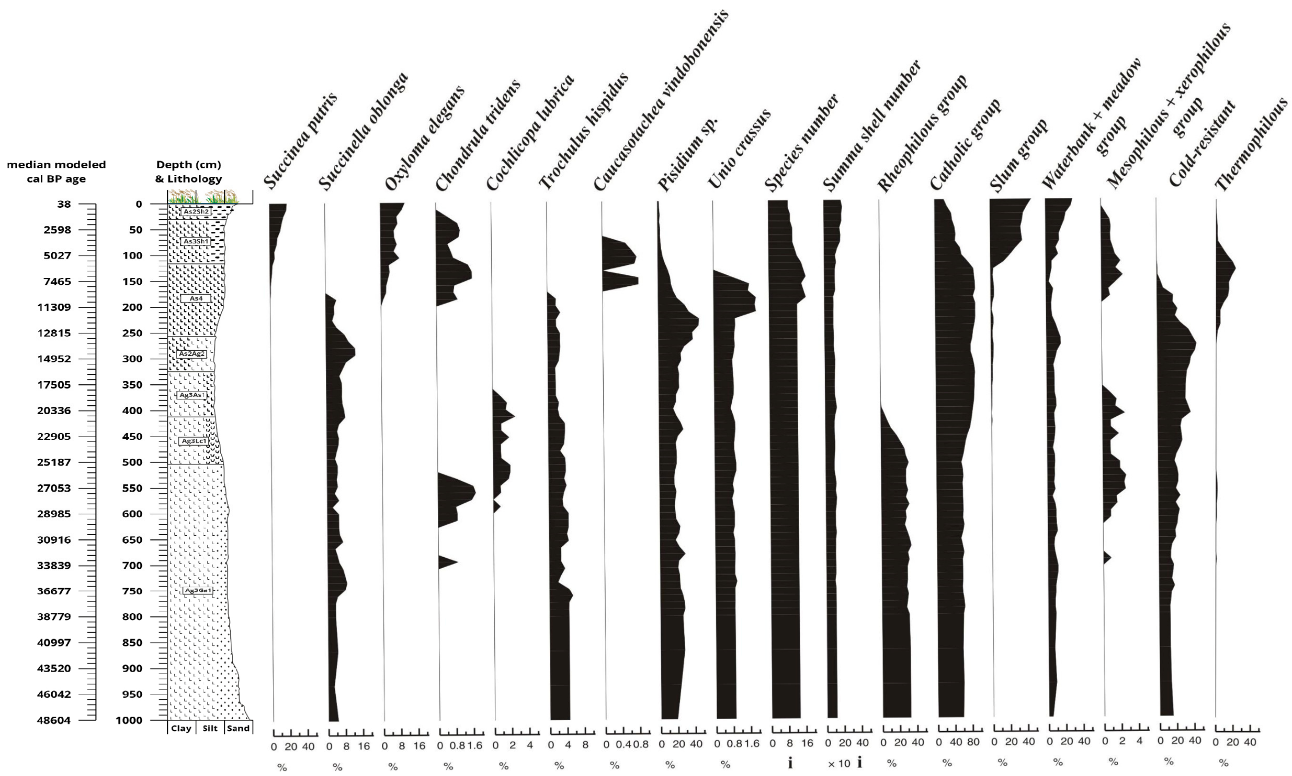

Figure 14. Quarter-malacological diagram 1: freshwater taxa in the Kunkápolnás undisturbed core sequence.

The water supply in the second half of the Holocene was cyclical, and the studied river basin may have periodically dried out during this period. Fauna elements living in a riparian environment were present throughout the sequence, but their proportion increased only in this last phase. The mesophilous and xerophilous taxa became dominant in the Holocene as well, but in the glacial period, between 29,000 and 24,000 years, such species (e.g., *Cochlicopa lubrica*, *Chondrula tridens*) also appeared in the sequence during the intensification of soil formation in the study area (Figure 14). During the glacial period, the proportion of cold-resistant elements (*Lymnaea glabra*, *Valvata pulchella*, *Succinea oblonga*, and *Trochulus hispidus*) was highly significant. These taxa coexisted with thermophilous elements during the glacial/Holocene transition and at the beginning of the Holocene, before disappearing from the sequence in the Early Holocene.

Cepaea vindobonensis, a character species of the Pannonian forest–steppe [138], appeared at the beginning of the Holocene, indicating the spread of Pannonian forest–steppe vegetation. At this time, the number of species in the malacofauna increased, and beyond the appearance of 9–10 taxa at the end of the glacial period, species numbers exceeded 10 taxa per sample during the Pleistocene/Holocene transition and the Early Holocene. This increase in species may have been due to the survival of glacial species that did not become extinct, whereas dispersing elements had already appeared in the section during the Holocene (Figures 14 and 15). From the end of the Early Holocene (7500 cal BP) onward, species abundance declined sharply, and the terrestrial fauna became dominated by thermophilous, mesophilous–xerophilous elements in the steppe-like environment that evolved during the last 7500 years, which was certainly dry for part of the year. This mosaic environment may have stabilized after 5000 cal BP years in the second half of the Holocene when the number of individuals doubled to more than 200 individuals per sample.

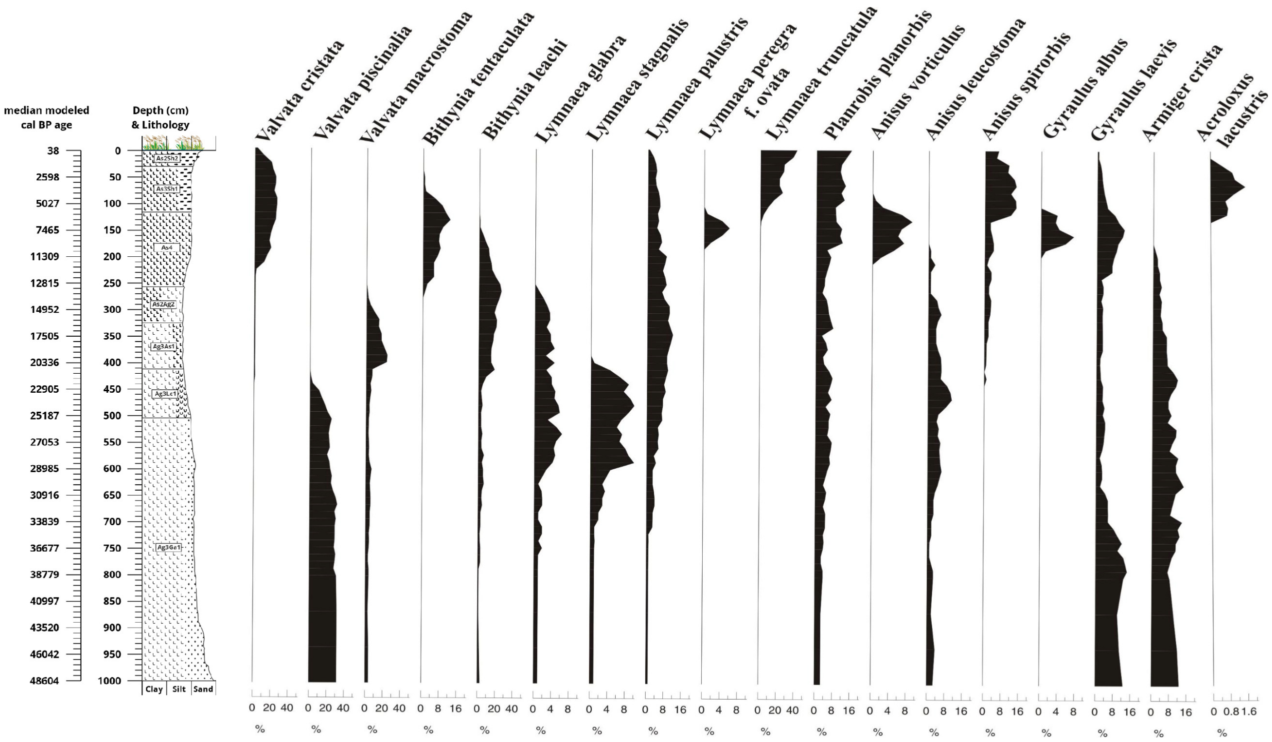

Figure 15. Quartermalacological diagram 2: terrestrial taxa and quartermalacological-based paleoecological groups in the undisturbed Kunkápolnás core sequence.

In the second half of the Holocene, the proportion of the group associated with a marshy environment also increased, along with the maximum of aquatic species indicating temporary water cover, and then, the vegetation of the Kunkápolnás marsh may have stabilized for the last 5000 years in the study area.

4. Discussion

A complete fluvial cycle has been revealed [105,139–143] in the studied riverbed of the so-called Róna basin at the edge of the Kunkápolnás marsh complex, which evolved from the carbonate fluvial sand sediment of the bedrock that formed about 50,000 years ago into a Holocene, organic-rich clayey rock silt (marsh) sedimentary layer. Trends in sedimentation parameters can be synchronized with the accumulation of major sediment layers, changes in the sediment-forming environment, and the climatic cycles of the past 50,000 years [120–123,125,129,130].

Pollen analysis was carried out on the entire undisturbed core section, the results of which are completely different from those of the previously published pollen studies in Hungary [48,49,51–57]. This became particularly obvious when based on the biomization approach [101,117]; the pollen composition of the undisturbed core drilling was compared with the pollen composition of the recent Eurasian biomes (Figure 16) and with the arboreal pollen (AP) from pollen cores in the Carpathian Basin (Figure 17). These results show that a boreal forest–steppe with a dominance of Pinus diploxylon-type pollen was established in the glacial period in the studied Kunkápolnás region. Previous pollen analyses have shown that Pinus-dominated taiga forest patches developed along former living river branches [48], and the pollen diagram (Figure 16) shows that the pollen composition of Kunkápolnás is typical of the recent Eastern and Western Eurasian forest–steppe/steppe boundary. The pollen, macrobotanical, and malacological data suggest that the first patches of alkaline vegetation were established during the cold maximum of the glacial period (Figures 12–15) in the study area.

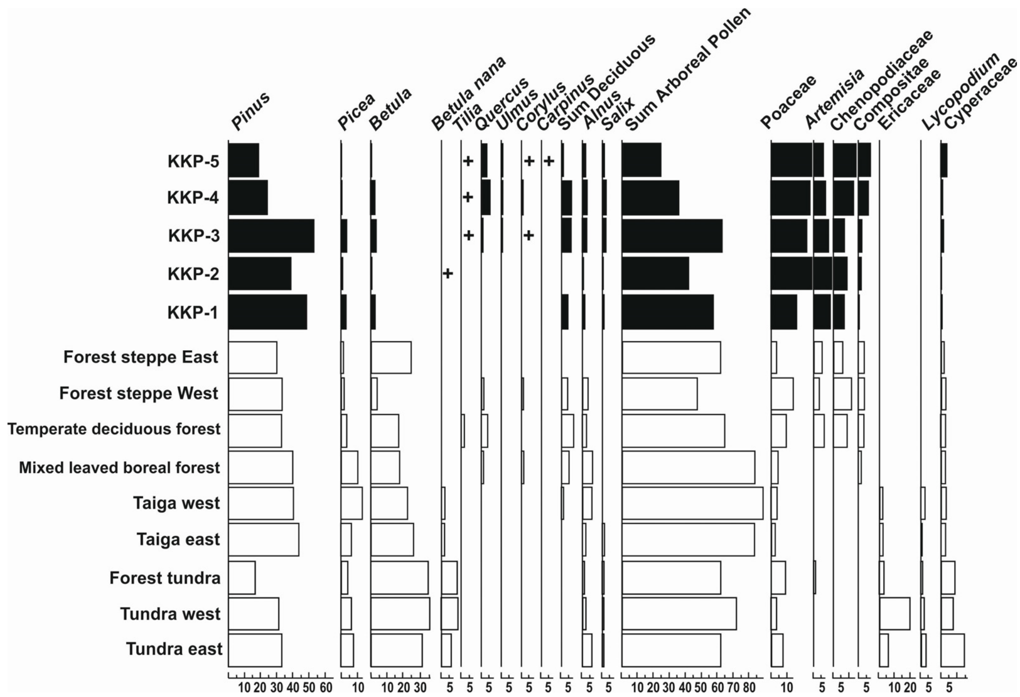

Figure 16. Zone-average pollen frequencies of selected pollen types from Kunkápolnás marsh plotted alongside mean values of major pollen types in various vegetation zones of the former Soviet Union. Surface pollen spectra are redrawn from [144]. KKP-1 = pollen spectra from Dansgaard–Oschger (Greenland Interstadial) events in the sequence of Kunkápolnás marsh; KKP-2 = pollen spectra from Heinrich (Greenland Stadial) events in the sequence of Kunkápolnás marsh; KKP-3 = pollen spectra from the Late Glacial Age in the sequence of Kunkápolnás marsh; KKP-4 = pollen spectra from early postglacial time (Early Holocene Age) in the sequence of Kunkápolnás marsh; KKP-5 = pollen spectra from late postglacial time (Late Holocene Age) in the sequence of Kunkápolnás marsh.

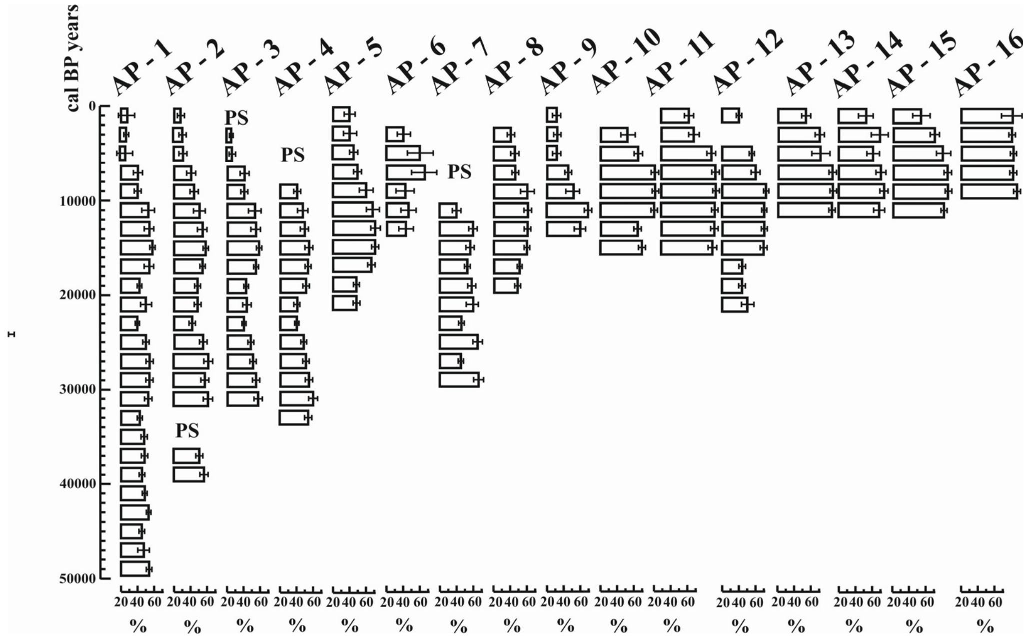

Figure 17. Abundance of pollen of woody taxa in Holocene records from Hortobágy and the Carpathian Basin. The range of values, as well as an indication of the most frequent value, is plotted for each site for 2 millennial intervals from 50,000 to 0 cal BP years. AP = arboreal pollen. 1. Kunmadaras, Kunkápolnás marsh; 2. Hortobágy, Halas Basin; 3. Hortobágy, Pap-ere; 4. Balmazújváros, Fecske-rét; 5. Izsák, Lake Kolon [48]; 6. Ecsegfalva, Lake Kiri [49]; 7. Kardoskút, Lake Fehér [50]; 8. Maroslele, Pana-hát [51]; 9. Hajós [52]; 10. Kelemér, Kis-Mohos [53]; 11. Nagy-Mohos, Kelemér [54] 12. Bátorliget, fens [55]; 13. Csaroda, Nyíres fen [56]; 14. Tiszadob, Sarló-hát [54]; 15. Nagybárkány, Nádas Lake [56]; 16. Sirok, Nyírjes Lake [57].

However, general alkalinization and a drier steppe phase became widespread in the region with the gradual warming of the climate from the Late Glacial to about 12,000–13,000 years, together with the process that resulted in the dominance of the *Matricaria* pollen type *Chenopodiaceae* and *Artemisia* pollen (Figure 12). This was also the time when plant remains (*Elatine* sp.) typical of alkaline vegetation and drier loess steppes appeared [32]. Then, at the beginning of Holocene warming, from about 11,000 years onward, a change in the dominance of pollen and the appearance of vegetation remains typical of drier loess–steppe environments (*Trifolium repens*, *Atriplex*) resulted in the expansion of dry steppe and alkaline marsh patches. Based on the analysis of the radiocarbon-dated pollen and macrobotanical and malacological material, a mosaic habitat complex of alkaline marshes and steppes, without any human influence, was established in the studied region at the end of the Ice Age, during the turn of the Late Glacial and the Early Holocene. It appears that in contrast to the mountain rims and hill regions of the Carpathian Basin [53], no forest phase was established in the area at the beginning of the Early Holocene, but a mosaic vegetation structure of a forest–steppe developed, where trees occurred only at the margins of the former watercourses, while their cut and transformed beds gradually filled up with sediments. These data are in good agreement with the previously reported paleoecological data on the mosaic environmental structure of the Carpathian Basin [145]. However, it seems that local environmental factors (micromorphology, alkaline soil, morphology, and groundwater) were extremely strong in the Kunkápolnás region, amplifying the essentially climate-driven alkalinization process (Figure 18), and therefore, the alkaline patches in the Pannonian forest–steppe region were formed on a regional scale [135,146–148] under the influence of locally evolved edaphic factors.

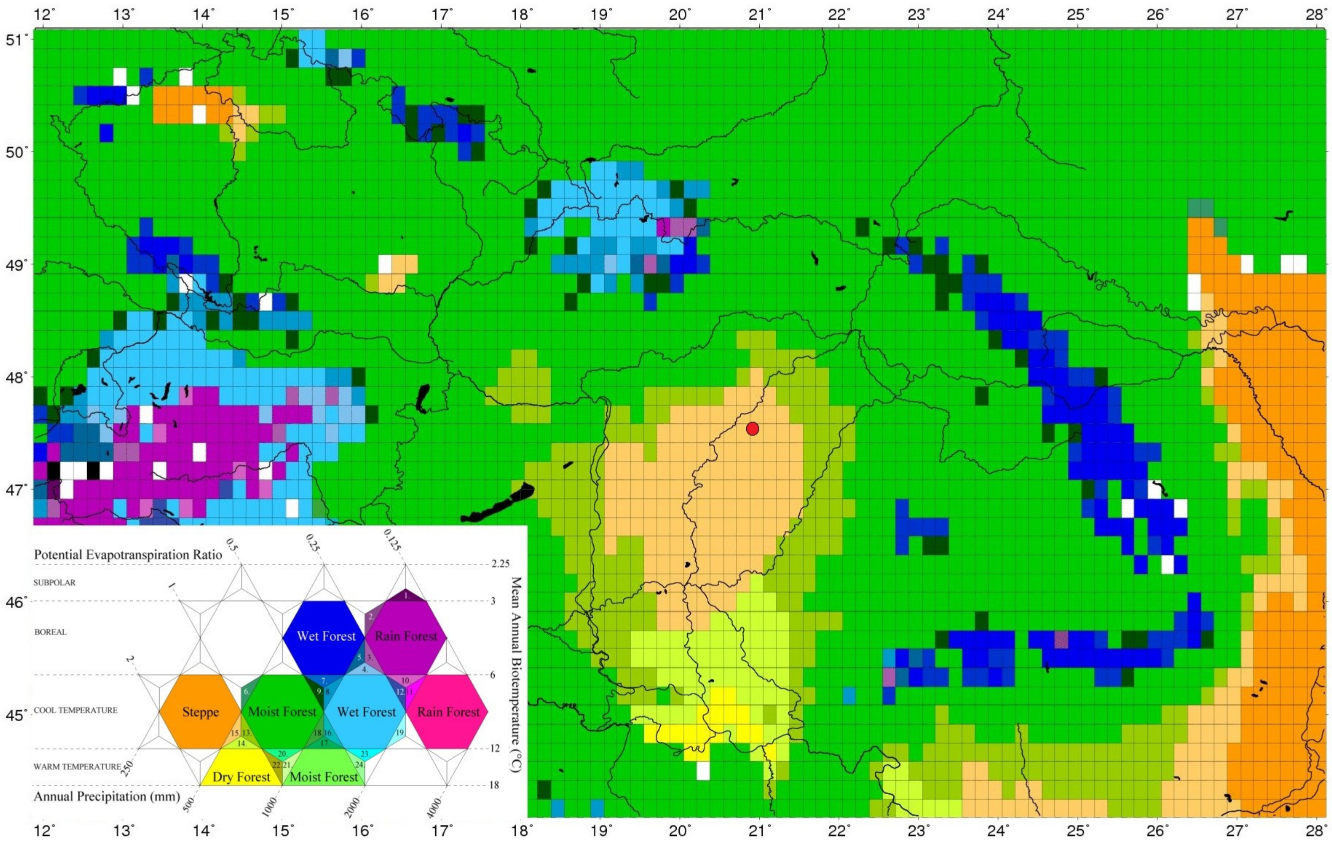

Figure 18. The Holdrige type classification of the vegetation of the Carpathian Basin [135,146–148]. •, study area. The explanation of the colors used in the map squares is given in the hexagons in the bottom left figure. The numbers between the hexagons are MAP (Mean Annual Precipitation) and MAT (Mean Annual Temperature) values.

The first pastoralist cultures (Pit Grave culture = Yamnaja = Kurgan culture), which appeared around 3300 BC, only reinforced ongoing natural processes [46] but did not fundamentally transform the vegetation of the Kunkápolnás region. Similarly, there were no significant changes in the landscape character of the region over the following millennia, when the land management by domestic animals gradually increased and eventually completely took over habitat management, i.e., the grazing role of large ungulates, such as the aurochs and the European bison, which became extinct during the Holocene [149].

Significant negative changes have been brought about to the natural areas of the wider Hortobágy region by the river management and agricultural intensification interventions of the last two centuries, including the drainage of marshes, the irrigation of pastures, and the creation of fishponds and rice fields. Hortobágy National Park, Hungary's largest protected area, was established in 1973 in the central part of the region, which has been relatively little affected by these interventions, and the natural alkaline grassland–wetland complexes continue to dominate the landscape to this day (Figure 2). The foundation of Hortobágy National Park 50 years ago put a halt to these negative processes. Since then, the site management organization, the Hortobágy National Park Directorate, initiated and implemented several habitat restoration projects aiming to preserve and restore the degraded natural vegetation mosaics. As a result of these consequent conservation efforts, water supply systems for altogether 5000 hectares of marshes have been established, and more than 1000 km of disused channels, dykes, and ditches were eliminated in the already 80,000 ha area of the National Park. These already-implemented, landscape-scale conservation measures, together with the recently planned restoration of the water regime of the central part of the Hortobágy area, will hopefully enable the conservation of this unique habitat complex's mosaic structure, along with the diverse fauna it hosts, for future generations.

In light of the recent scientific results providing evidence on the primary, natural origin of the alkaline grassland–wetland complexes of the site, as well as based on the limited occurrence of alkaline and sodic areas in Eurasia [150], the relevant Hungarian authorities might consider the nomination of the Hortobágy National Park—the Puszta property for the World Heritage List under the following natural criteria as well.

Criterion (vii): The flat and open landscape of Hortobágy National Park is an area of exceptional natural beauty, representing the highest scenic quality, with pleasing and dramatic patterns and combinations of landscape features, which provides it a distinctive character, including aesthetic qualities and topographic and visual unity.

Criterion (viii): The site is an outstanding example that represents the natural landscape and vegetation development of the Late Quaternary stage of Earth's history, including significant ongoing geological processes in the development of landforms and significant geomorphic features.

Criterion (x): Hortobágy National Park contains the most significant natural habitats for the in situ conservation of biological diversity in the temperate steppe zone, including those containing threatened species of outstanding universal value from the point of view of science or conservation.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/d16010067/s1: Video S1: Grassland–wetland mosaic habitats of the alkaline steppe in Hortobágy National Park, Hungary.

Author Contributions: Conceptualization, P.S. and G.S.; methodology, P.S., S.G. and T.Z.V.; software, S.G. and T.Z.V.; validation, P.S. and S.G.; investigation, P.S., S.G. and T.Z.V.; writing—original draft preparation, G.S., S.G., T.Z.V. and P.S.; writing—review and editing, G.S., S.G., T.Z.V. and P.S.; visualization, S.G., T.Z.V., P.S. and G.S.; supervision, P.S. and S.G.; project administration, P.S. and G.S.; funding acquisition, P.S. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflicts of interest.

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