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I dedicate this work to the kindest Ukrainian scientists who despite the horrors of the war have contributed a great deal to the current project, and to the Russian and Ukrainian people who do not follow the propaganda of violence and hatred. With the hope that soon our countries will find their way to live a peaceful and happy life as neighbours, I would like to start…

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Abstract

While many studies have documented changes of the northern latitudinal forest limit in Europe and its drivers, little is known about the southern latitudinal limit of the forest towards the steppe in Eastern Europe. Characterized by fertile chernozem soils, the region has been consequently anthropogenically changed, with more than 80% of the area used as cropland by the year 2000. Therefore, it is hard to estimate the natural extension of the forest-steppe zone and to predict the response of the ecosystems to the global warming in the future. For sustainable management strategies, nature conservation and land use should be based on the knowledge of the natural vegetation of the area, which can be obtained by palaeoecological studies.

This work contributes to the understanding of the vegetation dynamics of the East-European forest-steppe due to climate changes, human impact and fires since the Late Glacial period. The results of multi-proxy analyses of four sediment cores obtained from the northern, central and southern parts of the ecotone during the expeditions of 2009-2013 are presented in the dissertation. Combining all available records, we reconstruct the forest cover using the modern analogue technique and evaluate possible shifts in the forest limit and the character of the ecotone since the postglacial. With the use of transfer functions, we explore potential climate forcing that may have changed the vegetation in the ecotone during the postglacial.

The research shows that the vegetation of the East-European forest-steppe is highly sensitive to moisture availability caused by the northern hemispheric climate changes. Thus, the stadial periods of the Late Glacial caused the steppe spread while forest-steppe was developing during the interstadials within the study region. The region became an ecotone between forest and steppe zones by ~8 cal. kyr BP after the Holocene warming ~11.7 cal. kyr BP allowed the spread of forest into steppe. The spread of the broadleaf trees coincided with decreasing summer insolation and temperatures in the late mid-Holocene and late Holocene lowering evapotranspiration values and increasing the amount of available moisture. During the late Holocene the region became entirely forested including its southern limits.

The southern treeline is extremely sensitive to human activities. With the development and spread of agriculture, local societies induced deforestation and fires to clear the land. In the last 800 yrs the area of the ecotone became deforested reaching the minimum forest cover in the 17th century. The conversion of the forest-steppe into an agrarian steppe left over only very small patches of semi-natural vegetation today.

Considering the current global warming the southern tree line is likely to shift northwards bringing the area to the mid-Holocene conditions. Lower aridity index and therefore moisture availability will increase the risks of droughts affecting agriculture in the region.

Chapter I – Introduction

Since the pre-Industrial period to 2015 the mean land surface temperature has risen by 1.53°C (IPCC 2019). While climate change has adversely been impacting terrestrial ecosystems contributing to desertification and land degradation, the global population growth and changes in consumption of food, feed, fibre, timber and energy have caused unprecedented rates of land and freshwater use with agriculture accounting for around 70% of global fresh-water use. East-European forest-steppe is one of the world's major agricultural producers due to the occurrence of fertile chernozem soils and favourable climate conditions. By the year 2000, up to 80% of its territory was used as cropland (Ramankutty et al. 2008) leading to a noticeable decrease in thickness of the humus horizon (Khitrov et al. 2019). Almost no natural vegetation remains in the area but a few protected land plots of the Nature Reserves. Based on satellite images, the remaining woodland cover in the Mid-Russian Upland is estimated to be between 9% to 30% (Bartalev et al. 2011). Considering the risks of the ecosystem loss due to the climate change and anthropogenic pressure, the knowledge of the history of its formation and the response of its natural vegetation to climate changes may provide guidelines for nature conservation and restoration attempts.

East-European forest-steppe

Stretching over 2000 km from the Carpathian Mountains in the west to the Urals in the east, the belt of the East-European forest-steppe is a transition zone between temperate woodland in the north and west and true bunch-grass steppes in the south (Donita et al. 2004). It represents a mosaic of nemoral deciduous forest patches and meadow steppes, the distribution of which is determined by the relief, microclimate, soil composition as well as grazing and land use (Erdős et al. 2019). Under natural conditions, dry and warm southern slopes are occupied by steppes and dry grasslands while the forests prefer northern slopes, valleys, gorges, hollows and mountain tops. The position of forest-steppe at the junction of the contrasting natural zones and the intra-landscape mosaic of heterogeneous communities create an extraordinary variety of environmental conditions contributing to a high biodiversity (Chernov 1975; Neronov 2015).

The steppe assemblages generally occupy chernozem, solonetz and solonchak soils (Knapp 1979; Lavrenko and Karamysheva 1993) while forests grow on grey forest soil and occasionally on chernozem and solonetz (Erdős et al. 2018). The parent rock for the soil formation is mainly loess sediment (Velichko 2009).

The climate of the region is transitional from temperate to semi-arid. In the lowland part, the annual precipitation is relatively low within 400-600 mm decreasing towards the south and east with a dry period of at least two months in the late summer – early autumn (Donita et al. 2004; Erdős et al. 2018; Walter and Breckle 1994). Within the forest-steppe, the moisture balance is close to neutral. Summer is warm throughout the ecotone with an average temperature around 20-24°C. Mean January temperatures have a wide amplitude from 0 to -2°C in the southwest to -14 – -16°C in more continental parts.

Following the macroclimatic conditions, the composition of the forests and grasslands changes within the forest-steppe region from north to south and from west to east. The forest-steppe can be divided into two major provinces – sub-Mediterranean-subcontinental forest-steppe in the south with an annual temperature above 10°C and a subcontinental forest-steppe with an annual temperature below 10°C in the east (Fig. 1.1) (Donita et al. 2004). Sub-Mediterranean-subcontinental province is distinguished from the subcontinental one through a far higher proportion of thermophilous to xerothermic plant species with *Quercus pubescens*, *Q. robur*, *Q. pedunculiflora* and *Acer tataricum* in the forests and *Festuca valesiaca*, *Stipa*, *Botriochloa ischaemum*, *Chrysopogon gryllus* in herb-grass and meadow steppes.

Subcontinental meadow steppes and steppe-like grasslands comprising *Festuca rupicola, F. valesiaca, Stipa tirsa, S. pennata, Poa angustifolia, Agrostis vinealis* alternate with *Quercus robur* forests. Subcontinental forest-steppe vegetation exhibits a clear differentiation due to an increase in continentality eastwards which is expressed in a change of dominants and increasing role of eastern (West-Siberian, West-Siberian-North-Kazakh and West-Siberian-Kazakh-Mongolian) species (Donita et al. 2004). Therefore, subcontinental province of the ecotone can be further subdivided into Volyno-Podolian, Moldavian-Ukrainian, South Sarmatian, Central-Russian-Volgian and trans-Kamian-trans-Volgian meadow steppes (Fig. 1.1).

The westmost Volyno-Podolian meadow steppes have considerable amounts of *Carpinus betulus* and *Quercus petraea* in the forests and a high proportion of western European shrub and herb species (*Asperula cynanchica, Allium waldsteinii, Centraurea rhenata, Achillea pannonica, Euphorbia lingulata*). In the Moldavian-Ukrainian meadow steppes, pedunculate oak (*Quercus robur*) forests include *Carpinus betulus*, *Acer pseudoplatanus* and *Prunus avium* as well as *Crataegus betulus*, *Cornus sanguinea* and *Vinca minor*. *Thymus* is also widely distributed. The South Sarmatian subprovince includes salty lowlands of the ancient terraces of the Dnieper and Oka-Don region with salinated vegetation and local sedge swamps, reeds, wetland and alluvial forests. In the Central-Russian-Volgian meadow steppes *Carpinus betulus* is absent from the oak forests. Pannonian and East-European species dominate but many West-Siberian and West-Siberian-North-Kazakh species (*Artemisia latifolia, A. sericea*) occur. The easternmost trans-Kamian-trans-Volgian meadow steppes have the least proportion of the Central European floristic elements. *Acer campestre*, *Ulmus minor* and *Fraxinus excelsior* disappear from the broadleaf forests (Donita et al. 2004).

The study area chosen for the current project is located at the junction of the Central-Russian-Volgian, Moldovian-Ukrainian and South Sarmatian meadow steppes (Fig. 1.1). A special plant geographical importance of the study area comprises the nearby eastern border of the *Carpinus betulus* areal (Sikkema et al. 2016) and the southern border of *Picea abies* (Zerov 1950). Easy identification of the pollen grains of both species and their well-defined climatic requirements might help to trace climate changes since the Late Glacial.

Previous palaeoecological studies of the study region

The western part of the East-European forest-steppe is much better studied compare to its eastern part. Multiple palaeoenvironmental records allowed vegetation, climate and fire regime reconstructions of the region (Bozilova and Tonkov 1985; Feurdean et al. 2012; 2013; 2015; 2020; 2021; Florescu et al. 2018; Hájková et al. 2022; Juřičková et al. 2018; Kremenetski 1995; Magyari et al. 2010; Marinova and Atanassova 2006). The more eastern parts of the ecotone are significantly understudied (Borisova et al. 2006; Novenko et al. 2009; 2014a; Shumilovskikh et al. 2018; 2021b).

Since the first half of the 20th century, many works of the Soviet researchers have been published (Chiguryaeva 1941; Neustadt 1940; Pyavchenko 1958; Zerov 1950), yet there were some pollen identification issues (for instance, according to Spiridonova (1991), *Artemisia* pollen was referred to the *Salix* taxon in Chiguryaeva (1941)), the interpretation of the results was direct depending on the amount of pollen types, and due to the absence of radiocarbon dating, the interpretation was based on the stratigraphy and divided in phases. Some of the results of the Soviet researchers' works in the East-European forest-steppe are presented in the Table 1.1. According to them, the area was likely represented by pine-birch forests or forests-steppe (phase #2) prior to the broadleaf forests spread (phase #3).

With the development of the radiocarbon dating in the USSR in 1956 (Zaitseva et al. 1999), the works became more informative. However, there were still many points of disagreements. For example, Khotinsky (1984) demonstrated a change from a desert-steppe in the Late Glacial through xerophytic steppe in the early Holocene and mixed-grass mesophytic steppe in the middle Holocene for the region of the Ukrainian steppes. He underlined an exceptionally stable position of the forest-steppe border during the middle and late Holocene, in contrast to the tundra-forest border, fluctuating over 400-500 km distance. Such stability, however, was not proved by other studies. Thus, Spiridonova (1991) highlighted high dynamics of the forest-steppe ecotone suggesting large changes in the landscape through the Holocene from deciduous mixed-broadleaf forests through forest-steppe and steppe to semi-deserts. There was also no agreement on whether the mid-Holocene climate warming (referred to the Atlantic period) led to the warmer and dryer conditions (Isaeva-Petrova 1985; Serebryannaya 1976) or wetter and less continental (Kremenetsky 1987). Besides, the radiocarbon dates were rarely calibrated (e.g. Borisova et al. (2006)), just one radiocarbon date was often provided for a core or a soil section and then later correlated with the results from the other cores or soil sections based on the pollen composition (Spiridonova 1991).

Modern palynological works of the subcontinental part of the ecotone to the east of the Carpathian area include just few works mostly in the area of the Upper Don (Fig. 1.1, records of Podkosmovo, Don, Ustye) covering the late Holocene period (except Podkosmovo covering the middle and late Holocene) (Borisova et al. 2006; Novenko et al. 2009; 2014a; Shumilovskikh et al. 2019a) (Table 1.2). One of the reasons for the absence of long pollen records is the aridity of the forest-steppe zone which makes it difficult to find continuous palynological archives. A few palynological studies were carried out in the neighbouring broadleaf forest vegetation zone to the north from the study area (Novenko et al. 2014b; 2015; 2016b; 2017) (Table 1.2). Combining these records with the available records from the forest-steppe Shumilovskikh et al. (2018) showed the Holocene greatest expansion of forests between 4.5-2 cal. kyr BP.

However, due to the low data resolution in space and time, the existing records provide rather contradictive general reconstructions of Holocene vegetation and climate change, lack details of the forest-steppe dynamic and provide insufficient information on the role of humans and fire. Until now there have been no continuous well-dated palynological records available for the study region for the Late Glacial and Holocene.

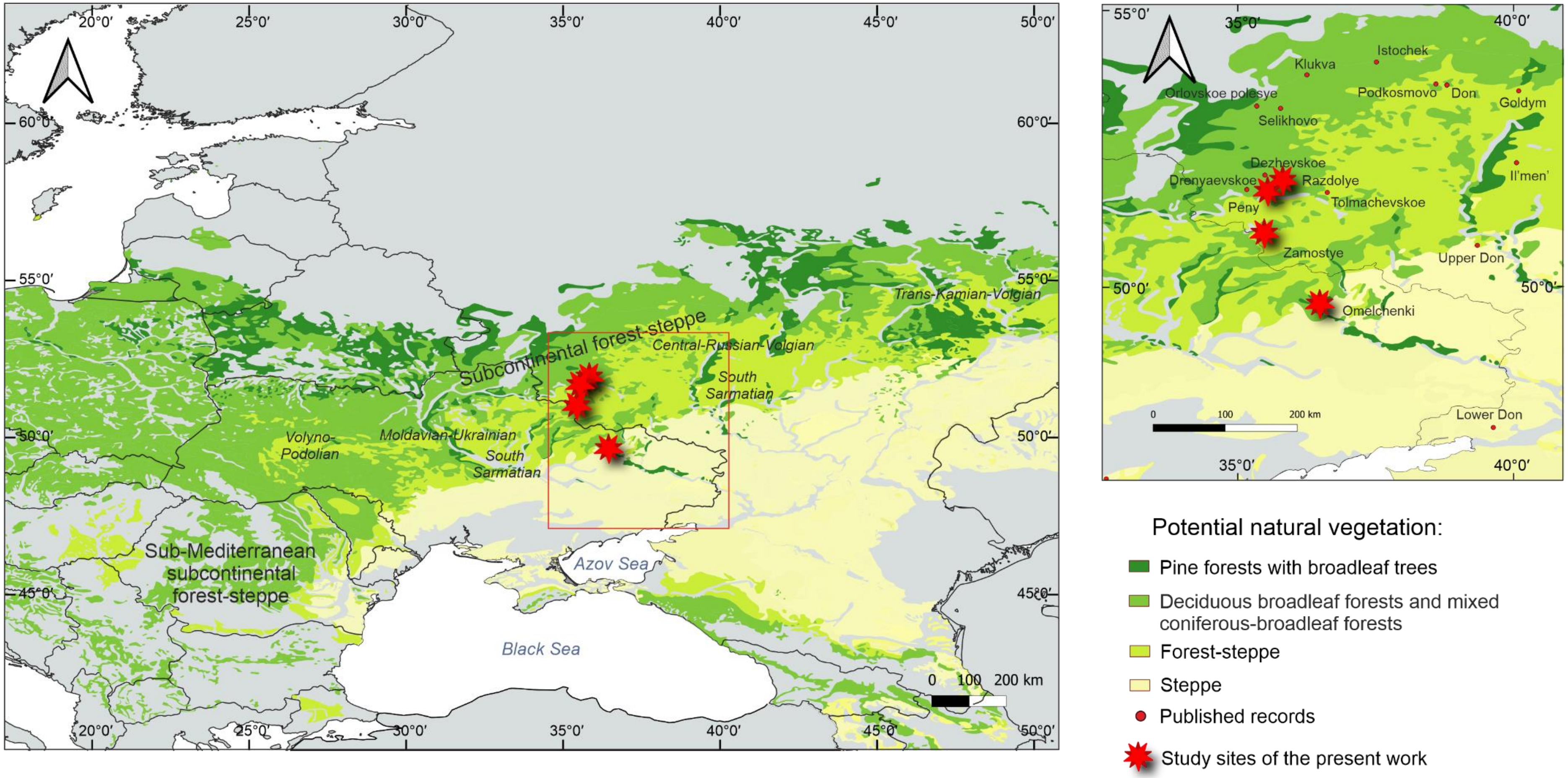

Fig. 1.1. Map of potential natural vegetation of the East-European forest-steppe and published records in the study area (after Bohn et al. (2004))

Table 1.1 – Results of some Soviet researchers' works of the beginning-middle of the 20th century (Fig. 1.1) (Spiridonova 1991)

Phase #	**Goldym** (Pyavchenko 1958)	**Dezhevskoe** (Pyavchenko 1958)	**Drenyaevskoe** (Pyavchenko 1958)	**Tolmachevskoe** (Pyavchenko 1958)	**Il'men'** (Pyavchenko 1958)	**South of the Penza Region**, **Russia** (Chiguryaeva 1941)	**Ukraine** (Zerov 1950)
4	Dominance of pine and birch, decrease of broadleaf taxa. Anthropogenic influence.	Steppe due to anthropogenic influence.	Steppe due to anthropogenic influence.	Increase of pine, decrease of alder and broadleaf taxa.	Decrease of broadleaf species, increase of birch and pine.	Phase of broadleaf forest. The author divided it into 4 stages due to the maximum of the taxa occurred in the spectra	Mixed forest phase, the dominance of pine with beech, hornbeam, fir. Decrease of oak in the second half of the phase.
3	Pine and broadleaf forests with oak, lime and hazel. No elm and hornbeam	Broadleaf forest-steppe	Forest-steppe	Broadleaf forests	Oak forest-steppe with an increase of birch and a decrease of alder, elm and hazel		Mixed forest, oak forest elements, presence of hornbeam
	Pine and broadleaf forests with oak, lime, elm, hazel and hornbeam						
2	Pine-birch forest-steppe. No broadleaf taxa.			Pine-birch forests	Oak forest-steppe with a significant amount of elm	Birch stage, little oak and alder	Pine or bine-birch forests
						Willow (most likely *Artemisia*) and pine. Little alder and broadleaf taxa.	
1	Forest-steppe with spruce-birch forests with oak, elm and later hornbeam.	Few woodlands in the beginning of the phase.	No data	No data	Steppe with a few trees close to water.	Birch stage. Little alder and oak.	Phase of early mixed forest (interstadial)
						Steppe	

Table 1.2 – Late Soviet and modern studies from the forest-steppe, broadleaf forest and steppe vegetation zones (Fig. 1.2). Provided reconstructed forest cover values were taken from Shumilovskikh et al. (2018)

Age (cal. yrs BP)	**Broadleaf forest zone**				**Forest-steppe**					**Steppe**	
	Klukva (Novenko et al. 2015)	**Istochek** (Novenko et al. 2017)	**Orlovskoe Polesye** (Novenko et al. 2014b)	**Selikhovo** (Novenko et al. 2016b)	**Podkosmovo** (Novenko et al. 2014a)	**Ustye** (Novenko et al. 2009)	**Don** (Novenko et al. 2009)	**SV-8** (Borisova et al. 2006)	**Sudzha** (Shumilovskikh et al. 2019a)	**Upper Don sites** (Spiridonova 1991)	**Lower Don sites** (Spiridonova 1991)
0	Anthropogenic disturbance (reconstructed forest cover 45-55%).	Agricultural landscape (reconstructed forest cover 30-35%).	Pine and mix-broadleaf forests. Anthropogenic impact.	Agricultural landscape (reconstructed forest cover 5-10%).	Agricultural landscape (reconstructed forest cover 9-15%).	Agricultural landscape.		No data	Agricultural landscape (reconstructed forest cover 12-18%).	Steppe/ forest-steppe.	
500	Mixed-broadleaf forests (forest cover 40-60%).	Mixed-broadleaf forests (forest cover 30%), anthropogenic disturbance.	Pine forests with increase of spruce and broadleaf trees.	Pine-broadleaf forests (forest cover 20-50%), disturbance.	Grasslands increase (forest cover 15-25%), anthropogenic disturbance.	Forest-steppe with broadleaf woodlands.		Mixed pine forests with broadleaf trees.	Oak-mixed forests (forest cover 30-37%), minor disturbance.		
1000											
1500			Pine-broadleaf forests.								
2000				Pine forests with broadleaf trees (forest							
2500		Mixed-broadleaf forests			Pine forests with	Mosaic vegetation of grasslands with patches of broadleaf trees.				Forest-steppe with	Forest-steppe with
3000									No data		

		(forest cover 40-50%).		cover 40-50%), moderate disturbance.	broadleaf trees and grasslands (forest cover 45%).					boreal species in forests.	boreal species in forests. Increase of grasslands at the end of the period
3500			No data			Meadow steppe with small-size forests of alder and birch on floodplains.				Forest-steppe.	
4000	Mixed-broadleaf forests with some disturbance.							Broadleaf forest-steppe.		Broadleaf forests.	Broadleaf forest-steppe.
4500						Forest-steppe with broadleaf woodlands.				Steppe with forests on floodplains, some fluctuations in vegetation cover.	
5000		Mosaic vegetation with patches of mixed-broadleaf forests and grasslands (forest cover 35-45%).		Mosaic vegetation with patches of pine forests and grasslands (forest cover 30-40%).	Meadow steppe with small patches of forests (forest cover 9-25%).						
5500											
6000	Mixed oak forests.										
6500						No data	No data				
7000											
7500		No data		No data	No data						
8000	Birch-dominated forests.							Herb-grass steppe/ pine forest-steppe.			
8500										Forest-steppe.	Steppe with forests on
9000											

9500	Pine/ pine-birch forests.										floodplains.
10000	No data									Two migrations of forest-steppe into steppe: 1 – pine-birch forests with spruce; 2 – pine and oak trees.	
10500											
11000											
11500								Dry steppe with pine and birch			
12000											
12500											
13000								Boreal/ dark coniferous forest-steppe including Scots pine, possibly *Pinus sibirica*, larch, birch tree, *Alnaster*, *Picea*			
13500											
14000											
14500								Pine and larch forest patches in dry/ meadow steppe			
15000											
15500											
16000											
16500											
17000											

Archaeological background

East-European forest-steppe is a vast region rich in history. The oldest archaeological finding of the region are charcoal lenses interpreted as campfire of primitive men dated to about 200,000 yrs BP (Zorin et al., 2014). The differences in climate and vegetation within the forest-steppe caused the differences in the development of archaeological cultures. Thus, the Neolithic revolution started in the west already by ~7.4-7.3 cal. kyr BP (Motuzaitė Matuzevičiūtė and Telizhenko 2016) while the eastern parts were still populated by forager communities for at least another 1-1.5 kyr (Anthony 1995). Due to these differences, this archaeological review will be focused on the changes within the Central-Russian-Volgian subprovince of the ecotone.

The area was populated in the Upper Palaeolithic. Thousands of Upper Palaeolithic sites have been identified and hundreds were excavated (Zaliznyak 2020). The most famous archaeological complexes include Kostenki (~42–20 cal. kyr BP) (Neugebauer-Maresch 2010), Avdeevo (~22–21 cal. kyr BP) (Medvedev et al. 2019), Buki (~22–17 cal. kyr BP) (Markova and Puzachenko 2022) and Divnogorie (~17–14 cal. kyr BP) (Sycheva et al. 2016). Major occupations of the people of the Palaeolithic age were hunting mammoth, reindeer, bison and horse as well as gathering (Dolukhanov and Arslanov 2009; Zaliznyak 2020).

The development of forest-steppe with the beginning of the Holocene following the climate warming ~11.7 cal. kyr BP (Borisova et al. 2006; Hájková et al. 2022; Lukanina et al. 2022; Schwörer et al. 2021) led to the change of fauna to non-herd animals such as red deer, wild boar and roe deer in the northern parts of the forest-steppe (Bibikova 1978). In the more open southern part, however, herd animals were still hunted (Stanko and Kiosak 2010) although many of them became extinct and were replaced (Dolukhanov and Arslanov 2009; Zalyznyak 2020). During the Mesolithic period (~10-7 cal. kyr BP), the hunting type economy reached its peak of development which might have caused its crisis. The early Mesolithic was represented by the Zimovniky archaeological culture (10-9 cal. kyr BP) replaced by the Donets culture in the late Mesolithic (9-7 cal. kyr BP) (Zalyznyak 2020).

The Neolithic revolution in Northern Eurasia occurred in the conditions of the thermal optimum established ~8-7 cal. kyr BP (Dolukhanov 2004). Neolithic farmers from the Near East spread agriculture to the East-European forest-steppe through the Balkan Peninsula by the bearers of Starčevo–Körös–Criș and subsequent Linear Pottery culture (LBK) (Motuzaitė Matuzevičiūtė 2020). The people of the Donets culture who lived in the study area since Mesolithic adopted agriculture not earlier than ~6 cal. kyr BP (*Hordeum* cultivation) (Anthony 1995; Zorin et al. 2014). However, it played a supporting role. Pit-Comb Ceramic culture penetrated the area in the end of the Neolithic period from the north (Shramko et al. 1977).

Due to the expansion of steppe and under the influence of the southern Balkan cultures, stock-breeding became the basis of the economy of the steppe population of the Copper Age cultures (Zalyznyak 2020). Around 5 cal. kyr BP the southern part of the study region was populated by the carriers of the Sredny Stog culture. Their economy was based on cattle breeding and especially horse breeding. The culture was strongly associated with the semi-nomadic Pit Grave (Yamnaya) culture, which formed somewhat later and was spread mainly in the steppe area (Shramko et al. 1977). Findings of querns implied some agricultural activities (Mallory and Adams 1997). According to Zorin et al. (2014) the northern more forested limits of the study region at that time were inhabited by the forager Finno-Ugric ethnic groups.

During the Bronze Age (end of the 5-3 cal. kyr BP) arable farming became the main branch of economy. In the steppe areas, however, cattle breeding was more developed. During 4.6-3.9 cal. kyr BP/26-19 centuries BCE the north of the region was inhabited by the semi-nomadic Catacomb culture tribes who then moved southwards ~3.8-3.6 cal. kyr BP/18-16 centuries BCE. In the north it was replaced by the Abashevskaya archaeological culture (4-3.7 cal. kyr BP/20-17 centuries BCE) engaged in cattle breeding and agriculture (Zorin et al. 2014). The Catacomb and Abashevskaya cultures were replaced by Srubnaya (3.6-3.2 cal. kyr BP/16-12 centuries BCE) and Sosnitskaya culture (second half of 2-beginning of the 1 cal. kyr BP) in the north-west, and later by the Bondarikha culture (3.2-2.7 cal. kyr BP/12-7 centuries BCE). Agriculture played an important role together with cattle breeding and bronze foundry in the economy of these cultures (Shramko et al. 1977).

The beginning of the Early Iron Age is strongly connected with the widespread use of iron since ~2.8-2.7 cal. kyr BP (Zorin et al. 2014) and the migration of agricultural tribes from the right bank of the Dnieper River to the forest-steppe of the left-bank and further to the Don River area. Scythian herdsmen dominated in steppe at that time. Shramko et al. (1977) write that during the Scythian times (7-4 centuries BCE) the forest-steppe area was dominated by the tribes of Melankhlens. Zorin et al. (2014), however, refer to them as to an agricultural Scythoid culture. To protect from the attacks of nomadic Scythians, local farmers fortified their settlements with wooden walls, earthen ramparts and ditches. ~2.5 cal. kyr BP (5th century BCE) the Yukhnov culture invaded the northern parts of the region. However, some Scythoid hillforts continued to exist after the Yukhnians conquered the lands and gradually disappeared among the conquerors (Zorin et al. 2014).

~2.1 cal. kyr BP (2 century BCE) nomadic Sarmatian tribes invaded the Black Sea steppe and further the forest-steppe. Scythians were forced out of the southern steppe region (Shramko et al. 1977; Zorin et al. 2014). The basis of the Sarmatian economy was the breeding of cattle, sheep and horses. Sarmatians did not build settlements, in summer they wandered with their herds in steppe and in winter they went down to the river banks to winter pastures (Zorin et al. 2014). Around the same time Zarubyntsi archeological culture appeared in the Middle and Upper Dnieper reaching the study region by the 2nd century CE. They cultivated fertile light forest soils and podzolized chernozems for growing millet, rye, wheat and barley, grazed cattle in the meadows of river floodplains, manually made simple pots from clay, and smelted iron from swamp ores (Zorin et al. 2014).

~1.7-1.5 cal. kyr BP (3-5 centuries CE) the Chernyakhiv archeological culture was spread on the vast territory of forest-steppe and steppe from the lower Danube in the west to the Donets River in the east including our study area (Lyubichev 2019). The basis of the subsistence economy was agriculture, and the population actively used the black soil (chernozem) of the region. They grew mainly wheat and barley but also millet and rye (Zorin et al. 2014).

At the end of the 1.6 cal. kyr BP (4 century CE) the Huns came from beyond the Volga River moving towards the decaying Roman Empire in the west. Due to the pressure from Bulgarian nomads in the Balkan Peninsula, the Slavic tribes were forced to partially abandon their land and carry away their skills of cultivating arable land, use of a heavy plow and building stone or clay stoves in their homes to the east (Zorin et al. 2014). Early Slavic sites were dated to the 1.5-1.3 cal. kyr BP (5-7 century CE) in the Kharkiv region (Shramko et al. 1977). The territory became part of Kievan Rus by the 1 cal. kyr BP (10 century).

The Saltovo-Mayaki culture was also spread in the south of the region ~1.2-1 cal. kyr BP (8-10 centuries CE) and was closely associated with the Khazar Khaganate. Several variants of the Saltovo-Mayaki culture represented different social-economic lifestyles from nomadism to semi-sedentary agropastoralism (Kiyashko 2016; Pletniova 1967). In the 10th century Kievan Rus defeated Khazar Khaganate and the forest-steppe part of the region was united under the Kievan Rus rule (Shramko et al. 1977).

Fires

Fire is an integral part of many ecosystems. For Central-Eastern Europe, Feurdean et al. (2020) showed that fire was one of the major factors impacting the formation of the forest-steppe vegetation since the beginning of the Late Glacial – Holocene transition. Furthermore, biomass burning is the high in the forest-steppe areas with 45% tree cover declining towards ~60% tree cover for the regions dominated by temperate forests. A higher tree cover provides moister and more wind-protected microclimate which decreases fuel flammability. Therefore, with the development of forest-steppe, the vegetation becomes prone to stronger fires affecting the species composition, biodiversity, canopy openness, as well as nutrient and hydrological cycles (Erdős 2014; Weddell 2001). Until now, there have been no palaeofire records from the East-European forest-steppe including both Ukraine and the south of Russia (Marlon et al. 2016). The role of fires in vegetation dynamics is unknown.

Study area

To get a deeper insight into vegetation and climate dynamics of the East European forest-steppe a project of "Holocene dynamics of the East-European forest-steppe: climate, human and fire impact" was funded by DFG (grant 422265568). A territory between the Kursk (Russia) and Kharkiv (Ukraine) regions was chosen as a study area (Fig. 1.1, 1.3). Located in the south-west of the Mid-Russian Upland between the rivers of Dnieper and Don, it is a part of subcontinental forest-steppe at the transition from the Moldavian-Ukrainian and South Sarmatian to the Central-Russian-Volgian meadow steppes (Bohn et al. 2004). The landscapes represent flat undulating watersheds of 200-250 m above sea level, dissected by a dense network of river valleys, ravines and gullies.

Highly divers and rich in continental species forest-steppe of the study area include meadow steppes with *Stipa tirsa, S. pennata, S. capillata, Festuca rupicola, F. valesiaca, Carex humilis*, *C. pediformis, Helictotrichon desertorum*, *Artemisia latifolia, A. sericea, Campanula wolgensis* alternating with maple-oak, lime-oak and ash-oak forests (*Quercus robur, Acer tatarica, Tilia cordata, Fraxinus excelsior*) (Bohn et al. 2004). South-eastern European xerophytic herb- and grass-rich pine and oak-pine forests (*Pinus sylvestris, Quercus robur*) are

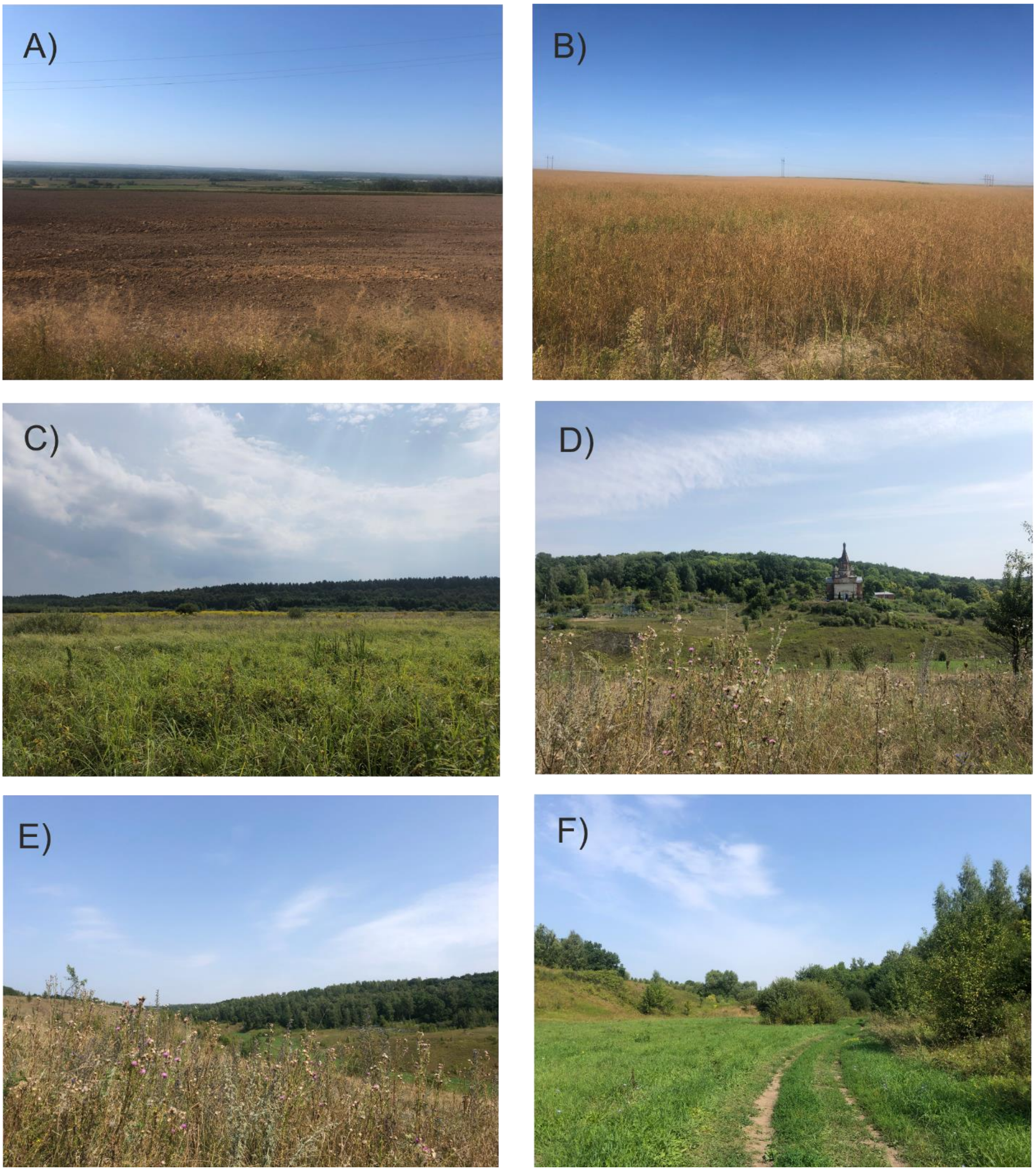

Fig. 1.2. East-European forest-steppe landscape in august 2021: plough fields (A, B) and an overgrazed and abandoned meadow (C) in the north-west of the Kursk region; views along the way from the Pesochnoe khutor to the village of Aleksandrovka (D, E, F) in the Kursk region, Russia

found on sandy soils. In moist and wet sites, East-Sarmatian hardwood alluvial forests (*Quercus robur, Ulmus laevis*) with the fern *Matteuccia struthiopteris* in combination with poplar and willow alluvial forests (*Populus nigra, Salix alba*) as well as willow shrub and alder carrs (*Alnus glutinosa*) are typical. The study area comprises the nearby eastern border of *Carpinus betulus* (Sikkema et al. 2016) and the southern border of the *Picea abies* (Zerov 1950) areal.

True steppe (west and central Pontic herb-rich grass steppes with *Stipa tirsa, S. lessingiana, S. ukrainica, Bromus riparius* and *Paeonia tenuifolia*) replaces the forest-steppe in the south (Karamyeva 2004). To the north, it is replaced by lime-pedunculate oak forests (*Quercus robur, Tilia cordata*) with *Fraxinus excelsior, Acer campestre* and *A. tataricum* (Ogureeva et al. 2004).

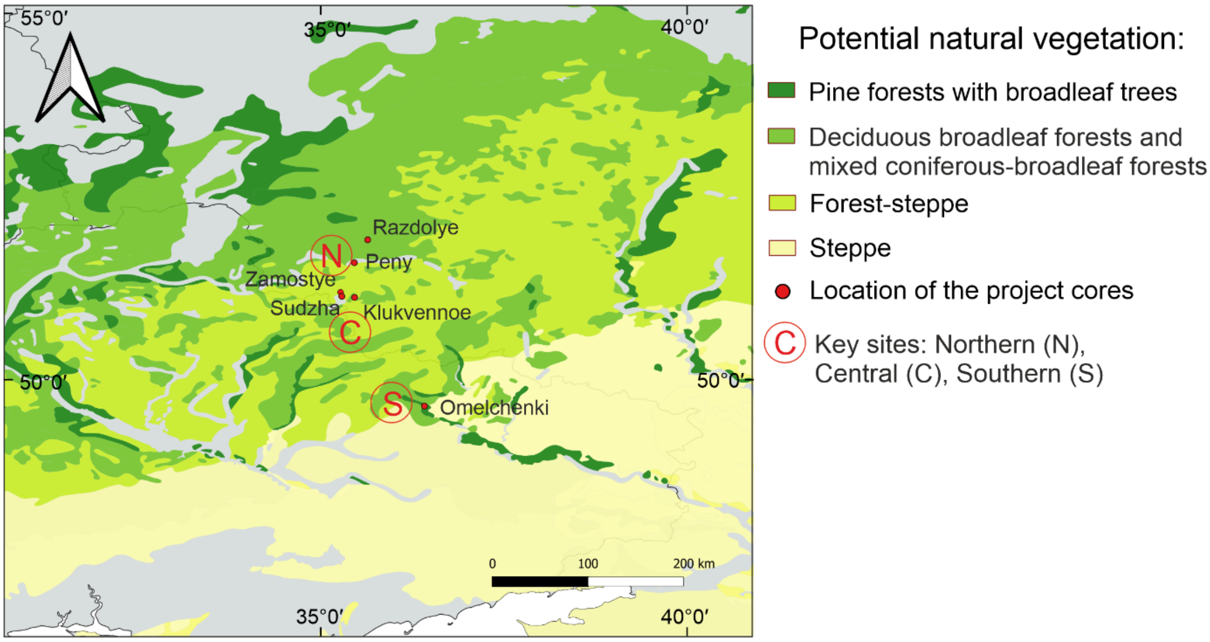

Fig. 1.3. Map of potential natural vegetation of the study area (Bohn et al. 2004) and the project cores

Three key sites (N, C, S) were chosen along a north-south gradient of the forest-steppe: a northern site (N) at the border of the forest-steppe to the forest zone, a central site (C) in the middle of the forest-steppe zone, and a southern site (S) at the border with the steppe zone (Fig. 1.3). Ten sediment cores were obtained during three field campaigns (2009, 2013 and 2016) in the three key regions, and six out of them have been processed and studied (Fig. 1.3). Two oldest and longest cores from the central and southern key sites – Zamostye and Omelchenki – became the main records for my dissertation.

Both sediment cores were obtained in 2013. Originating from an overgrown oxbow lake next to the Sudzha river in the Kursk region, Russia, Zamostye core covers the last 14,800 years providing a valuable insight into the formation of the forest-steppe vegetation since the Late Glacial. Omelchenki core from the southern key site was taken from a peatbog close to the Siverskyi Donets river in the Kharkiv region, Ukraine, and covers the last 9,800 years showing the fluctuations of the southern tree line throughout the Holocene. These cores were studied for pollen, non-pollen palynomorphs, macroremains, loss-on-ignition, macro- and micro-charcoal by myself. First lithological descriptions were carried out in the field and in detail in the laboratory.

Palynological analysis of the other two cores from the northern key site presented in the dissertation were carried out by Alisa Kasianova (Peny core) and Monika Schmidt (Razdolye core). My contribution included LOI of the Peny core and the statistical analysis of its charcoal record.

To assess the pollen spectra of the archives and provide further quantitative reconstructions of climate and forest cover, 60 surface samples from semi-natural environments have been collected in all the three key regions during the field campaigns. My task included their processing and palynological investigation. Using modern analogue technique (Overpeck et al. 1985) and weighted averaging partial least squares regression (Braak and Juggins 1993), I performed climate reconstructions for all the available project cores from the study region, including Zamostye, Omelchenki, Peny, Razdolye, Sudzha (Shumilovskikh et al. 2019a) and Klukvennoe (unpublished data of Lyudmila Shumilovskikh) (Fig. 1.3).

Main tasks and aims

The main goal of the work was to reconstruct the dynamics of the East European forest-steppe ecotone in space and time in terms of the forest composition and change of the ecotone border throughout the Holocene under global climatic changes, human impact, pastoral pressure and fire. We aimed to test several hypotheses:

1) Whether the development of the East-European forest-steppe in the study region occurred in the beginning of the Holocene replacing steppe landscapes and corresponded with the establishment of warm and wet conditions in the Northern Hemisphere;

2) The maximum of the broadleaf trees in the study region occurred in the beginning of the late Holocene similar to the northern Upper Don forest-steppe (Shumilovskikh et al. 2018);

3) A total deforestation and replacement of the natural vegetation by agricultural landscapes in the study area started in the last 400 years, corresponding to the Russian colonisation (Shumilovskikh et al. 2018).

Specific research questions addressed were:

- Did the forest-steppe borders in the study area change during the Holocene and how did these changes correspond to the global climate change?
- How did the forest composition change during the Holocene?
- How does the tree succession correspond to the vegetation history of the western part of the East-European forest-steppe?
- How similar is the history of the study region to the Upper Don forest-steppe, located to the north-east?
- What was the role of disturbances such as deforestation, pasture, fire in the history of the study region?

- What climate variables could be reconstructed through quantitative methods?

Materials and methods

Pollen and NPP

1 cm^3 of wet sediment was taken for the palynological analysis of the cores of Zamostye, Omelchenki, Peny and Razdolye in 1 to 4 cm resolution. For the surface pollen samples, 1 cm^3 of mixed material was taken from each sample. The processing technique followed Faegri and Iversen (1989) and included the treatment with 10% HCl, 48% HF and acetolysis for 3 minutes. The samples were sieved through 200 µm metallic mesh and 5 µm nylon mesh using ultrasound bath for less than 1 minute. To calculate the pollen concentration and influx, 1 *Lycopodium* spores' tablet was added per sample (batch number 1031, 20848 ± 1546 spores per tablet) prior to the chemical treatment (Stockmarr 1971). The samples were then counted to at least 300 or 500 terrestrial pollen grains per sample excluding Cyperaceae under 400× to 1000× magnification. The percentages of the pollen and NPP were calculated relative to the pollen sum of terrestrial plants. To identify the pollen types, we used Beug (2004) and a reference collection of the University of Göttingen, and for NPP – NPP Image Database (Shumilovskikh et al. 2022). Local pollen zones were defined using CONISS (Grimm 1987) while their number was determined by the broken stick model (Bennett 1996) and visually based on the changes in dominant and indicator taxa. Moss pollsters and litter samples taken for the palynological analysis of the modern pollen spectra were additionally treated with 10% KOH prior to the treatment with HF and acetolysis.

Marco- and micro-charcoal

To study the local fire regime, 1 cm^3 of sediment was taken for the macro-charcoal analysis in 1 or 2 cm resolution. The samples were treated following Stevenson and Haberle (2005): 10% KOH, 6% H_2O_2 and sieved through 125 µm metallic mesh. The charcoal was counted under 100× magnification. The results were processed in CharAnalysis version 0.9 (Higuera 2009). Microscopic charcoal was processed and calculated simultaneously with pollen and NPP.

LOI and macroremains

1 cm^3 of the sediment was taken in 1 or 2 cm resolution for LOI analysis. The treatment followed Heiri et al. (2001) and included drying the samples at 105°C for 24 hours, burning at 550°C for 4 hours and at 950°C for 2 hours.

For the analysis of macroremains, entire 1-cm thick core sections were sieved through 250 µm metallic mesh. Remained sediment was studied under 40× to 100× magnification. Cappers et al. (2006) and the Göttingen University reference collection were used to identify the seeds.

Forest cover reconstructions

The reconstructions of the forest cover were performed using modern analogue technique (MAT) based on matching analogues between modern and fossil pollen assemblages (Overpeck et al. 1985). The data set of modern analogues consisted of 726 modern pollen samples from a wide variety of landscapes in Eastern Europe and Siberia (Novenko et al. 2014a) and was combined with estimates of forest cover 20 km around the site from MODIS satellite images (Hansen et al. 2003). Calculations were carried out using the ‘analogue’ package (Simpson 2007). Squared-chord distances were used as a measure of similarity between pollen assemblages and weighted mean of the k-closest analogues. The number of the nearest analogues was defined automatically using the lowest root mean square error of prediction for the leave-one-out errors.

Climate reconstructions

For quantitative climate reconstructions, modern analogue technique (MAT) (Overpeck et al. 1985) and weighed averaging partial least squares transfer function (WAPLS) (Braak and Juggins 1993) were used. Modern pollen dataset included 2287 samples from Eastern Europe and northern Asia including the modern samples collected in the East-European forest-steppe. Modern climate data was acquired from the WorldClim Version 2 (Fick and Hijmans 2017) database and the Global Aridity Index and Potential Evapotranspiration Climate Database v2 (Trabucco and Zomer 2018). Calculations were carried out using the ‘rioja’ package (Juggins 2022).

Outline of the manuscripts and personal contribution

The dissertation consists of five manuscripts. Three of them have been published in peer-reviewed international journals, one manuscript has been submitted and one is being prepared for publication. Formatting of manuscripts is presented as required by different journals. Complete pollen diagrams are presented in the appendix.

The first manuscript “*Vegetation and fire history of the East-European forest-steppe over the last 14,800 years: A case study from Zamostye, Kursk region, Russia*” (by Ekaterina Lukanina, Lyudmila Shumilovskikh and Elena Novenko, published in *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 605, 111218 (2022), https://doi.org/10.1016/j.palaeo.2022.111218) presents a continuous well-dated vegetation and fire history of the central part of the Don-Dnieper forest-steppe area starting from the Late Glacial. The forest cover reconstruction gives an idea of the natural forest cover in the study area throughout the Late Glacial and the Holocene. The vegetation changes are then compared with the published records from the East-European forest-steppe and the climate changes in the Northern Hemisphere. Personal contribution included subsampling, laboratory treatment of the samples for radiocarbon dating, loss-on-ignition, pollen, NPP, macroremains’, macro- and micro-charcoal analyses, the analyses of the listed proxy, the analysis of the results, statistical calculations, interpretation, preparation of all the figures and tables (but the supplementary figures 2.3 and 2.4), writing and revision of the manuscript.

The second manuscript “*Did Holocene climate drive subsistence economies in the East-European forest-steppe? Case study Omelchenki, Kharkiv region, Ukraine*” (by Ekaterina Lukanina, Mikhail Lyubichev, Jens Schneeweiss, Erdmute Schultze, Kyrylo Myzgin and Lyudmila Shumilovskikh, published in *Quaternary Science Reviews*, vol. 305, 108004 (2023), https://doi.org/10.1016/j.quascirev.2023.108004) focuses on the human-environment interactions at the southern limits of the East-European forest-steppe throughout the Holocene and the human impact on the southern treeline of the temperate forests in Eastern Europe. The vegetation changes were compared with the archaeological data from the study area which allowed to discuss the connection of the subsistence economies of the forest-steppe population with the climate changes. Personal contribution included subsampling, laboratory treatment of the samples for radiocarbon dating, loss-on-ignition, pollen, NPP, macroremains’, macro- and micro-charcoal analyses, the analyses of the listed proxy, the analysis of the results, conceptualization, statistical calculations, interpretation, preparation of all the figures and tables (but the supplementary figures 3.1 and 3.2), writing and revision of the manuscript.

The third manuscript "*1,100-years history of transformation of the East European forest-steppe into arable land: Case study from Kursk region (Russia)*" (by Alisa Kasianova, Monika Schmidt, Oleg Radyush, Ekaterina Lukanina, Jens Schneeweiß, Frank Schlütz and Lyudmila Shumilovskikh, published in *Anthropocene*, vol. 42, 100385 (2023), https://doi.org/10.1016/j.ancene.2023.100385) discusses the human-related changes in vegetation and their connection with the historical events over the last 1,100 years. Personal contribution included the loss-on-ignition analysis of the Peny core, statistical calculations of the macro-charcoal results and the revision of the manuscript.

The fourth manuscript "*Modern pollen spectra from the East-European forest-steppe reflect land use patterns rather than climate*" (by Ekaterina Lukanina and Lyudmila Shumilovskikh, submitted to *Vegetation History and Archaeobotany*) is focused on the study of surface pollen samples from the East-European forest-steppe. Here we aimed to study: 1) how the regional vegetation is reflected in the pollen spectra; 2) the main trends in the distribution of pollen spectra and the main factors affecting it; 3) which surface samples can be used for quantitative pollen-climate reconstructions. Personal contribution included subsampling, laboratory treatment of the samples for the palynological analysis, pollen analysis, the analysis of the results, conceptualization, statistical calculations, interpretation, preparation of all the figures and tables, writing and revision of the manuscript.

The fifth manuscript "*Climate dynamics in the East-European forest-steppe since the Late Glacial*" (by Ekaterina Lukanina, Lyudmila Shumilovskikh, Thomas Giesecke, Olga Rudenko and Elena Novenko, in prep.) is focused on the pollen-based quantitative climate reconstructions of the East-European forest-steppe ecotone. We provide the estimations of climate change since the Late Glacial for the project cores and compare them to the corresponding forest cover reconstructions and previously made climate models of the Northern Hemisphere. Personal contribution included the analysis of the available pollen records, collection of data for the modern pollen training set, extraction of modern climate data, statistical calculations and modelling, interpretation, preparation of all the figures and tables, writing of the manuscript.

Table 1.3 – List of the samples processed and analysed by myself

Analysis	*Records*	*Total*
Pollen	66 Zamostye, 52 Omelchenki, 60 surface samples	178
NPP	66 Zamostye, 52 Omelchenki	118
Micro-charcoal	66 Zamostye, 52 Omelchenki	118
Macro-charcoal	120 Zamostye, 150 Omelchenki	270
Macroremains	9 Zamostye, 14 Omelchenki	23
LOI	208 Zamostye, 137 Omelchenki, 44 Peny	389

Overall, 154 pollen and 70 NPP taxa including plant and animal remains, algae, fungi, spores and other have been identified.

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Chapter II – Manuscript 1

Vegetation and fire history of the East-European forest-steppe over the last 14,800 years: a case study from Zamostye, Kursk region, Russia

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Abstract

The East-European forest-steppe extends from the Carpathian to the Ural Mountains, representing a mosaic of broadleaf deciduous forest patches and meadow-steppe, where up to 80% of the territory has been converted to croplands. Here we examine the Late Glacial and Holocene history of the forest-steppe of the East European Plain to better understand its sensitivity to climate fluctuations, fire and human impact, and also the timing of its transition into the modern agro-pastoral landscapes. We studied a radiocarbon-dated sediment core from the village of Zamostye (Kursk region, Russia), which provides a continuous record of vegetation change for the last 14,800 years. We conducted an analysis of pollen, non-pollen palynomorphs, loss-on-ignition, macro- and mirco-charcoal and macroremains, and applied a modern analogue technique to the pollen data to reconstruct forest cover. The pollen data reveal high sensitivity of the vegetation in this region to moisture availability caused by the northern hemispheric climate changes and permafrost. The region was occupied by a pine forest-steppe during Bølling/Allerød but transformed into a cold steppe during the GI 1d and Younger Dryas events. Around 11.7 cal kyr BP the climate warming triggered an expansion of birch trees into the steppe but the lack of moisture and strong fire activity hindered the development of pine and broadleaf forests for more than a millennium. Vegetation turnover occurred at ~10.3 kyr BP, when the vegetation became dominated by pine. Pine and mixed deciduous oak forests continued to dominate through the Middle to Late Holocene reaching their maximal extension by 4.4 cal kyr BP. During the Late Holocene, human impact was detected for the Late Bronze Age, Early Iron Age, Roman period and Early Middle Ages. However, natural forests were recovering after a decrease in human activities. We demonstrate that the forest-steppe of the East European Plain has experienced a total deforestation in the 17th century and has remained open although climate conditions could have allowed the recovery of pine-broadleaf mixed forests.

Introduction

The East-European forest-steppe forms a transitional zone between the mesophilous deciduous broadleaf forests and the true bunch-grass steppe (Bohn et al. 2004). Stretching over 6000 km from the Carpathian Mountains to the Urals, it occupies lowlands and hilly areas between ca. 90 and 500 m a.s.l. (Erdős et al. 2018). Climatically, the southern distribution of deciduous trees is determined by soil moisture availability during the summer months. The increase in aridity from north to south causes the formation of forest-steppe as an ecotone zone between the temperate climate zone VI and the semi-arid steppe climate zone VII (Walter and Breckle 1994). The climate is characterized by the presence of dry period of at least two months in the late summer – early autumn (Bohn et al. 2004; Walter and Breckle 1994). Within the zone, the mesoscale mosaic of forest and steppe patches is determined by the exposition and edaphic factors. Furthermore, steppe vegetation is supported by grazing and fire through physical elimination of young trees, changing nutrient content, and physical properties of soils (Bohn et al. 2004; Chytrý et al. 2022; Walter and Breckle 1994). Heterogeneous landscape allows the interplay of all these factors and leads to high species richness and biodiversity of the forest-steppe zone (Bátori et al. 2018; Chytrý et al. 2022; Erdős et al. 2018).

On a longitudinal gradient, the East-European forest-steppe is divided in two provinces: 1) sub-Mediterranean-subcontinental forest-steppe in the south and 2) subcontinental forest-steppe in the north (Bohn et al. 2004). The first province is characterized by a sub-Mediterranean climate with an annual temperature >10°C supporting herb-grass steppes and meadow steppes (*Festuca valesiaca*, *Stipa*, *Botriochloa ischaemum*, *Chrysopogon gryllus*), alternating with oak forests (*Quercus pubescens*, *Quercus robur*, *Quercus pedunculiflora*) with *Acer tataricum* (Bohn et al. 2004). The second province has a lower annual temperature (<10°C) and an increase in continentality from west to east expressed by the change in both grassland and forest dominants. The westernmost Volyno-podolian subprovince (Fig. 2.1a) has a high proportion of European herb species with the dominance of *Carpinus betulus* and *Quercus petraea* in the forests. The Moladavian-Ukranian meadow steppes are typical for the East-European forest-steppes. The dominance of *Quercus robur* is associated with *Carpinus betulus*, *Acer pseudoplatanus*, and *Prunus avium*. In the Central-Russian-Volgian meadow steppes Pannonian and East-European species dominate and West-Siberian and West-Siberian – North-Kazakh species occur; *Carpinus betulus* disappears from the mixed oak forests while *Fraxinus excelsior* is still present. In the easternmost trans-Kamian-trans-Volgian subprovince the number and importance of the Siberian floristic elements increase further; *Fraxinus excelsior*, *Acer campestre* and *Ulmus minor* are absent in the forests while *Tilia cordata* plays a more important role (Bohn et al. 2004).

In theory, the forest-steppe represents a mosaic of broadleaf deciduous forest patches and meadow-steppe or steppified meadows (Bohn et al. 2004). However, up to 80% of the territory is converted to croplands (Khitrov et al. 2019; Ramankutty et al. 2008). The occurrence of chernozems and, in contrast to the steppe zone, rare droughts provide the basis for agriculture development in the forest-steppe zone (Boonman and Mikhalev 2005). The modern climate warming induces an increase in drought and fire frequencies in arid regions leading to a decrease in harvesting yields and, consequently, affects the social, economic and political life of millions of people as well as biodiversity (IPCC 2019). The current fragmentation of natural and semi-natural habitats due to the more intensive human land use makes the forest-steppe and its biota very sensitive to macroclimatic changes (Chytrý et al. 2022). Therefore, studies on natural variability and resilience of affected ecosystems are highly requested for development of reliable management strategies for the near future.

The late Quaternary vegetation history provides guidelines for understanding the natural ecosystems' responses to climatic changes (Birks and Birks 2005; Willis and Birks 2006). However, comparatively little is known about the East-European forest-steppe region. Most of the well-dated pollen studies focus on the southern and western parts of the region. They allow to trace the long-term vegetation dynamics of sub-Mediterranean subcontinental forest-steppe (Bozilova and Tonkov 1985; Feurdean et al. 2015; 2021; Magyari et al. 2010; Marinova and Atanassova 2006) and of Volyno-Podolian (Schwörer et al. 2021) and Moldavian-Ukranian (Kremenetski 1995) subprovinces of the subcontinental forest-steppe (Fig. 2.1a). Going further east, the records become sparse and fragmented, with the easternmost trans-Kamian-Volgian subprovince lacking continuous well-dated records with the exception of the Late Holocene history of the Kungur-Krasnoufimsk forest-steppe in the boreal zone (Shumilovskikh et al. 2021b). However, in the Central-Russian-Volgian subprovince, twelve dated records exist (Fig. 2.1b), but most of them have poor chronological control and are fragmented (Suppl. table 2.1).

In order to establish a continuous vegetation history of more continental Central-Russian-Volgian subprovince of the East-European forest-steppe region, we carried out palynological studies in the Kursk region (Russia). Located in the middle of the forest-steppe zone, the region is highly sensible to past and present climatic changes. While the region is highly exploited by an intensive agriculture, the remains of natural forest and steppe vegetation are still present in the Tsentralno-Chernozemny Nature Reserve (Central Black Earth Nature Reserve) (Council of Europe 2022). In 2013 we were able to obtain the Zamostye core in the western part of the Kursk region, Russia (Fig. 2.1b). The core covering the last ~14.8 kyr BP was studied for pollen, non-pollen palynomorphs (NPP), macroremains, loss-on-ignition (LOI) and charcoal. The aim of the study is to provide insights into the formation of the East-European forest-steppe vegetation and evaluate how climate, fire and humans have shaped the vegetation.

Geographical setting

Geomorphology and geology

The Zamostye site (51.18481 °N, 35.27988 °E, 135 m a.s.l.) is situated in the south-west of the Mid-Russian Upland in the south of the East European Plain. The landscapes represent flat undulating watersheds of 200-250 m above sea level, dissected by a dense network of river valleys, ravines and gullies. The studied oxbow lake is located in the valley of the Sudzha River belonging to the Dnieper River basin. The territory is characterized by a thick loess mantle, loess-like clays and loams, which are parental material for chernozem and phaeozem soil formation (Sycheva 2012; Velichko 2009).

Climate

The climate is transitional from temperate, moderately humid to semi-arid in steppe (Donita et al. 2004). According to the closest weather station to the study site in the town of Oboyan in the Kursk region, ~70 km to the east from the village Zamostye, the mean annual temperature is 7.3 °C with the average January temperature of -5.6 °C and average July temperature of 20.3 °C (mean temperatures for the period 1990-2020). Annual precipitation is ~630 mm/year with the lowest amount of precipitation in February/April ~40-41 mm and the highest in July ~78 mm. (Kazakov 2004-2021).

Vegetation

The potential natural vegetation represents a mosaic of deciduous broadleaf, aspen-birch (*Populus-Betula*) and pine (*Pinus sylvestris*) forest patches with herb-rich grass steppes. The limiting factor for tree growth is the amount of soil moisture, especially during the summer months. The dominant tree species are *Quercus robur* growing together with *Acer plantanoides*, *Fraxinus excelsior, Corylus avellana* and *Tilia cordata* (Bohn et al. 2004; Shahgedanova 2003). The meadow steppe vegetation is dominated by *Filipendula vulgaris*, *Trifolium montanum*, *Onobrychis arenaria*, *Rhinanthus alectorolophus*, *Bunias orientalis*, *Bromus riparius*, *Festuca rupicola*, *Carex humilis*, *C. praecox*, *Poa angustifolia*, *Stipa pennata* (Bohn et al. 2004).

The study site represents a wetland overgrown by *Phragmites* and surrounded by alder trees and grasslands with ruderal vegetation due to its location in the village of Zamostye.

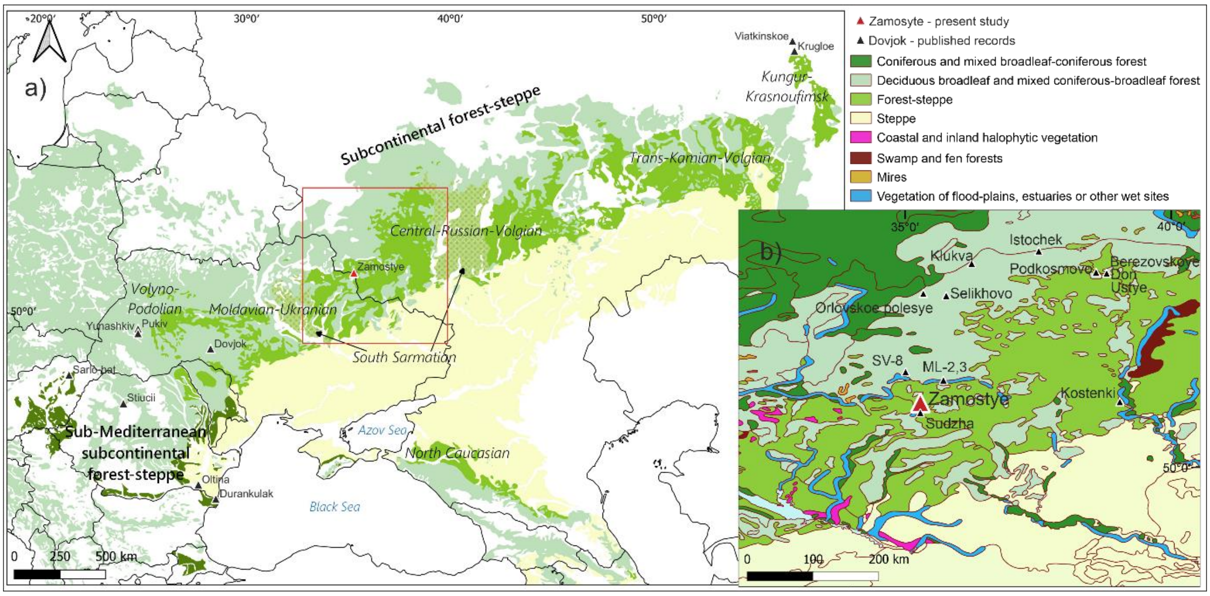


Fig. 2.1. a) Map of potential natural vegetation of the East-European forest-steppe (based on the map of (Bohn et al. 2004); b) Map of potential natural vegetation of the study region in the Central-Russian-Volgian subprovince of the forest-steppe. More information about the published records can be found in Supplementary table 2.1

Settlement history

The East-European forest-steppe was populated during the LGM and the Late Glacial. There are several famous archaeological complexes including Kostenki (~42-20 kyr BP) (Neugebauer-Maresch 2010), Avdeevo (~22-21 kyr BP) (Medvedev et al. 2019), Buki (~22-17 kyr BP) (Markova and Puzachenko 2022) and Divnogorie (~17-14 kyr BP) (Sycheva et al. 2016). There are 148 archaeological sites in the study area (Kashkin 2015; Shumilovskikh et al. 2019a) belonging to almost all the epochs including the Late Palaeolithic. The main activities of the Neolithic tribes presented by just 8 archaeological sites in the region, included hunting, gathering and fishing. The Bronze Age was one of the most populated periods in the region of Zamostye in terms of the number of settlements. The were 74 known settlements and temporary sites within a 20 km radius around the study site (Shumilovskikh et al. 2019a). However, the majority of the archaeological sites were broadly dated to the Bronze Age based on ceramics and fragments of bronze artefacts, while two of the sites could be related to the Early (e.g. Zamost'e-Poselenie 1) and sixteen – to the Late Bronze Age (e.g. Cherkasskaya Konopelka-Poselenie 3; Kniazhiy 1-Poselenie 1). In terms of cultures, eight sites reveal the presence of the Srubnaya culture and eight – of the Bondarikhinskaya culture (Kashkin 2000). Their subsistence economy was mainly based on cattle breeding with less extensive agriculture, fishing and gathering (Zorin et al. 2014). The settlements of the Early Iron Age (7th – 1st century BCE) represented by Scythoid and Yukhnov archaeological cultures were much less present in the region. During the late Roman period the number of sites increased to nineteen: seven sites of the Chernyakhov culture are known, four – of Kiev, four sites belong to both cultures and four are not defined (Kashkin 2000; Shumilovskikh et al. 2019a). The Early Medieval Period (7th – 10th century CE) is famous for the archaeological settlement complex Gornal. It was one of the centres of the Severians (Romny culture), a tribe confederation of the Slavs from the 8th – 10th centuries. The fortification was founded in the 8th century AD and existed until the 70s of the 10th century, when it was burned possibly due to a military invasion of the Kievan Rus (Morgunov 2014). Crop cultivation and animal husbandry (Kashkin 2000; Veretyushkina and Gorbanenko 2015) are well known for this period. The Kievan Rus period (XI-XIII century) was interrupted by the Mongol invasions. The last occupation phase started in the 17th century with southern expansion of the Tsardom of Russia. In 1661 Sudzha town was founded (Babin 2015) and functioned as a military post until the fire in 1725 and then developed into a trade and handcraft centre (Ozerov and Babin 2015).

Materials and methods

Sediment core and chronological framework

Zamostye sediment core was obtained with a Russian corer from an overgrown oxbow lake near the Sudzha River in July 2013 and consists of two sister cores – “Zamostye I” (0-176 cm from surface) and “Zamostye II” (25-250 cm). The two cores were taken close to each other with overlapping segments. The sediment description was carried out directly after obtaining the core. LOI measurements followed Heiri et al. (2001). In total, 208 samples of 1 cm^3 were dried at 105 °C for 24 hours, burnt at 550 °C for 4 hours and at 950 °C for 2 hours.

To determine the chronology, 11 AMS radiocarbon dates were carried out in Poznań Radiocarbon Laboratory in Poland. We calibrated the ages and created the age-depth model using R, version 4.0.4 (R Core Team 2021) and the package ‘clam’ version 2.3.8 (Blaauw 2010; Blaauw et al. 2021) with the Intcal20 calibration curve (Reimer et al. 2020).

Pollen, NPP and micro-charcoal

In total, 66 samples in 1 to 4-cm resolution were obtained for palynological, NPP and micro-charcoal analysis. Laboratory treatment followed the standard processing technique by Faegri and Iversen (1989) included 10% HCl, 48% HF left overnight and acetolysis for 3 minutes. The samples were then sieved through 200 µm metallic mesh and 6 µm nylon mesh using an ultrasound bath for less than 1 minute. Before the chemical treatment, one

Lycopodium spores' tablet (batch number 1031, 20848 ± 1546 spores per tablet) was added to each sample to calculate palynomorphs concentration and influx (Stockmarr 1971).

Beug (2004) and Göttingen University reference collection were used for pollen identification and NPP Image Database (Shumilovskikh et al. 2022) – for NPP. 300 pollen grains of terrestrial plants per sample under 400× to 1000× magnification were counted. Due to the low pollen concentration (<2000 grains/cm^3) three samples that contained less than 300 grains and one sample with less than 100 counts were excluded from the pollen diagram.

The percentages of the pollen, NPP types and micro-charcoal were calculated relative to the pollen sum of terrestrial plants excluding Cyperaceae and aquatics. To visualize the data we used Tilia software version 2.6.1 (Grimm 1991-2019, 1991). To identify the pollen zones we applied cluster analysis using CONISS (Grimm 1987). The number of the main pollen zones was determined by the broken stick model (Bennett 1996), while the subzones were distinguished visually based on the changes of dominant and indicator taxa. To identify the main trends in changes of pollen spectra in a temporal context we performed a Principal Component Analysis (PCA). Furthermore, we excluded rare taxa occurring less than 4 times in the dataset and used a square root transformation to reduce the effect of extreme values. The analysis was carried out using the R packages 'vegan' version 2.5-7 (Oksanen et al. 2020) and 'ellipse' version 0.4.2 (Murdoch and Chow 2020) for correlations with 95% confidence intervals.

Forest cover reconstruction

Reconstructions of forest cover were performed using MAT based on matching analogues between modern and fossil pollen assemblages (Overpeck et al. 1985). The dataset of modern analogues consists of 726 modern pollen samples from a wide variety of landscapes in Eastern Europe and Siberia (Novenko et al. 2014a), combined with estimates of forest cover 20 km around the site from MODIS satellite images (Hansen et al. 2003). Calculations were carried out using the 'analogue' package (Simpson 2007). We used squared-chord distances (SCD) as the measure of similarity between pollen assemblages and weighted mean of the k-closest analogues. The weights used are the inverse of the dissimilarity, $1/d_{jk}$, for each of the k-closest analogues (Simpson 2007). The number of the nearest analogues (k) used for the model was defined automatically using the lowest root mean square error of prediction (RMSEP) for the leave-one-out errors (Suppl. Fig. 2.3). In this approach, the prediction for each sample in the training set is based on k-closest analogues excluding that sample.

Macro-charcoal

Macro-charcoal analysis was performed in 2-cm resolution. The samples were treated following Stevenson and Haberle (2005): 10% KOH, 6% H_2O_2 and sieved through 125 µm metallic mesh. The charcoal was identified under 100× magnification. Four morphological types were identified using Jensen et al. (2007).

Macroremains

We analyzed 14 samples for macroremains to track the changes in local vegetation and sediment composition. The entire 1-cm thick section of the core was sieved through 250 µm and studied under 40× to 100× magnification. We used Cappers et al. (2006) and Göttingen University collection to identify the seeds of the plants. To identify the zones of macroremains we applied a cluster analysis using CONISS (Grimm 1987).

The data obtained in this study was submitted to PANGAEA Data Publisher for Earth & Environmental Science.

Results

Lithological characteristics

The sediment of the core changes from blue, silty clay at the bottom to organic sediment in the middle and then to sands in the upper part intercalated by organic-rich layers at 74-59 cm and 17-0 cm. Visible plant remains are frequent in the upper part of the core.

The LOI results complement the visual description of the core. The top (2-8 cm) and the middle parts (84-200 cm) of the core are rich in organic material. The sediment at 10-82 cm and 202-250 cm consists mostly of the mineral particles. The carbonates' content is ~1-2% for most of the record. Based on the LOI results we combined the first 25 cm of the Zamostye core I with the main Zamostye core II to obtain the composite core from Zamostye.

Table 2.1 – Lithology and LOI values of the composite core from Zamostye

Core	**Depth, cm**	**Description**	**LOI 550 ºC (mineral part,%)**
Zamostye I	0 – 17	Dark brown organic mud with plant remains	61 – 93
	17 – 25	Grey and greyish brown sands	94 – 99.6
Zamostye II	25 – 59	Grey and brown sands with plant remains and black inclusions	90 – 99
	59 – 74	Brown well decomposed organic mud with black inclusions	83 – 91
	74 – 83	Grey and brownish grey sand	89 – 97
	83 – 191	Dark brown decomposed organic mud, with sand at 97 – 109 cm	21 – 80
	191 – 209	Greenish brown organic mud with white inclusions	67 – 86
	209 – 220	Blackish brown organic silt	88 – 95
	220 – 236	Blue–greenish grey silt	96 – 97
	236 – 250	Blue silty clay with black inclusions	97

Radiocarbon dates and age-depth model

Radiocarbon dates in the lower part of the core (218-123 cm) are consistent. Three ^{14}C dates in the upper part show inversions. Samples from 88 cm (^{14}C 565 ± 30 BP) and 118 cm (^{14}C 315 ± 30 BP) consist of *Alnus* wood possibly from roots, which showed an inversion when dated. A bulk sample from 117 cm (^{14}C 3425 ± 35 BP) showed rather old age possibly due to the higher carbonate content and higher chance for the hardwater effect (Shotton 1972). These samples were excluded from the age-depth model (Fig. 2.2, Table 2.2). The model was based on linear interpolation between the dated levels and extrapolated below the lowermost available date. All the ages in the publication are provided in calibrated years BP (before present is related to 1950).

According to the age-depth model, the Zamostye core covers the last ~14,800 years (Fig. 2.2). Sedimentation rate in the lower part of the core (250-96 cm) varies between 0.07 and 0.14 mm/year increasing to 0.86-1.2 mm/year at 96-33 cm and up to 41.7 mm/year in the uppermost part (33-0 cm). Influx data are sensitive to bias and error caused by sedimentological changes. The lithology and the age-depth model of the sediment core show remarkable changes in sedimentary conditions and rates during the last ~500 years of the record. If influx anomalies in the upper part of the core are caused by sedimentological reasons, it is possible that other features in the influx data are influenced by similar reasons.

Table 2.2 – Radiocarbon dates of the sediment core from Zamostye

Sediment core	**Depth, cm**	**Dated material**	**Lab. code**	**Age, ^{14}C year BP**	**Age, cal. BP (probability)**	**Best Age, cal. BP**
Zamostye I	33	Vegetative grass remains	Poz-122529	105.84 ± 0.36 pMC	Modern	-55
Zamostye II	88	Bulk (1.7% carbonates)	Poz-132085	360 ± 30	316-400 (48.4%) 422-494 (45.8%) 405-408 (0.8%)	405
Zamostye II	88	*Alnus* remains (presumably roots)	Poz-121538	565 ± 30*	588-641* (53.5%) 526-563 (41.5%)	-
Zamostye II	96	Bud scale, leaf, *Carex bicarpillata*, Poaceae seeds	Poz-83087	440 ± 30	457-529 (93.9%) 342-348 (1.1%)	498
Zamostye II	117	Bulk (2.2% carbonates)	Poz-132723	3425 ± 35*	3571-3727* (79%) 3792-3824 (11.1%) 3746-3770 (4.9%)	-
Zamostye II	118	*Alnus* remains (presumably roots)	Poz-121580	315 ± 30*	303-464* (95%)	-
Zamostye II	123	Bulk (2% carbonates)	Poz-128969	2545 ± 30	2694-2747 (41%) 2497-2595 (39.2%) 2613-2640 (14.4%)	2635
Zamostye II	144	Bud scale, leaf, *Carex* seeds	Poz-83088	4700 ± 35	5320-5425 (59%) 5431-5482 (24.6%) 5527-5574 (11.1%) 5514-5516 (0.3%)	5419

Zamostye II	160	*Carex tricarpillata* seeds	Poz-125577	6690 ± 40	7476-7620 (92.1%) 7638-7658 (2.9%)	7555
Zamostye II	176	*Carex tricarpillata* seeds	Poz-83089	8620 ± 50	9525-9699 (93.4%) 9493-9509 (1.6%)	9599
Zamostye II	218	Bulk (1% carbonates)	Poz-125578	10510 ± 50	12454-12686 (85.4%) 12268-12303 (3.5%) 12194-12229 (3.2%) 12326-12353 (2.9%)	12523

* – dates excluded from the age-depth model

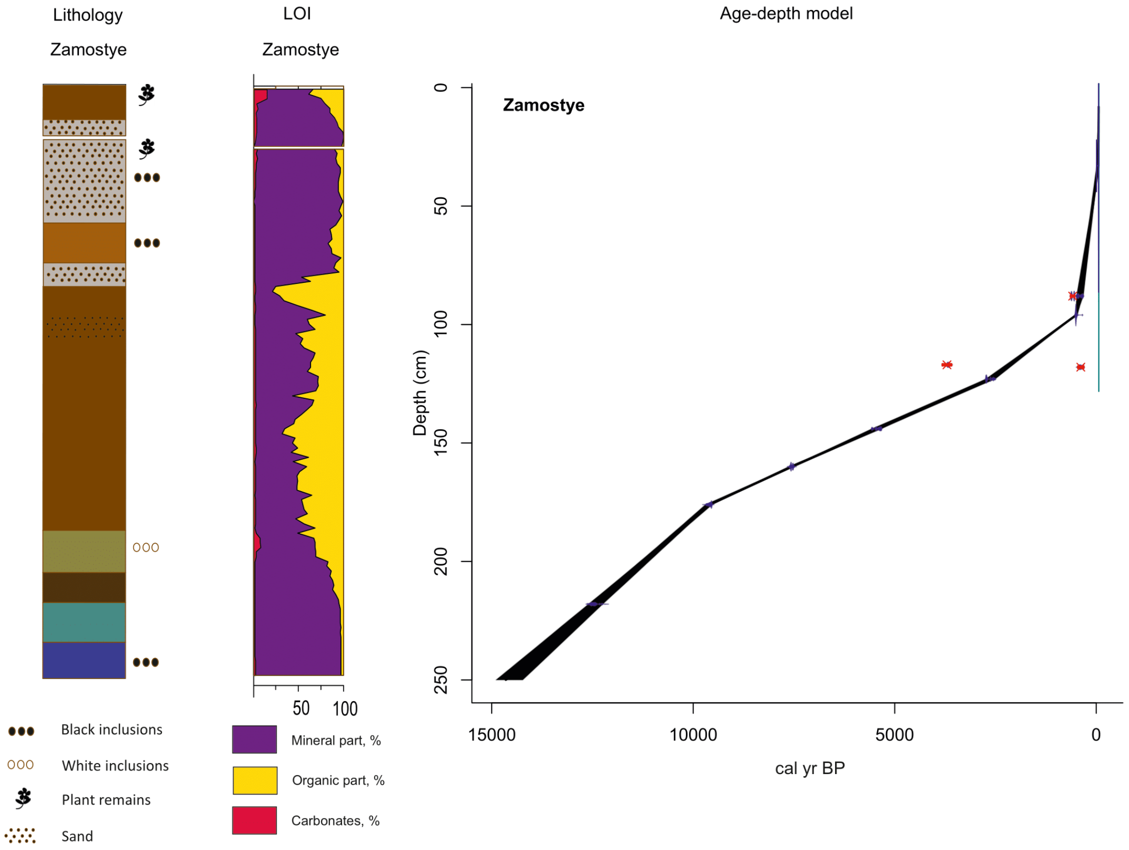


Fig. 2.2. Age-depth model, LOI and the lithology of the Zamostye core

Pollen

Temporal resolution of the pollen record varies considerably. The lowermost part of the core (250-176 cm) has a resolution of ~70 to ~280 years between the samples. In the middle (124-176 cm) it decreases to ~500-530 years. The uppermost part (8-96 cm) has the best resolution of 1 to 50 years.

A total of 110 pollen taxa were identified. The pollen diagram was divided into 4 local pollen zones (ZAM) and several subzones (Fig. 2.3).

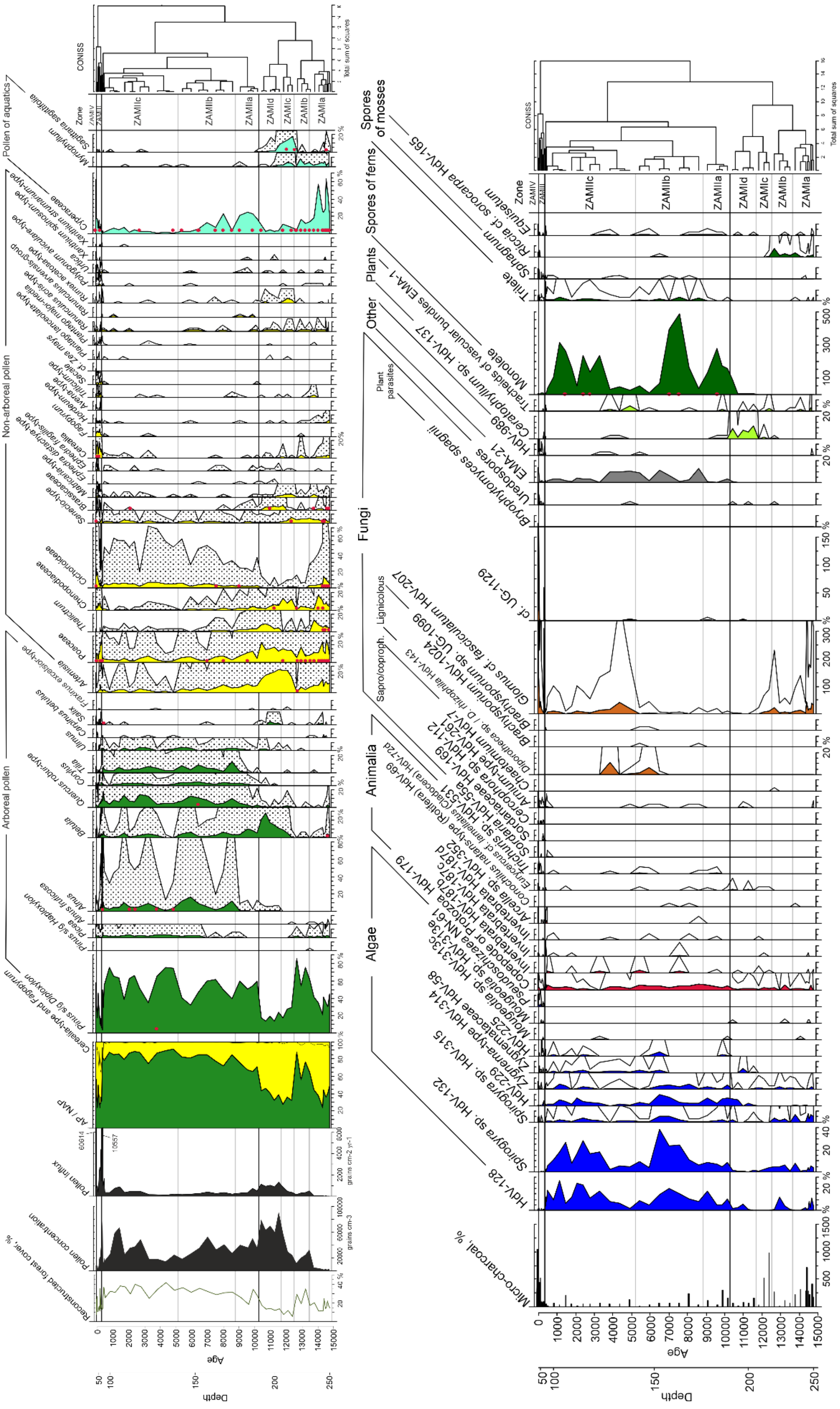


Fig. 2.3. Chosen types of pollen and NPPs of the Zamostye core. Red dots mark the clumps of pollen or spores representing the local presence of the taxon

The local pollen zone ZAM-I (250 – 186 cm; ca. 14.8-10.3 kyr BP) is characterized by the distinct changes in arboreal (AP) and non-arboreal pollen (NAP), based on which we divided the zone into 4 subzones. In the subzone ZAM-Ia (250 – 234 cm; ca. 14.8-13.6 kyr BP) NAP dominates the spectra (44-76%) with Cyperaceae, Poaceae (8-25%), *Artemisia* (6-16%), Chenopodiaceae (2-17%), *Thalictrum* (up to 14%) and Cichorioideae (3-13%). *Pinus* s/g *Diploxylon* (21-52%) dominates among the trees accompanied by *Alnus fruticosa* (following modern taxonomy *Alnus alnobetula* subsp*. fruticosa* (2013)), *Betula*, *Picea*, *Pinus* s/g *Haploxylon* and *Salix* as well as broadleaf deciduous trees (*Carpinus betulus, Quercus, Tilia*).

In the next subzone ZAM-Ib (234 – 218 cm; ca. 13.6-12.5 kyr BP) AP increases up to 56-87% due to an increase in *Pinus* s/g *Diploxylon* up to 86%. Poaceae (5-18%), *Artemisia* (1-7%) and *Senecio*-type (4-6%) dominate among the herbs.

The subzone ZAM-Ic (218 – 206 cm; ca. 12.5-11.7 kyr BP) is dominated by NAP (64-73%) with major abundance of *Artemisia* (18-26%), Chenopodiaceae (8-14%) and Poaceae (13-16%). Among the trees, *Pinus* s/g *Diploxylon* decreases to 17-29%, while *Betula* increases to 9%. *Picea* disappears. Some Cerealia-type pollen grains occurred. These pollen grains likely represent some naturally occurring Poaceae with Cerealia-type pollen grains (e.g. *Agropyron, Elymus*, *Bromus*, *Glyceria*, *Ammophila arenaria* (Beug, 2004).

During the ZAM-Id (206 – 186 cm; ca. 11.7-10.3 kyr BP) AP slowly increases from 39 to 44%. *Pinus* s/g *Diploxylon* decreases (14-24%) while *Betula* reaches the maximum values of 28%. *Alnus*, *Corylus* and *Ulmus* have continuous curves; *Fraxinus excelsior*-type and *Quercus* are present. From this subzone on *Alnus fruticosa* disappears. Among the herbs, *Artemisia* (15-27%), Poaceae (13-23%), Chenopodiaceae (2-6%) and *Thalictrum* (3-9%) are dominant.

The next zone ZAM-II covers almost 10,000 years (186 – 82 cm; ca. 10.3-0.35 kyr BP) and is characterized by the dominance of AP throughout the zone. The most dominant taxon is *Pinus* s/g *Diploxylon*. ZAM-II is divided into three subzones.

During ZAM-IIa (186 – 170 cm; ca. 10.3-8.8 kyr BP) AP further increases (66-75%) with the dominance of *Pinus* s/g *Diploxylon* (51-60%) and *Betula* (4-10%). *Corylus*, *Quercus*, *Tilia*, *Ulmus* increases and *Picea* appears at the end of the subzone. The most represented NAP taxa are Poaceae (5-12%), *Artemisia* (6-9%), Chenopodiaceae (2-4%), Cichorioideae (2-4%) and *Thalictrum* (2-4%).

ZAM-IIb (170 – 142 cm; ca. 8.8-5.2 kyr BP) is characterized by AP dominance throughout the phase (72-85%), presented by *Pinus* s/g *Diploxylon* (32-62%), *Alnus* (2-17%), *Quercus* (4-13%), *Tilia* (2-12%) and *Corylus* (1-5%). Cichorioideae (3-6%), Poaceae (1-7%) and *Artemisia* (3-9%) are abundant among the herbs.

In the ZAM-IIc (142 – 82 cm; ca. 5.2-0.35 kyr BP), AP further increases up to 75-93%, especially in the values of *Pinus* s/g *Diploxylon* reaching 76%. *Alnus* also reaches its peak of 73% during the phase.

The third zone ZAM-III (82 – 42 cm; ca. 350-20 cal yr BP) shows abrupt reduction of AP to 24%. *Pinus* s/g *Diploxylon* (6-46%), *Quercus* (1-10%) and *Alnus* (7%) remain the most abundant tree taxa. Considerable changes occur among the NAP composition: Cerealia-type (4-19%), Poaceae (4-29%), Cichorioideae (2-19%), Chenopodiaceae (2-10%), *Triticum*-type (up to 8%), *Fagopyrum* (2-9%), *Secale* (1-10%), *Artemisia* (1-9%) and *Ephedra fragilis*-type (up to

9%) dominate. *Avena*-type occurred in the pollen record for the first time. Many other NAP taxa such as *Urtica* and *Polygonum aviculare*-type reach their peaks during the phase.

The last ZAM-IV zone (42 – 8 cm; ca. 1930 CE – present) is characterized by further increase in NAP (39-86%). The dominant tree taxon remains *Pinus* s/g *Diploxylon* (10-58%). The most abundant NAP taxa are Cichorioideae (14-63%), Poaceae (3-7%), Cerealia-type (2-6%) and Chenopodiaceae (1-7%). One pollen grain of cf. *Zea mays* occurred. Pollen influx shows distinct anomalies during the last two pollen zones ZAM-III and ZAM-IV.

The dataset used for PCA included 64 terrestrial pollen taxa and 66 samples. The first two components explain 26.6% of the total variance (Fig. 2.4). The first PC axis is oriented between positive scores of *Tilia*, *Pinus* s/g *Diploxylon*, *Ulmus* and other tree taxa and negative scores of *Polygonum aviculare*-type, Cerealia, Chenopodiaceae, *Fagopyrum*, Poaceae, etc. The second axis is oriented between the positive scores of *Thalictrum* and *Artemisia* and the negative scores of *Fagopyrum*, *Secale* and *Quercus*. Sample scores are organized in four distinguishable groups corresponding to the local pollen zones differentiated by CONISS.

The model applied for the forest cover reconstructions shows that three analogues provide the lowest leave-one-out errors RMSEP = 10.709 and R^2 = 0.651 (Suppl. Fig. 2.3). The SCD show the highest values during the Late Glacial, Early Holocene and the last 300 years, indicating no analogue situations (Suppl. Fig. 2.4). Using 5 percentile as a threshold (Simpson 2007), SCD below 0.23 provides good estimations for the Holocene. Forest cover estimations vary between 5 and 35% in the ZAM-I, increase to 18-42% in the ZAM-II, decrease to 11-35% in the ZAM-III and to 8-26% in ZAM-IV (Fig. 2.3).

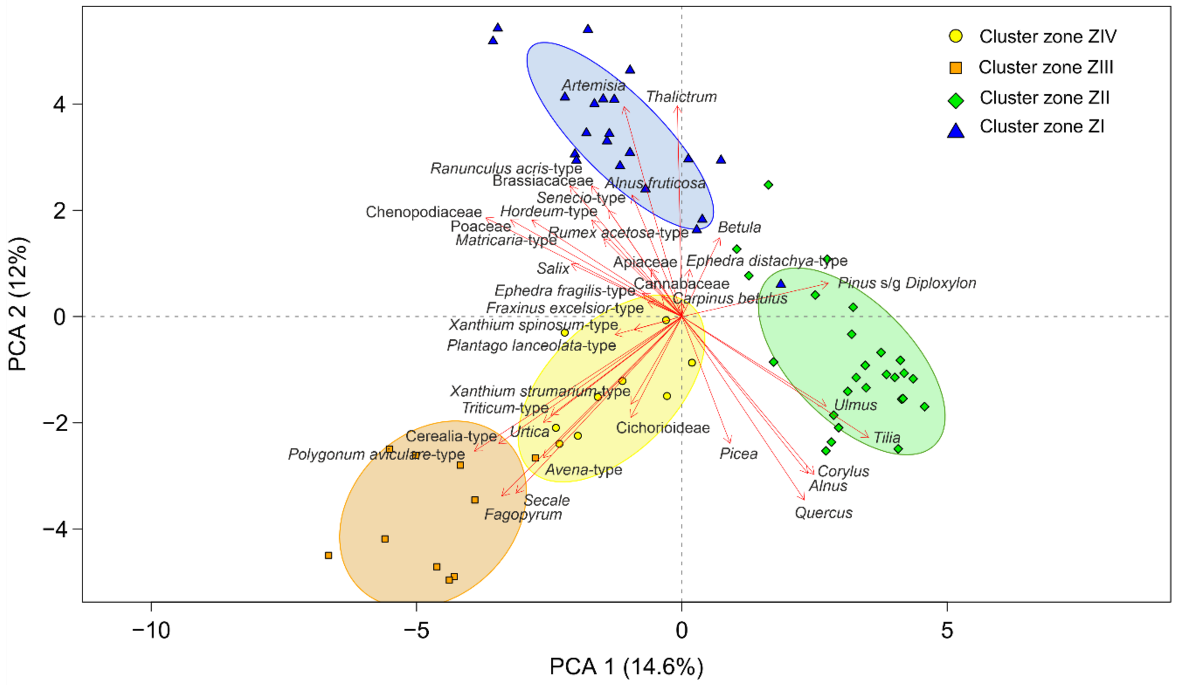


Fig. 2.4. PCA analysis of the pollen record from Zamostye

NPP results

We identified a total of 58 NPP types, including algae, animal and plant remains, fungi, spores of mosses, *Equisetum* and ferns and other non-pollen palynomorphs (Fig. 2.3).

During ZAM-Ia, ZAM-Ib and ZAM-Ic the most represented NPP types were algae *Spirogyra* sp. (HdV-132 and HdV-315 up to 8%), HdV-128 (12%), HdV-179 (4%), chlamydospores of *Glomus* cf. *fasciculatum* (HdV-207 up to 45%), moss spores *Riccia* cf. *sorocarpa* (HdV-165, 8%) and the tracheids of vascular bundles of plants (EMA-1, 3%). In the ZAM-Id phase the listed taxa either decreased or disappeared, while the remains of *Ceratophyllum* sp. (HdV-137) reached the highest values of 12%.

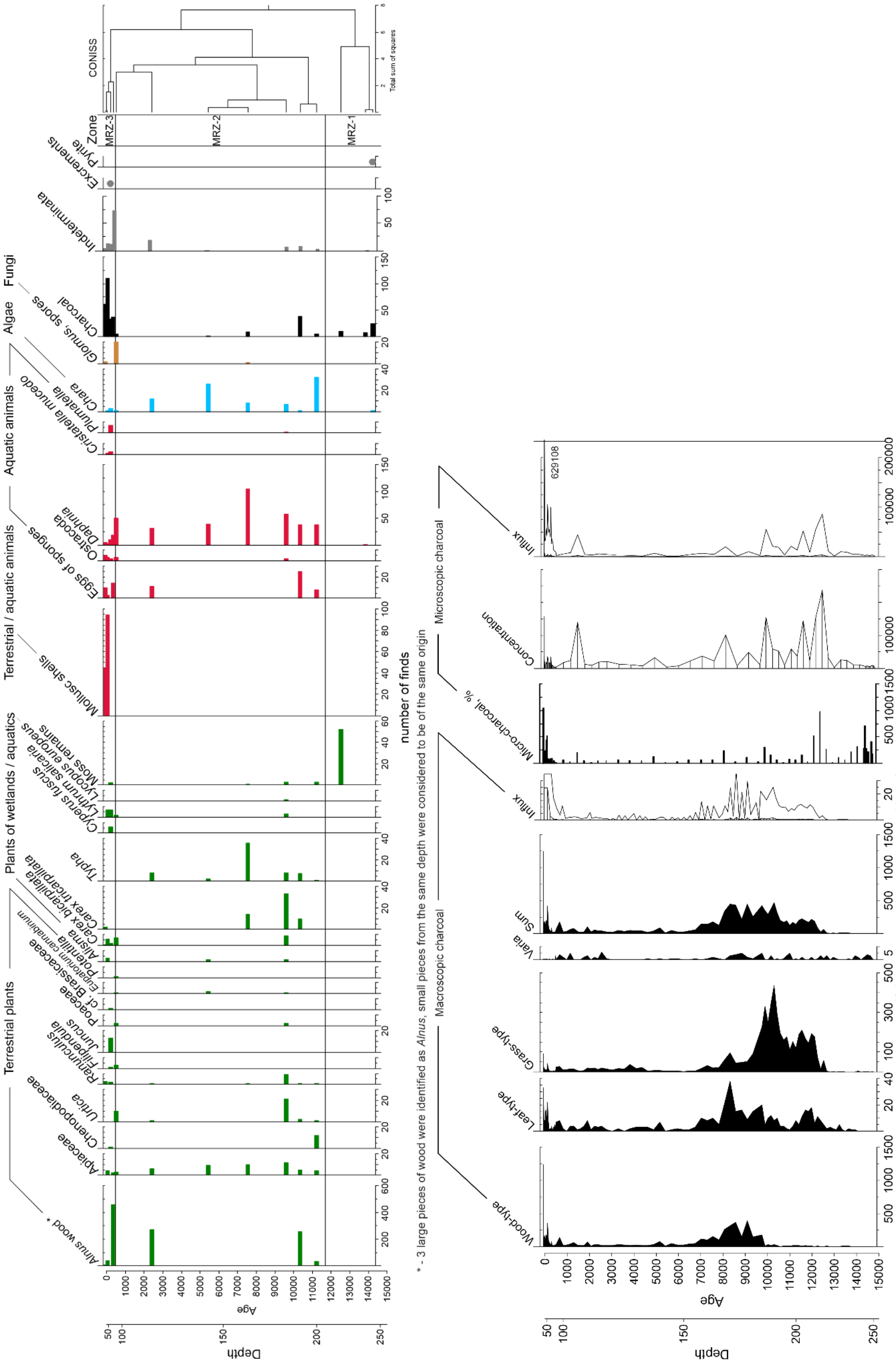
In ZAM-II pollen zone algae became very abundant (up to 77%). *Spirogyra* sp. (38%) and HdV-128 (27%) remained dominant. Other algae types increased: HdV-225 up to 4%, *Zygnema*-type (HdV-314) up to 5% along with the algae HdV-179 (8%) and EMA-21 (13%). Remarkably the values of the monolete fern spores increased up to 488%. In the time period ~6-4 kyr BP the number of algae, HdV-179 and the fern spores decreased significantly. At the same time fungi types *Glomus* (42%) and *Diporotheca* (HdV-143, 11%), tracheids of vascular bundles of plants (EMA-1, 5%) and EMA-14 (2%) increased.

In the last two pollen zones ZAM-III and ZAM-IV algal types, HdV-179 and fern spores decreased or completely disappeared. In ZAM-IV coprophilous fungal types such as *Arnium* (HdV-261, 7%), Sordariaceae, *Cercophora*-type increased. cf. UG-1129 (112%) and *Glomus* (247%) dominated NPP spectra.

Macroremains

We identified 48 types of macroremains, including 31 types of plant remains like seeds, wood pieces, bud scales, leaves and roots, 11 types of animal remains, algal and fungal types and others. 30 types are presented on the diagram (Fig. 2.5). Based on the cluster analysis results and the changes in the macroremains composition, the record was divided into 3 macro-remain zones (MRZ).

In the MRZ-1 (~14.8-11.7 kyr BP, 3 samples) very few types occurred: few eggs of *Daphnia*, moss remains, pyrite and charcoal. Starting from MRZ-2 (~11.7-0.45 kyr BP, 7 samples) high number of wooden particles (c.f. *Alnus*), seeds of Apiaceae, Chenopodiaceae, *Urtica*, *Carex, Alisma, Typha* and other taxa, eggs of sponges and *Daphnia*, ostracods and *Chara* remains were found. MRZ-3 (~0.45 kyr BP – present, 4 samples) is characterized by sharp increases in *Glomus* spores and charcoal, appearance of mollusk shells and *Cristatella mucedo* remains. There was also an increase in the amount of *Carex bicarpillata*, *Alisma*, *Potentilla* and *Lythrum salicaria* fruits and seeds.



* - 3 large pieces of wood were identified as *Alnus*, small pieces from the same depth were considered to be of the same origin

Fig. 2.5. Macroremains' and charcoal diagrams of the core Zamosyte

Charcoal

There is little charcoal in the record from 14.8 kyr to ~12.5 kyr BP (Fig. 2.5). Between ~12.5 kyr and ~9.5 kyr BP mainly grass-type macro-charcoal occurred. This sharp increase in macro-charcoal corresponds to high micro-charcoal concentration and influx values in the same time period. Leaf-type charcoal was also present. The highest values of grass-type macro-charcoal (436 particles per sample) for the record correspond with ~10.3 kyr BP.

High amounts of wood-type charcoal particles (176 particles per sample) appeared in the record starting from ~9.7 kyr BP with the peaks in ~9.1 and ~8.6-8.1 kyr BP (387 and 259-366 particles per sample, respectively). Leaf-type maximum matches the wood-type with the peak ~8.3 kyr BP.

With respect to the macro-charcoal influx and concentration, large number of charcoal particles were accumulated between ~12 kyr and ~8 kyr BP (charcoal concentration up to 365 particles cm^{-3}, accumulation rate 2.4 particles cm^{-2}yr^{-1}). During the Middle and Late Holocene (after ~7 kyr BP) charcoal concentration decreased to 2-57 particles cm^{-3} and accumulation rate – to 0.0008-0.4 particles cm^{-2}yr^{-1}. During the last 1000 years macro-charcoal concentration raised up to 102 particles cm^{-3} and accumulation rate reached the maximum of 24.6 particles cm^{-2}yr^{-1}. From the 18th century until the present day the wood-type charcoal reached its maximum (1237 particles per sample) as well as micro-charcoal influx.

Micro-charcoal influx and concentraion values were high bettwen ~13 kyr and ~9.5 kyr BP reaching 3413 particles cm^{-2}yr^{-1} for influx and 237607 particles cm^{-3} for concentration. During the Middle and Late Holocene the number of micro-charocal particles was low. There were peaks in micro-charcoal ~1.5 kyr BP (influx – 1768 particles cm^{-2}yr^{-1}, concentration – 140128 particles cm^{-3}) and in the last 300 years (influx rose up to 629108 particles cm-2yr-1, concentration – 157277 particles cm-3). The latter, however, likely represents an influx anomaly due to sedimentological reasons.

Interpretation and discussion

Local wetland development

Sedimentation at the Zamostye site started at ~14.8 kyr when an oxbow lake was formed as a meander of the river Sudzha. HdV-179 indicates shallow open freshwater conditions (Geel et al. 1983), supported by finds of *Daphnia* eggs and pollen of *Myriophyllum*, a submerged aquatic plant growing in still or slow-moving water (Pełechaty et al. 2014). Zygospores of *Chara* reveal calcareous water conditions. Marsh plants, such as *Sagittaria sagittifolia* and *Sparganium,* were growing in shallow fens around the lake. Spores of liverworts *Riccia* indicate bare soils alongside open water until the Younger Dryas (Geel et al. 1983). Similar, chlamydospores of *Glomus* cf. *fasciculatum* evidence soil erosion in the lake surroundings (Anderson et al. 1984) during 14.8 and 12.7 kyr BP and reduce after.

The beginning of the Holocene from ~11.5 kyr BP showed the peaks in *Ceratophyllum* and *Chara* – macrophytes growing together in deeper lakes with good light and oxygen availability (high water transparency), higher pH, low total phosphorus concentration and a high species diversity (Pełechaty et al. 2014). An increase in organic content (Fig. 2.2) suggests an increase in the lake productivity. Alder trees were growing on the lake shore (Fig. 2.5).

Shallow lake conditions persisted during almost the entire Holocene, which is indicated by high amounts of algae such as HdV-128, *Spirogyra*, *Zygnema*, HdV-229, HdV-225 and the shores of the lake were overgrown by ferns from the beginning of the Holocene. By ca. 6 kyr BP drier local conditions are suggested by the reduction of algae and increase in

Glomus. The increase in *Diporotheca* sp. (HdV-143) likely indicate a development of the alder carr (Prager et al. 2006). After ~4 kyr BP shallow lake conditions were reestablished.

During the period between ca. 600 and 1500 yr BP (core depth 97-109 cm; Fig. 2.2) organic sediment of the core contains some sand inclusions indicating the possibility of increased fluvial activity.

In the 17th century the process of Sudzha town construction changed the landscape drastically. Total deforestation caused land erosion leading to a rapid overgrowth of the lake (Fig. 2.3 and 2.5). Sand layers appearing from 74-83 cm are likely connected with these changes (Fig. 2.2). Abundant Cyperaceae, *Sphagnum*, appearance of a *Sphagnum* parasite *Bryophytomyces sphagni* and a testate amoebae *Arcella*, as well as the disappearance of most of the algae and aquatics suggest formation of a mire. A sharp increase in *Glomus* indicates the local presence of Cyperaceae roots (Kołaczek et al. 2013).

Vegetation history

The pollen record from Zamostye presents the vegetation history for the last 14,800 years. In order to estimate the dynamics of the forest-steppe, we compared MAT reconstructions to the modern forest cover around the site of 13% and to the estimates for forest/forest-steppe border of ~30% (Fig. 2.6). The data of the Russian Federal Forestry Agency based on which the MODIS forest cover estimations were made (Novenko et al. 2014a) consider the forest cover of the forest-steppe zone to be ~10-25%, for broadleaf, coniferous and mixed forest - ~30-45% and more than 50% - for taiga (Vorobyev 1985).

Late Glacial (~14.8-12.9 kyr BP)

During the Last Glacial Maximum (20-18 kyr BP) the vegetation of the East European Plain differed considerably from modern vegetation. Pollen-based reconstructions suggest a predominance of periglacial tundra and steppe over a large area of northern Eurasia (north of 57°N) to the west, south and east of the Scandinavian ice sheet. Periglacial steppe and forest-steppe vegetation dominated in the latitudinal band from western Ukraine, where temperate deciduous forests grow today (Binney et al. 2017; Borisova et al. 2006; Tarasov et al. 2000; Velichko 2009; Velichko et al. 2011). After the Late Glacial termination, forests developed on the European continent in response to warmer and wetter conditions. The Greenland interstadial 1 (GI 1) evidenced by $\delta^{18}O$ record of NGRIP (Svensson et al. 2008) lasted from ~14.7 to ~12.9 kyr BP and was interrupted by two cold events GI 1d at ~14.0 and GI 1b at ~13.2 kyr BP (Rasmussen et al. 2014).

The Late Glacial spread of trees is clearly reflected by the pollen record of Zamostye. At 14.8 kyr BP, the record reveals the presence of forest-steppe (AP up to 56%) with the dominance of *Pinus sylvestris* accompanied by *Betula*, *Picea, Alnus fruticosa, Salix* and possibly *Pinus sibirica* (ZAM-Ia). Reconstructed forest cover reached 25% suggesting the presence of open forests or forest patches. Heterogeneity of the relief allowed the coexistence of different habitats with steppes on the watersheds and patches of trees in the wetter areas along the rivers. At ~14.3 kyr BP, AP strongly declined to 24% and the study area was occupied by a mosaic of dry and meadow steppe indicated by Poaceae, *Artemisia,* Chenopodiaceae, *Ephedra fragilis* and *Thalictrum*. This cold event likely corresponds to GI 1d (Svensson et al. 2008), although chronological control in the lower part of Zamostye is poor. Arboreal pollen was still present during this short cold phase and forest cover estimates declined to 11-12%. The following Greenland interstadials GI 1a-c had a longer duration

(Svensson et al. 2008), favourable temperatures and higher precipitation values compared to the previous phases. Such climate favoured the development of forests (AP 77-87%) in the study area and the reconstructed forest cover reached 35%. The forest patches consisted mainly of *Pinus*, *Picea* and *Betula* and were possibly accompanied by *Quercus* and *Tilia* (ZAM-Ib). The meadow steppe communities were likely spread over well-drained watersheds.

Forest composition during the Late Glacial was very similar across the lowlands of Central and Eastern Europe. Biome reconstructions indicate the spread of taiga in Central and Eastern Europe (Binney et al. 2017) mainly due to the spread of *Pinus sylvestris, Picea*, trees and shrubs of *Betula* (Borisova 2008; Litt et al. 2003; Novenko 2016; Velichko et al. 2011). Records from Volyno-Podolian forest-steppe show very high AP values up to 90% dominated by *Pinus sylvestris* in association with *Betula*, *Picea* and *Salix* (records of Pukiv and Yunashkiv, Fig. 2.1a) (Hájková et al. 2022). Similar values are characteristic for Zamostye and other records from the Central-Russian-Volgian forest-steppe (records SV-8, ML-2, MK-3, Fig. 2.1b) (Borisova et al. 2006; Panin et al. 2017). The forest composition in the latter region is similar to the northern records (Khotinsky and Klimanov 1997; Schwörer et al. 2021) characterized by the presence of boreal elements such as *Pinus* s/g *haploxylon*-type (*Pinus cembra* and *Pinus sibirica*) and *Larix*, indicative for colder and/or more continental climate. Some eastern locations (Shkurlat III, Kostenki 12) were occupied by *Picea* to a higher degree, suggesting wetter soil conditions possibly through permafrost (Levkovskaya et al. 2015; Spiridonova 1991).

Climatic reconstructions of the Late Glacial show significant variations during the period. Using the arealogram method (Grichuk 1969), Borisova et al. (2006) provided climate reconstructions for the Bølling-Allerød vegetation of the Seim and Svapa Rivers (SV-8 record, Fig. 2.1). The upper Yenisey River in Siberia was identified as an analogue for the beginning of the period with the mean January temperature of -23°C, mean July temperature of 17°C and mean annual precipitation values of 450 mm indicating strong continentality. During Allerød winters became milder with the mean January temperature of -16°C, mean July temperature of 18°C and mean annual precipitation of up to 700 mm, however remaining colder and more continental than at present.

Due to the dating and temporal resolution problems, the correspondence of terrestrial pollen records from Central Europe to NGRIP is not always straight forward. Some records show three warm phases (Meiendorf, Bølling, Allerød), some only two (Bølling, Allerød) and some do not reveal any cold phases (Litt et al. 2003). The pollen records in the modern forest-steppe region are also not consistent. Thus, both records from the western forest-steppe do not show any drastic changes in vegetation composition in response to the Late Glacial stadials (Hájková et al. 2022). In contrast, the more eastern forest-steppe region reveals high sensitivity to the GI 1d, reflected by the pollen record from Zamostye as well as by SV-8 from the fluvial deposits of the Svapa River (Borisova et al. 2006). Similar sensitivity of vegetation to the cold event GI 1d is indicated in the studies from the southern regions e.g. 22-GC3 from the Black Sea, where the climatic fluctuations are reflected by pollen, geochemistry and dinoflagellate cyst records (Shumilovskikh et al. 2012) or by $\delta^{13}C$ record from the Sofular Cave (Fleitmann et al. 2009). Beside chronological problems of terrestrial records, differences in sensitivity of vegetation to Older Dryas can be explained by its short duration between 70 to 90 years (Seierstad et al. 2005). Such short periods are difficult to trace using pollen records known for their delayed response to abrupt climate changes (Shumilovskikh et al. 2014). More continental regions likely experienced stronger impact of cold and dry climate on tree growth and/or pollen production and reacted sensitively to climate change.

Younger Dryas (~12.9-11.7 kyr BP)

The Younger Dryas cold event is indicated by the lowest temperatures for the last 15 kyr in the NGRIP $\delta^{18}O$ (Fig. 2.6) (Svensson et al. 2008). The period is known for the cooling of the North Atlantic Ocean, expansion of sea ice, changes in atmospheric circulation in the Northern Hemisphere causing regionally dry conditions and more continental climate (Schenk et al. 2018). However, Younger Dryas had different spatial impact on climate and environment in Europe. Chironomid-based reconstructions (Heiri et al. 2014) and a global climate simulation together with a compilation based on plant indicator species (Schenk et al. 2018) reveal a latitudinal gradient with a significant drop of July temperatures in the north but a weak change in the southern regions. Climate models show positive precipitation anomalies (Younger Dryas versus modern) along the western seaboard of Europe and across the Mediterranean, while negative precipitation anomalies occur over the Fennoscandian ice sheet, the North European Plain, and as far south as the Alps (Rea et al. 2020).

The pollen record from Zamostye located at 51°N provides important insights into the regional vegetation response to the Younger Dryas. The pollen record clearly reflects the spread of the *Artemisia*-dominated dry steppe, indicating the driest conditions in the last 15 kyr. Estimated forest cover decreased to ~5%. Tree patches were presented mostly by *Betula* and *Pinus sylvestris*. Tree taxa requiring sufficient soil moisture like spruce and Siberian pine disappeared. Other regional records also clearly reflect Younger Dryas cooling by maximum of *Artemisia*, the dominance of birch and pine among the trees and the absence of *Picea* (Borisova et al. 2006; Panin et al. 2017). In contrast, the central part of the East European Plain was occupied by periglacial pine-birch forest-steppe with spruce (Khotinsky and Klimanov 1997; Novenko 2016) suggesting higher soil moisture to the north from the study region, most possibly due to changes in permafrost. Pollen-based reconstructions suggest high summer temperatures which led to a retreat of permafrost boundary already during Allerød to the north of the East European Plain (Velichko et al. 2002). Borisova et al. (2006) identified a region-analogue flora in the middle reaches of the Biya River in the northern Altai Mountains, reconstructing a drop in mean annual precipitation to 450 mm and a slight decrease in annual temperatures with the mean January temperature about -18°C and July 15°C. Also reconstructions based on GEOMAP palaeoclimatic model (Muratova et al. 1993) show the depletion of precipitation of ~150 mm/year for the study area in comparison with the present values. A strong decrease in precipitation in the Younger Dryas caused dry soil conditions leading to elimination of local populations of spruce and Siberian pine.

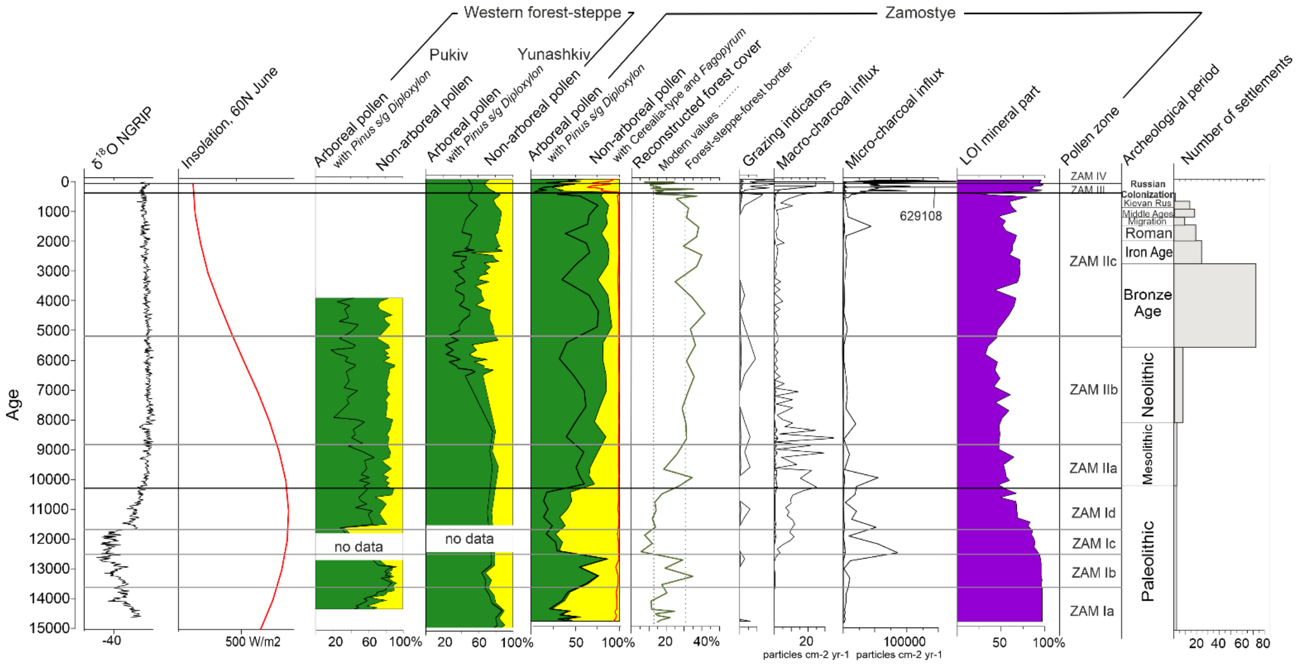


Fig. 3.6. Summary diagram of the North Atlantic climate changes, pollen records from the western Volyno-Podolian forest-steppe, vegetation and fire records of Zamostye and archaeological periods of the study area: δ18O from NGRIP core from Greenland (Svensson et al. 2008), June insolation (Berger and Loutre 1991), pollen records of Pukiv and Yunashkiv (Hájková et al., 2022), Zamostye pollen, charcoal and the reconstructed forest cover data (forest-steppe – forest border values (after Ershov 2007; Novenko et al. 2014b) and the archaeological periods of the study area (based on Shumilovskikh et al. 2019)

Early Holocene (~11.7-8.2 kyr BP)

Increasing temperature and greater moisture availability promoted a rapid forest spread in Europe from the onset of the Holocene. At the continental level, birch and pine forest density increased and replaced tundra parkland vegetation in the north, while thermophilous trees expanded rapidly in the south (Lang 1994; Novenko 2016; Zanon et al. 2018). The pollen record from Zamostye provides unique insights into the process of the forest spread into the steppe in more continental regions of Europe.

The forest cover estimates at Zamostye increased from ~12-14% in the beginning to 32-35% at the end of the period, indicating a slow establishment and spread of forests. The vegetation development during the Early Holocene is clearly divided into two parts. The period between 11.7 and 10.3 kyr BP is reflected by a dominance of *Artemisia* steppe and a distinctive increase of the pioneer tree *Betula* up to 28% associated with pine. Dry *Artemisia* steppe has been slowly and steadily replaced by meadow-steppes dominated by Poaceae, Cichorioideae and *Thalictrum*. *Ephedra* points to dry climate conditions and/or the presence of dry habitats, which can be found in the forest-steppe region even today (Zolotukhin et al. 2015). Overall, the vegetation during this period was dry with a trend to milder conditions towards the second part of the Early Holocene. The results from Zamostye differ strongly from the western Volyno-Podolian forest-steppe (Fig. 2.1a), where a visible increase of broadleaf deciduous taxa started already at 11.5 kyr BP (Fig. 2.6). The Early Holocene pollen records here are dominated by pine associated with *Betula*, *Quercus*, *Corylus* and *Ulmus* as well as *Picea*. *Fraxinus excelsior* joined the forest composition already at ~11 kyr BP and *Tilia* – at ~10 kyr BP (Hájková et al. 2022). At Zamostye, continuous curves of *Quercus*, *Ulmus* and *Corylus* suggest the presence of small populations of these trees already by 11 kyr BP. However, insufficient soil moisture might have hampered the development of the mixed-broadleaf forests in the more continental Central-Russian-Volgian region, indicating a dry climate during the insolation maximum (Fig. 2.6). Moreover, the maximum in macro-charcoal and micro-charcoal influx in the beginning of the Holocene (Fig. 2.5) suggests strong regional and local fires, most likely limiting the forest spread (Feurdean et al. 2020).

The vegetation turn-over at Zamostye occurred ~10.3 kyr BP (ZAM-II), when *Pinus sylvestris* replaced *Betula* and the area became dominated by open forests with the reconstructed forest cover 32-35% (Fig. 2.3). Between ~10.3 and ~8.8 kyr BP the landscapes were covered by meadows and pine-birch forest patches with broadleaf trees *Quercus*, *Tilia*, *Ulmus* and *Corylus*. From ~9.1 kyr BP *Picea* appears sporadically in the pollen diagram most likely reflecting long-distance transport of the spruce spread in the north (Klukva, Fig. 2.1b) (Novenko et al. 2015) or west (Pukiv and Yunashkiv, Fig. 2.1a) (Hájková et al. 2022). The distinctive changes in vegetation at Zamostye at ~10.3 kyr BP are very likely associated with an increase in available moisture. Furthermore, timing of the pine expansion here corresponds to a synchronous expansion of *Corylus* in Western Europe at ~10.5 kyr BP (Giesecke et al. 2011). Although Zamostye and further records from the East European Plain lack hazel maximum (Khotinsky 1977; Lang 1994), both types of vegetation development could be triggered by large-scale climatic changes.

Around 8.6 kyr BP broadleaf taxa *Quercus*, *Tilia*, *Ulmus* and *Alnus* reached their peaks (Fig. 2.3), while the forest cover reached 30%. Our record is in accordance with Spiridonova (1991), who suggested the development of forests over almost all of Mid-Russian Upland between 9 and 8.7 kyr BP. The closest record SV-8 (Borisova et al. 2006) represents the Early Holocene in one sample only and indicates the presence of pine-birch forests with an admixture of broadleaf tree species. The indicator species approach applied in this study showed that the mean January temperature was around -15.5 °C, mean July temperature was 19 °C and mean annual precipitation was around 550 mm. These results agree with the climate reconstructions based on the best modern analogue technique applied to the pollen record from the Klukva peatbog to the north (Fig. 2.1b) (Novenko et al. 2019), suggesting an annual temperature of 3-5 °C and precipitation close to 600 mm. Overall, the region was characterized by cooler and dryer climate compared to the modern conditions.

Middle Holocene (~8.2-4.2 kyr BP)

The cooling event ~8.2 kyr BP reflected in the NGRIP core divides the Early and Middle Holocene (Walker et al. 2018). It is associated with a weakened Atlantic meridional overturning circulation (AMOC) due to the catastrophic meltwater released from glacial lakes of Agassiz and Ojibway into the North Atlantic during the depletion of the Laurentide Ice Sheet (Hoffman et al. 2012; Matero et al. 2017). This short-lived episode is reflected in pollen records and vegetation models as a vegetation response to the temperature drop in the north and to the temperature and precipitation drop in the south (Li et al. 2019). The reduction of forest areas at Zamostye is also evidenced by the decrease in AP to 72% and forest cover to ~29%. The broadleaf component declined and *Artemisia* and meadow steppe taxa increased in the study area for ~500 years indicating long-term dry conditions. Pollen diagrams within the forest-steppe show different responses to the 8.2 kyr event. While the western records show a short-term decline in *Picea, Ulmus, Corylus* (Hájková et al. 2022), southern and eastern records show the spread of steppe (Spiridonova 1991). These changes are interpreted as a vegetation response to the decline of available moisture likely caused by the decrease in precipitation.

After the 8.2 kyr event, AP values increased and became more stable for the rest of the Holocene varying between 72 and 91% reflecting the forest cover of 29-42%. The region was most likely occupied by pine-mixed-broadleaf forests with patches of meadow steppes. At ~7 kyr BP forest cover estimates exceeded 30%, indicating the dominance of forests over steppe. The reconstructed forest cover at Zamostye is in line with the regional northern sites from the broadleaf forest vegetation zone suggesting the presence of open forests. The Istochek and Selikhovo forest sites (Fig. 2.1b) show only slightly higher values of 30-45% in the forest cover. Only the forest-steppe site of Podkosmovo was dominated by steppe with only ~10-13% of forests (Novenko et al. 2014a; Shumilovskikh et al. 2018).

The pollen record from Zamostye shows prominent millennial scale vegetation variability starting from the mid-Holocene. Pine dominated phases during ~7.9-6.3, 5-3.6, 2.8-1.9, 1.5-0.6 kyr BP alternating with phases of broadleaf forest maxima during ~6.3-5, 3.6-2.8, 1.9-1.5 kyr BP (Fig. 2.6). Such distinct fluctuations of ~1500-2500 years in the climatically sensitive forest-steppe region might reflect climate changes. We speculate that such periodical climate changes might have impacted the vegetation development during the Holocene through changes in water balance in favour of broadleaf forests or pine forests. However, this observation has to be validated by further records in the region.

Starting from 7 kyr BP, forests gradually expanded around Zamostye and by ~4.5 kyr BP reached their maximal extension. This strongly contradicts with records from central Europe, where maximum forest cover occurred already at ~8 kyr BP (Novenko 2016; Zanon et al. 2018). Similar to Zamostye, the sites from the north including Istochek (Novenko et al. 2017), Orlovskoe Polesye (Novenko et al. 2014b), Selikhovo (Novenko et al. 2016b), Podkosmovo (Novenko et al. 2014a), SV-8 (Borisova et al. 2006) were getting forested between 5 and 4.5 kyr BP, indicating the movement of the forest border to the south-east (Shumilovskikh et al. 2018). This widespread shift of forest into the steppe areas is documented by the tree pollen maxima in pollen sequences of the Mid-Russian Uplands in the Don and Oka River basins (Klimanov and Serebryannaya 1986; Novenko et al. 2009; 2012; 2016b; Serebryannaya 1981; Spiridonova 1991). In the eastern Trans-Kamian-Volgian province of the forest-steppe zone forests reached their maximum extent between 5-3.2 kyr BP (Blagoveshchenskaya 2006). Similarly, the pronounced moist phase between 4.7 and 3.7 kyr BP was evidenced in Transylvania, leading to a change in the forest composition towards more mesic tree species (Lake Stiucii, Fig. 2.1a) (Feurdean et al. 2015). This over regional trend of forest development in the late Middle Holocene can be explained by the onset of a global cooling evidenced by the NGRIP core (Svensson et al. 2008), glacier advances in the Northern Hemisphere (Solomina et al. 2015), regional climate reconstructions from the Klukva peatbog (Novenko et al. 2019), expansions of peatlands in the forest-steppe of the East European Plain (Volkova et al. 2020) and by general circulation models (Wanner et al. 2008). The decrease in summer temperature in combination with a possible change in the atmospheric circulation probably led to considerable changes in evapotranspiration towards more mesophitic conditions and changes in vegetation.

Late Holocene (4.2 kyr BP – present)

During the Late Holocene vegetation at Zamostye experienced a strong human impact. The first drastic change occurred ~3.8-3.3 kyr BP when AP values dropped to 75% caused by a strong reduction of pine. The forest cover estimates decreased to 25%. The deforestation occurred at the same time with the findings of Cerealia, *Fagopyrum*, *Plantago major-media* and *Rumex acetosa* suggesting agricultural and pastoral land use (Fig. 2.3). These activities are closely related to the presence of Bronze Age settlements in the vicinity of the study site. An increase in the settlement activity in the Late Bronze Age by the bearers of the Srubnaya (18th – 12th BCE) and the Bondarikhinskaya (11th – 9th centuries BCE) cultures is clearly reflected in the pollen diagram of Zamostye by contemporary strong deforestation, increase in agricultural markers and an increased erosion, suggested by the high values of the *Glomus*-type (Fig. 2.3). The subsistence economy of both cultures was based on cattle breeding and less extensive agriculture (Zorin et al. 2014). The findings of *Fagopyrum* pollen could also imply the possibility of buckwheat cultivation, although we cannot exclude it as a ruderal marker (Klerk et al. 2015).

By ~2.8 kyr BP anthropogenic pressure at Zamostye decreased and AP values went up to 87% reflecting the reduction of human settlements in the Early Iron Age (Fig. 2.6). Forest cover estimates increased to 37%, reaching 40% by ~2.4 kyr BP representing the reforestation of the territory.

The next drop in the forest cover to 30% and AP to 80% occurred ~2.1-1.8 kyr BP. Small peaks in Cerealia-type and *Plantago lanceolata*-type in the record and an increase in the number of macro-charcoal particles ~1.9 kyr BP indicate human activities that can be attributed to the Roman and Late Roman periods. Archaeologically, there are only two Roman period sites known due to the ceramics of the late Zarubinets or early Kiev cultures. During the late Roman period the number of sites increased to nineteen: seven sites of the Chernyakhov culture are known, four – of Kiev, four sites belong to both cultures and four are not defined (Kashkin 2000; Shumilovskikh et al. 2019a). Although Zarubinets, Cherniakhov and Kiev cultures are known by their developed slash-and-burn agriculture and pastoral activities (Rodinkova et al. 2020; Zorin et al. 2008), the signal of anthropogenic indicators is rather weak in the pollen diagram of Zamostye as well as in the neighbouring Sudzha (Fig. 2.1b) (Shumilovskikh et al. 2019a). It is likely that the low topographical position of the archives, the proximity to the river and therefore higher forest cover with pine or oak around the sites caused signal depletion from herbs. It is consistent with palynological studies from the hemiboreal zone (Ershova and Krenke 2014), showing that early signs of developed agriculture can be seen only in the areas of intensive economic development immediately around the settlements, and only when agriculture covers large areas does the pollen signal become visible in the regional records.

Further deforestation at Zamostye coincides with a strong increase in the markers of agricultural activities (Cerealia-type, *Fagopyrum*, *Hordeum*-type), ruderals (*Ranunculus arvensis*, Brassicaceae), trampling (*Polygonum aviculare*-type) and grazing indicators (*Plantago lanceolata*, *Ranunculus acris,* coprophilous spores and eggs of intestine parasite *Trichuris*) starting at ~1.1 kyr BP. The timing of this increase in human indicators is closely related to the Early Medieval Period and the functioning of the most famous regional archaeological site Gornal, located 15 km south from the Zamostye study site. Various agricultural instruments were found in the Gornal fortification such as sickles, skythes, ard ploughs, millstones, which together with the findings of *Triticum aestivum/compactum, Triticum dicoccum, Secale cereale, Hordeum vulgare, Avena sativa* in storage rooms evidence crop cultivation (Veretyushkina and Gorbanenko 2015). Bones of goats, sheep, cattle and pigs document animal husbandry (Kashkin 2000). Smaller settlements of the Romny culture were located close to our study site – Kurilovka-Gorodishche and Kniazhiy 1-Selishche (Kashkin 2000). Although the pollen diagram has rather low temporal resolution for the period, there is a decrease in anthropogenic indicators and some reforestation up to 37% of the estimated forest cover in the 15th century, suggesting less human activity in the area of Zamostye during the Late Middle Ages (13-17th century).

In the 17th century the area experienced total deforestation: AP suddenly decreased from 93 to 32%, forest cover estimates reached the modern values of 13-15% (ZAM-III). The finding is in accordance with the total deforestation in the southern East European Plain in the 17th-18th century evidenced by almost all of the regional pollen sites displaying agricultural landscape and anthropogenic disturbance due to the expansion of the Russian State (Khotinsky 1984; 1993; Serebryannaya 1981)(Novenko et al. 2009; 2012; 2014a; 2015; 2016b; Spiridonova 1991) (Chendev et al. 2016; Shumilovskikh et al. 2018). At Zamostye, the increase in primary and secondary anthropogenic indicators (Behre 1981) is strongly related to the increased settlement activity and the foundation of the town Sudzha in 1661. Following historical documents, the Cossacks built the town over one or two years (Babin 2015) using mainly oaks and some elms to build the walls (Ozerov and Babin 2015). The deforestation is evidenced by a strong decrease in *Pinus*, *Quercus* and *Tilia* in the diagram of Zamostye, while a 13% decrease in *Quercus* is evidenced in the pollen diagram of Sudzha (Shumilovskikh et al. 2019a). The opening of the landscapes occurred at Zamostye in ~1610, ~50 years earlier than Sudzha was built. However, this can be explained by uncertainties in the chronology. The town Sudzha functioned as a military post until the fire in 1725 and then developed into a trade and handcraft centre (Ozerov and Babin 2015). In the 19th century, 90.7% of the population were engaged in agriculture with cultivation of rye, oat, wheat, buckwheat, sunflower, tobacco, sugar beet and hemp (Berezhnaya 2015). The first five crops are clearly reflected in the diagram of Zamostye by *Secale*, *Avena*-type, *Triticum*-type, *Fagopyrum* and *Senecio*-type and the cultivation of barley can be suggested by the high values of *Hordeum*-type. Strong grazing in the surroundings is suggested by *Rumex acetosa*-type, *Plantago lanceolata*-type, *Polygonum aviculare*-type, *Plantago major-media*-type as well as by coprophilous fungal spores and eggs of intestine parasite *Trichuris* infecting domestic animals or humans (Revelles and Geel 2016). Historical data indicate that horses and oxes were used for ploughing while sheep and cattle were for domestic use (Berezhnaya 2015).

The upper part of the diagram (ZAM-IV) is dominated by Cichorioideae which increased drastically up to 63% and contributed to an increase in SQD and no analogue situation (Suppl. Fig. 2.4). The occurrence of Cichorioideae clumps in the pollen spectra implies the local presence of the plants possibly due to active pastural activity in the area (Florenzano et al. 2012).

Fire history

The fire history of the East European forest steppe is much less investigated than the vegetation history. Most of the records originate from the sub-Mediterranean subcontinental forest-steppe (Fig. 2.1a), spanning the Holocene (Feurdean et al. 2015; 2020; 2021). The micro- and macro-charcoal records of Zamostye provide unique insights into the fire activity in the subcontinental forest-steppe during the Late Glacial and the Holocene.

Micro- and macro-charcoal concentration and influx were low during the Late Glacial (14.8-12.5 kyr BP) (Fig. 2.6), suggesting low fire activity. Low fire in open pine-dominated forests is surprising because a high amount of available flammable fuel can be assumed. In contrast to the Holocene, the Last Glacial Maximum was characterized by the maximum extent of permafrost in the Northern Hemisphere (Lindgren et al. 2015), which started melting with an onset of warming, likely increasing surface runoff (Wang et al. 2021). This connection is assumed to have formed "red layers" in the Black Sea sediments (Bahr et al. 2008) as a strong surface runoff from Dniester and Dnepr regions during 18-14.8 kyr BP was caused by frozen soils. Meltwater pulses from the north contributed to the Black Sea freshwater discharges into Marmara Sea until 14.7 kyr BP (Aloisi et al. 2015). In our study region, loess-paleosol sequences from the Aleksandrovskiy surface mine demonstrate cryogen features during the Late Glacial documenting that permafrost was still present at the time (Sycheva 2012). Incisions in the LGM terraces and the formation of large river palaeochannels indicate a higher than present water runoff during 18-13 kyr BP. The floods also rose above the present-day levels as indicated by large levees and overbank loams on LGM terraces (Panin et al. 2017). In our opinion, fire activity in flammable vegetation was hampered by the presence of water or water saturated soil, decreasing flammability through fuel moisture.

Another possible explanation is a change in the charcoal source area. High floods (Panin et al. 2017) and the topographical position of the Zamostye basin in the River Sudzha valley suggests that the lake shore vegetation cover was rather low (see section 4.1 for details), supporting low local fire regime. Bare soils and high erosion are evidenced by *Riccia* cf. *sorocarpa* (HdV-165) and *Glomus* cf. *fasciculatum* (HdV-207), respectively (see section 4.1). Relatively high percentages of microcharcoal indicate the presence of fires during 14.8-13.8 kyr BP when the forest cover varied between 10 and 25%. Open landscapes facilitated easy transport of charcoal particles from distant fires. During 13.8-12.5 kyr BP, microcharcoal percentages decrease but the concentration and influx of micro- and macro-charcoals slightly increased, suggesting a more local charcoal source area possibly due to a denser vegetation cover and the development of forests.

Fire activity strongly increased during the Younger Dryas as suggested by the micro- and macro-charcoal records. Severe and/or frequent burnings occurred in dry steppe environments documented by pollen. The dominance of grass-type charcoal particles during the Younger Dryas also indicated the dominance of grasslands (Fig. 2.5). Although the reconstructed forest cover declined to 5% (Fig. 2.6), local vegetation cover very likely increased as indicated by the higher pollen concentration (up to 57,241 pollen grain/cm^3) and influx values (up to 822 pollen grain/cm^{3}yr) and a decrease in *Riccia* and *Glomus* (Fig. 2.3, see section 4.1 for details). Grassland vegetation is adapted to frequent fires and provides enough fuel for short and frequent fires (Leys et al. 2018; Neary and Leonard 2020).

The Holocene fire regime at Zamostye is in line with the long-term fire dynamics in Central and Eastern Europe with an Early Holocene maximum, Middle Holocene minimum and anthropogenic increase in the Late Holocene (Feurdean et al. 2020). At Zamostye, there are differences in timing of fire maxima derived from micro- and macro-charcoal records. Peaks in micro-charcoal influx and concentrations started in the Younger Dryas and lasted until ~10 kyr BP, indicating high regional fire activity. Lower micro-charcoal input occurred together with a change in fuel source from grass to wood, indicated by macro-charcoal (Fig. 2.5) possibly due to the local presence of trees around the lake. Although forest cover increased up to 30% at ~10.3 kyr BP, shore vegetation was initially mostly represented by grasslands, indicated by grass-type charcoal peaks.

Charcoal loads decreased strongly at ~7 kyr BP, when the reconstructed forest cover exceeded 30% and remained high (up to 42%) for the next five millennia. Feurdean et al. (2020) demonstrated that biomass burning decreases in temperate regions when the forest cover exceeds 60% and 65% for boreal zones. It is explained by a reduced amount of solar radiation reaching the forest floor resulting in a more moist and wind-protected microclimate underneath canopies which decreases fuel flammability. However, forest cover estimates in our study were reconstructed using MAT and cannot be directly compared to the values based on the semi-quantitative pseudobiomisation method (Fyfe et al. 2015). Nevertheless, both studies demonstrate the same trend – a lower fire activity during the maximal forest development.

The fires that occurred over the last 2000 years are most likely connected to the settlement activities in the area: the expansion of populations of Zarubinets, Chernyakhov or Kiev cultures during the Late Roman period and the later foundation of the Gornal centre by the Romny culture in the Early Medieval (compare to section 4.2.5). A strong increase in charcoal in the upper 80 cm of the sediment core is strongly related to the construction of the town of Sudzha. At least two fires burning the wooden Sudzha fortress were documented historically in 1665-1668 and 1725 (Ozerov and Babin 2015). From the 18th century till the present the wood-type charcoal reaches its maximum as well as macro- and micro-charcoal influx likely due to the constant use of wood for the heating of the houses in the nearby town.

Conclusions

Zamostye study site was a shallow lake which existed from 14.8 kyr BP until the last ~400 yrs, when it was overgrown by peat. The core provides unique Late Glacial and Holocene pollen and charcoal records allowing the reconstruction of vegetation changes and fire activity of the continental part of the East-European forest-steppe. Pollen data reveal high sensitivity of vegetation in this region to moisture availability caused by the northern hemispheric climate changes. The spread of pine forest-steppe, which started ~14.8 kyr BP, was interrupted by a cold event at ~14.3 kyr BP (GI 1d) favouring grass steppe. From 13.9 to 12.7 kyr BP, the region was covered by forest-steppe with *Pinus sylvestris*, *Picea*, *Betula, Pinus sibirica* and *Alnus fruticosa*. The presence of spruce and low fire activity during the Late Glacial were likely related to permafrost, disappearing by the end of Allerød. This contributed to an enhanced aridity during the Younger Dryas, causing the spread of dry *Artemisia* steppe.

At ~11.7 kyr BP the warmer climate of the Holocene triggered the development of birch forest-steppe, but the lack of moisture and strong regional and local fire activity hindered the development of broadleaf forests for more than a millennium. Vegetation turnover occurred ~10.3 kyr BP, when the vegetation became dominated by pine. Around 8.6 kyr BP the forest-steppe was represented by pine-broadleaf mixed forests with *Quercus*, *Tilia*, *Ulmus* and *Corylus*. The cooling event ~8.2 kyr BP caused a reduction of woodlands and their broadleaf component at Zamostye for ~500 years. Starting from ~7 kyr BP, forests gradually expanded and by ~4.4 kyr BP reached their maximal extension (42%), which is correlated to the onset of the northern hemispheric climate cooling. During the Late Holocene, human impact was detected in the Late Bronze Age, Early Iron Age, Roman period and Early Middle Ages, correlating well with archaeological data. However, natural forests were recovering after a decrease in human activities. Total deforestation, similar to the modern one, occurred in the 17th century and was related to the southern expansion of the Tsardom of Russia.

Our palaeoecological study demonstrated that the regional vegetation of the forest-steppe of the East European Plain has experienced strong anthropogenic pressure since the 17th century and has remained open although climate conditions could have allowed the recovery of pine-broadleaf mixed forests. This highlights the need for tailored management for the nature protection of diverse steppe habitats. Semi-natural openness should be actively achieved by selective lumbering, prescribed fires, moderate grazing or traditional mowing. However, if the current climate warming reaches the Middle Holocene thermal maximum, it might favour the steppe vegetation and therefore the protection of forests to keep the heterogeneity of the forest-steppe will be necessary.

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Supplementary material

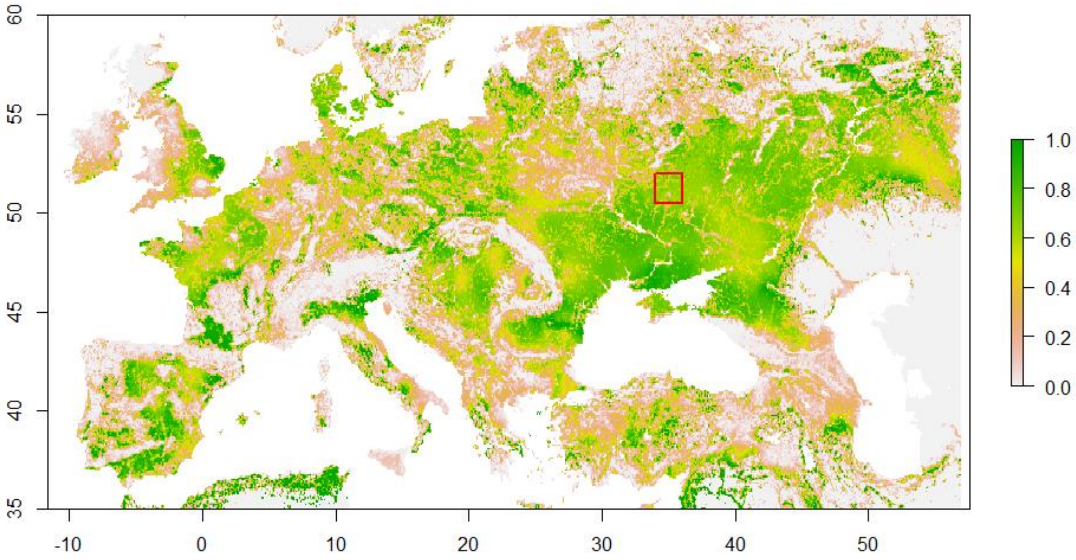

Fig. S2.1. Map of the territories used as cropland for the year 2000 (Ramankutty et al. 2008) where 0.0 – not used for agriculture, 1.0 – used 100% of the land. Red rectangle marks the study area

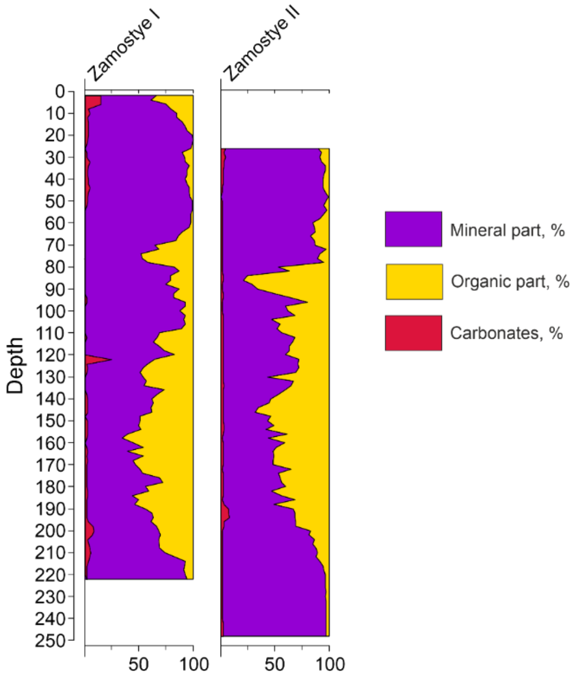

Fig. S2.2. LOI results of the Zamostye I and Zamostye II cores

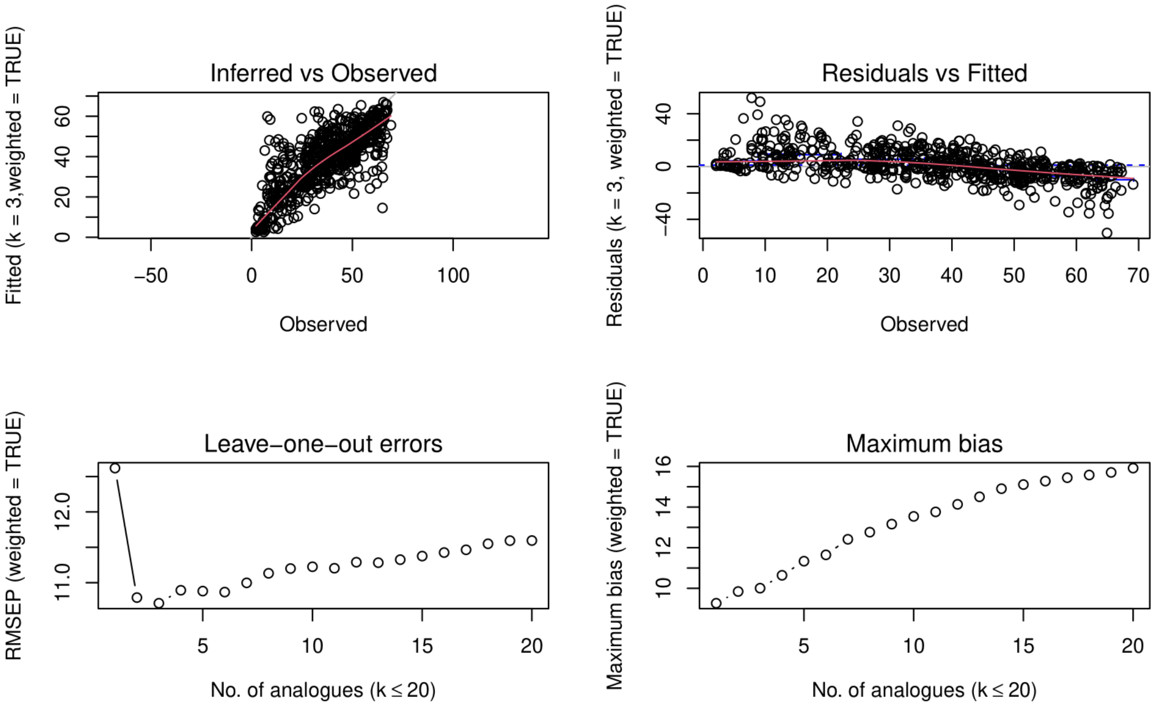

Fig. S2.3. Modern Analogue Technique (MAT) for the forest cover reconstructions

Fig. S2.4. SCD values of the forest cover reconstructions

Table S2.1. Published pollen records from the East-European forest-steppe and the southern border of the broadleaf forest zone

Site	Country	Covered time period	Reference
Durankulak 3	Bulgaria	Late Holocene	Marinova and Atanassova (2006)
Lake Oltina	Romania	Middle-Late Holocene	Feurdean et al. (2021)
Lake Stiucii	Romania	Late Glacial-Holocene	Feurdean et al. (2015)
Sarlo-hat	Hungary	Holocene	Magyari et al. (2010)
Dovjok	Ukraine	Middle-Late Holocene	Kremenetski (1995)
Pukiv, Yunashkiv	Ukraine	Late Glacial-Holocene	Hájková et al. (2022)
Sudzha	Russia	Late Holocene	Shumilovskikh et al. (2019a)
SV-8, ML-2, ML-3	Russia	Late Glacial, Holocene, fragmented	Borisova et al. (2006), Panin et al. (2017)
Orlovskoe polesye	Russia	Late Holocene	Novenko et al. (2014b)
Selikhovo	Russia	Middle-Late Holocene	Novenko et al. (2016b)
Klukva	Russia	Holocene	Novenko et al. (2015)
Istochek	Russia	Middle-Late Holocene	Novenko et al. (2017)
Podkosmovo	Russia	Middle-Late Holocene	Novenko et al. (2014a)
Don, Ustye,	Russia	Middle-Late Holocene	Novenko et al. (2009)
Berezovskoye	Russia	Middle-Late Holocene	Novenko et al. (2012)
Don river archeological sites incl. Kostenki	Russia	Late Glacial, Holocene, fragmented	Spiridonova (1991)
Krugloe	Russia	Late Holocene	Shumilovskikh et al. (2021b)
Viatkinskoe	Russia	Late Holocene	Shumilovskikh et al. (2019b)

Chapter III – Manuscript 2

Did Holocene climate drive subsistence economies in the East-European forest-steppe? Case study Omelchenki, Kharkiv region, Ukraine

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Key words: vegetation history; fire history; palynology; charcoal; human impact; Holocene; Eastern Europe

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Abstract

Climate is often considered a primary driver of important historical events and its role is crucial for the existence of sedentary cultures at the ecological borders of agriculture such as the East-European forest-steppe. We investigate how the forest-steppe vegetation and climate changes impacted societies through time and vice versa the role of the human impact on the southern border of the ecotone. For this, we obtained a sediment core from a mire next to the village of Omelchenki in the Kharkiv region, Ukraine, covering the last ~9,800 yrs for multi-proxy analysis including pollen, non-pollen palynomorphs, macro-remains, loss-on-ignition, macro- and micro-charcoal, and applied a modern analogue technique to the pollen data to reconstruct forest cover. In the first half of the Holocene the fluctuations of the southern tree line correspond with the changes of the cultures with forager economies. The mid-Holocene spread of steppe promoted stock breeding as a basis of the Copper Age cultures' economy. The early late-Holocene increase in available moisture and the following forest spread contributed to the transition from nomadism to farming. Sufficient moisture attributed to the forest spread allowed the cultures' agricultural success. We conclude that the Holocene climate and environmental changes supported the changes in subsistence bases throughout the Holocene. Our data highlight a high sensitivity of forests in their southern limits to anthropogenic pressure, which emphasizes the possibility of their potential spread further south. However, considering the current global warming the southern tree line is likely to shift northwards bringing the area to the mid-Holocene conditions increasing risks for agriculture.

Introduction

Climate is often considered a primary driver of important historical events starting with the changes in Natufian communities in South-Western Asia with the Late Glacial termination and the onset of the Holocene (Moore et al. 2000; Weiss and Bradley 2001), and the following Neolithic revolution on a global scale. The Mid-Holocene climate change coincided with cultural and socio-environmental changes and the adoption of agriculture throughout Europe (Motuzaitė Matuzevičiūtė and Telizhenko 2016; Warden et al. 2017; Weinelt et al. 2021). When debating over the development and fall of civilizations, social, political and economic reasons are first to be expected. Numerous examples demonstrate that since ancient times people were able to cope with climate change and environmental risks with a proper management (Abate 1994; Douglas et al. 2015; Feinman and Carballo 2018). However, as a major natural driving force, climate defined the borders of the vegetation zones and therefore the way of life of people including culture and economy (Schneeweiss and Rjabogina 2014).

The leading role of climate for existence of sedentary cultures is expected at the ecological borders of agriculture like the East-European forest-steppe. Stretching from the eastern foothills of the Carpathian Mountains until the western slopes of the Urals the band of the East-European forest-steppe represents a natural or near-natural mosaic of forest patches and grasslands located between the mesophilous deciduous broadleaf forests and true bunch-grass steppes (Donita et al. 2004; Erdős et al. 2019). On one hand, the presence of fertile black soil – chernozem – makes the forest-steppe very attractive for agriculture. Compare to arid steppe, the ecotone has more precipitation and therefore less risks for crops' growth while the occurrence of forests provides wood for building and heating. On the other hand, meadow steppes and open territories are attractive for raising of grazing animals. Located at the junction of the natural zones, forest-steppe potentially allows all types of subsistence economy – foraging, pastoralism and agriculture – thrive within its limits. Throughout the Holocene the study region was populated by the nomadic and semi-nomadic Yamnaya (Pit Grave), Sredny Stog and Catacomb cultures as well as by the later Scythians, Sarmatian tribes and Saltovo-Mayaki culture (Shramko et al. 1977). Among agricultural societies, Srubnaya, Bondarikha, Zarubyntsi, Chernyakhiv, Penkivka and Romny cultures were spread. Farming has become the base of economy in the Bronze Age, not earlier than in the 4th millennium BP (2nd millennium BCE) (Shramko et al. 1977), although agriculture appeared in the western part of the East-European forest-steppe already by ~7.2 cal. kyr BP (Motuzaitė Matuzevičiūtė and Telizhenko 2016).

Cultural and economic development usually goes in line with the environment. When facing a climate change, people try to adapt to the changing environment (Douglas et al. 2015; Scarborough et al. 2012). Previous studies from different parts of the Eurasian forest-steppe demonstrated high sensitivity of societies to climatic and environmental changes (Schneeweiss and Rjabogina 2014). In the Baraba forest-steppe in Siberia, the mid-Holocene spread of steppe induced the transition to livestock breeding while the expansion of coniferous forest in the late Holocene promoted strengthening of hunting and fishing (Zhilich et al. 2017). Wetter climate conditions in the Bronze Age allowed sedentarism in the Transural steppe where mobile pastoralism was otherwise traditional (Stobbe et al. 2016). We suggest East-European forest-steppe might have experienced similar trends when the changes in the treeline were followed by the change in the subsistence bases.

Earlier studies have shown that the East-European forest-steppe is a dynamic system. Sensitive to the North Atlantic changes (Lukanina et al. 2022), the ecotone was dominated by dry steppe during the cold and dry Younger Dryas stadial (Borisova et al. 2006; Muratova et al. 1993; Spiridonova 1991). Milder climate conditions of the Holocene allowed the spread of forest into steppe (Novenko et al. 2015; Novenko 2016). The maximum extent of forest occurred in the late Holocene and its decline coincides with the constantly increasing anthropogenic pressure. Pollen studies indicate that without human impact the area would probably be more forested than currently believed (Feurdean et al. 2021; Hájková et al. 2022; Lukanina et al. 2022; Novenko et al. 2014a; Shumilovskikh et al. 2018). Environmental fluctuations of the ecotone would have likely had an impact on prehistorical societies.

In the present study, we investigate how the vegetation and climate changes of the East-European forest-steppe impacted human societies through time and vice versa. For this, we conducted a study on the vegetation and fire history of the southern border of the ecotone. A sediment core obtained from a mire next to the village of Omelchenki (Kharkiv region, Ukraine) and covering the last ~9,800 yrs was studied by multi-proxy analysis including pollen, non-pollen palynomorphs (NPP), macro-remains, loss-on-ignition (LOI), macro- and micro-charcoal. We applied a modern analogue technique to the pollen data to reconstruct forest cover and estimate the forest-steppe dynamics, and compared our data to the archaeological records.

Study area

Geography, climate and vegetation

Omelchenki study site (49.63969°N, 36.41677°E, 88 m a.s.l.) is located next to the village of Omelchenki south from the city of Kharkiv in the Zmiiv district of the Kharkiv region, Ukraine. It belongs to the Siverskyi Donets River valley which is a part of the Don River basin in the south of the East-European Plain. The territory is located in the area of continuous loess cover (Velichko 2009) which is parental material for chernozem soils widespread all over Ukraine including the study region (Baliuk et al. 2017). The relief is polymorphic from lowland plains to hilly and plateau landscapes fissured by valleys (Donita et al. 2004). Forests occupy well-drained northern slopes, damp hollows, gorges, floodplain terraces and alluvial plains as well as hill and mountain tops while steppe and dry grassland vegetation occurs predominantly on southern slopes and plateau with clay and silt-rich soils.

According to the Ukrainian Hydrometeorological Center, in the close-by city of Kharkiv, the average January temperature is -6 °C while the average July temperature is 21 °C. Annual precipitation is 525 mm/year with the least amount of precipitation in the periods of February-April and September-October (28-41 mm/month). However, the number of days with various amounts of precipitation is the lowest for the period of August-October which impacts the soil water balance limiting the spread of forests (Donita et al. 2004).

Dominated by oak *Quercus robur*, broadleaf forests make up a substantial proportion of forests of the East-European forest-steppe. *Acer, Fraxinus, Corylus* and *Tilia* occur in mixtures. *Carpinus betulus* is present in the western part of the forest-steppe but disappears from the forest stands of our study region (Donita et al. 2004; Sikkema et al. 2016). Meadow steppes rank amongst the most species-rich plant communities predominated by *Filipendula vulgaris, Trifolium montanum, Onobrychis arenaria, Rhinanthus alectorolophus, Bunias orientalis, Tragopogon pratensis* subsp. *orientalis, Viola rupestris, Bromus piparius, Festuca* *rupicola, Carex humilis, C. praecox, Poa angustifolia, Stipa pennata* as well as *Artemisia latifolia* and *A. sericea* (Donita et al. 2004).

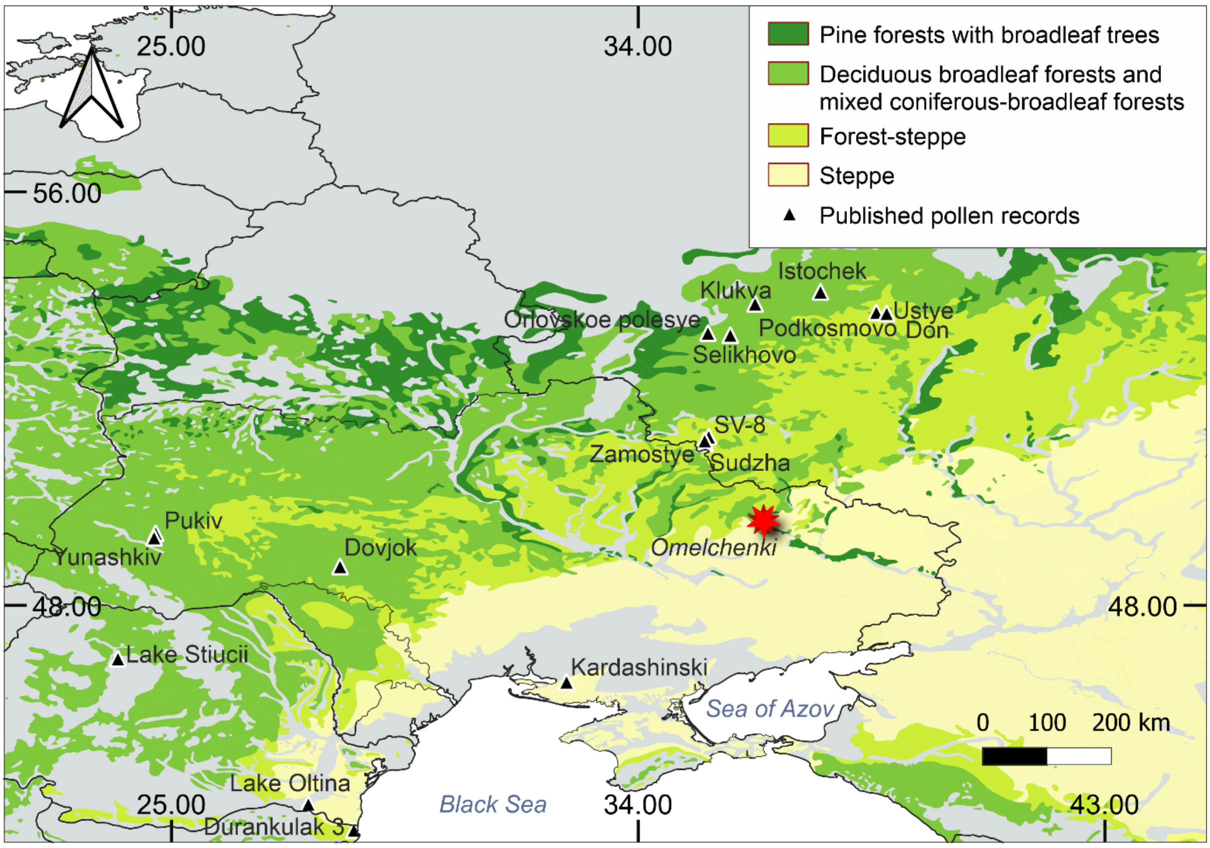

Fig. 3.1. Map of modern potential natural vegetation of the East-European forest-steppe (after Bohn et al. (2004))

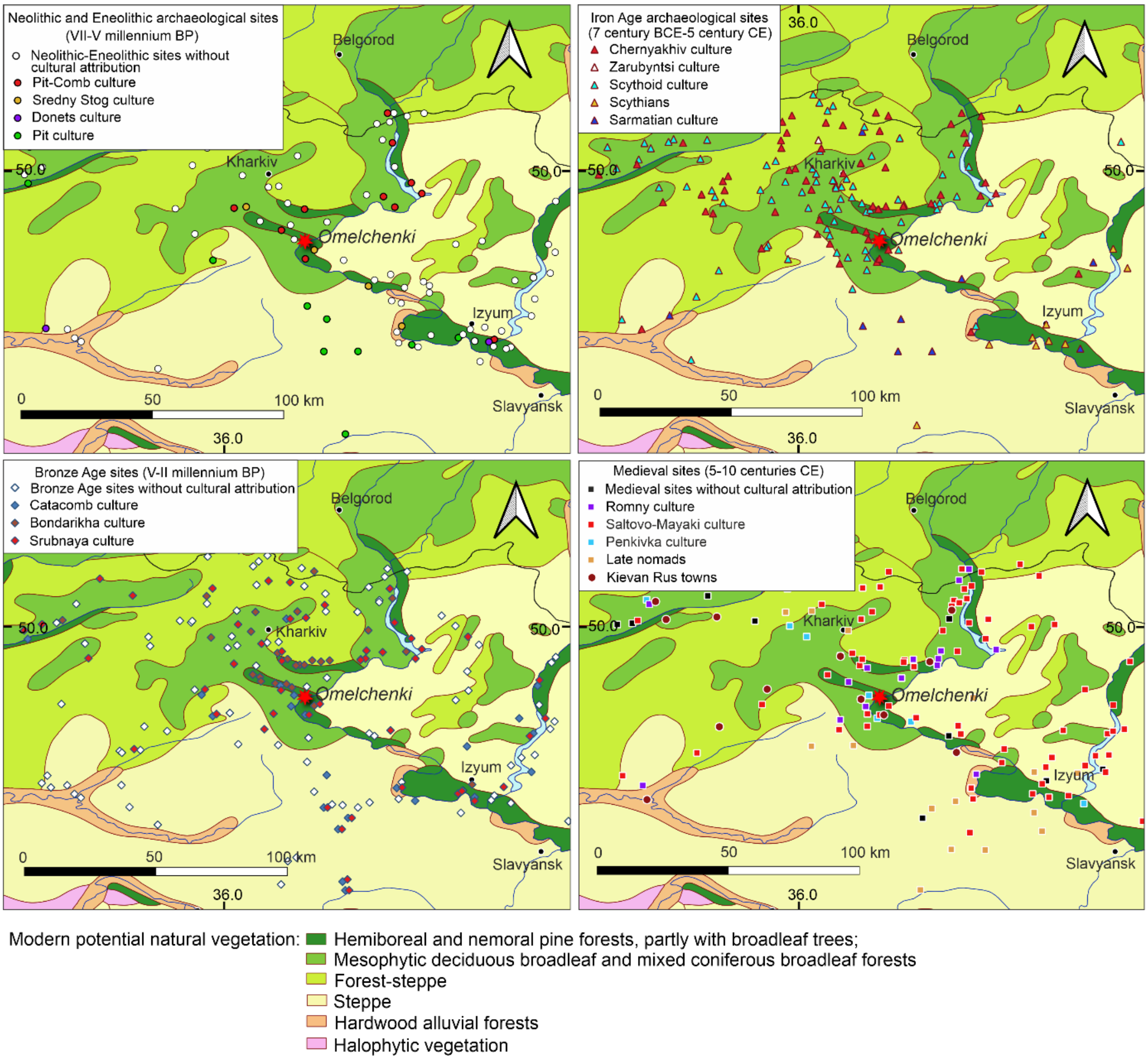

Fig. 3.2. Map of modern potential natural vegetation (Bohn et al. 2004) and archaeological sites of the study area (Fig. S3.3, Table S3.1) (Shramko et al. 1977)

Archaeological background

Favourable for people throughout Palaeolithic (Spiridonova 1991; Velichko 2009), the area of the modern East-European forest-steppe region was quite populated already since the Upper Palaeolithic times. By now, thousands of Upper Palaeolithic sites have been identified and hundreds were excavated (Zaliznyak 2020). Hunting activities were the main occupation of the inhabitants of then periglacial Eastern Europe which included hunting mammoth, reindeer, bison and horse (Dolukhanov and Arslanov 2009; Zaliznyak 2020). Climate warming of the beginning of the Holocene ~9.7 kyr BCE (~11.7 cal. kyr BP) resulted in expansion of deciduous and pine forests (Borisova et al. 2006; Hájková et al. 2022; Lukanina et al. 2022; Schwörer et al. 2021) and the change of fauna to non-herd animals such as red deer, wild boar and roe deer in the northern parts of the forest-steppe (Bibikova 1978). In the more open southern part, however, herd animals were still hunted (Stanko and Kiosak 2010) although many of them became extinct and were replaced, e.g. the Pleistocene horse was replaced by tarpan, and bison was replaced by aurochs (Dolukhanov and Arslanov 2009; Zalyznyak 2020). The Mesolithic period (~8-5 kyr BCE) is considered the highest phase of development of hunting economy which might have become the reason for its crisis. Early Mesolithic was represented by the Zimovniky culture in the Siverskyi Donets River valley (8-7 kyr BCE) replaced by the Donets culture in the Late Mesolithic period (7-5 kyr BCE) (Zalyznyak 2020).

The Donets (Dnieper-Donets) culture developed to the Neolithic stage. The Neolithic revolution in Northern Eurasia occurred in the conditions of the thermal optimum established ~6-5 kyr BCE (Dolukhanov 2004). Neolithic farmers from the Near East spread agriculture to the East-European forest-steppe through the Balkan Peninsula by the bearers of Starčevo–Körös–Criș and subsequent Linear Pottery culture (LBK) (Motuzaitė Matuzevičiūtė 2020). In western Ukraine, the first evidence of agriculture dates back to ~5.4-5.3 kyr BCE at the LBK settlement of Ratniv-2 (Motuzaitė Matuzevičiūtė and Telizhenko 2016). The agricultural expansion to central Ukraine was undertaken by farmer groups from the Cucuteni-Trypillia culture who followed the forest-steppe belt to the Dnieper River no earlier than the first half of the 5th millennium BCE (Anthony 1995; Motuzaitė Matuzevičiūtė 2020). According to Anthony (1995) the Dnieper River area was a boundary between the farmers of the Trypillia culture and the eastern forager communities of the Dnieper-Donets culture of our study area for 1000-1500 yrs. Due to the expansion of steppe and under the influence of the southern Balkan cultures ~5-3 kyr BCE, stock-breeding became the basis of the economy of the steppe population (Zalyznyak 2020).

The East-European forest-steppe area remained divided into two large cultural areas throughout the Neolithic period: early farmers and herdsmen in the south-west and hunting and fishing tribes in the north-east and along the Dnieper (Tovkailo 2020). Our study area was populated by people from the forager Dnieper-Donets culture settled on the dunes in floodplains. Livestock breeding (pigs, cattle) and agriculture (*Hordeum* cultivation) appeared only in the later stages (Zorin et al. 2014). Pit-Comb Ceramic culture penetrated the area in the end of the Neolithic period from the north (Shramko et al. 1977).

In the beginning of the Copper Age around 3 kyr BCE the study region was populated by the carriers of the Sredny Stog culture. Their economy was based on cattle breeding and especially horse breeding. The Sredny Stog culture was strongly associated with the semi-nomadic Yamnaya culture, which formed somewhat later and was spread mainly in the steppe area (Shramko et al. 1977). The findings in the Yamnaya culture settlement of Mykhaylivka to the south from the study area suggested cattle breeding as well as sheep/goat, horse and pig. Findings of querns implied some agricultural activities (Mallory and Adams 1997). Yamnaya culture has also brought metallurgy to the region (Klochko 2018).

During the Bronze Age (end of the 3rd – beginning of the 1st millennium BCE) arable farming becomes the main branch of economy. The spread of bronze casting and the proximity of mines and smelters in the neighboring Donetsk region favoured economic development (Shramko et al. 1977). In the steppe areas, however, cattle breeding was more developed. During the first half of the 2nd millennium BCE our study area was inhabited by the Catacomb culture tribes (18-16 centuries BCE) – semi-nomadic herdsmen for whom agriculture played a supporting role. Since the middle of the 2nd millennium BCE the Catacomb culture was replaced by the Srubnaya culture (16-12 centuries BCE) and later by the Bondarikha culture (12-7 centuries BCE). Agriculture played an important role together with cattle breeding and bronze foundry in the economy of these cultures (Shramko et al. 1977).

The beginning of the Early Iron Age is strongly connected with the widespread use of iron in the 8th-7th centuries BCE and the migration of agricultural tribes from the right bank of the Dnieper River to the forest-steppe of the left-bank and further to the Don River area. Scythian herdsmen dominated in steppe at that time. Shramko et al. (1977) write that during the Scythian times (7-4 centuries BCE) the Siverskyi Donets forest-steppe area was dominated by the tribes of Melankhlens. Zorin et al. (2014), however, refer to them as to an agricultural Scythoid culture. To protect from the attacks of nomadic Scythians, local farmers fortified their settlements with wooden walls, earthen ramparts and ditches.

In the 2nd century BCE nomadic Sarmatian tribes invaded the Black Sea steppe and further the forest-steppe. Scythians were forced out of the southern steppe region (Shramko et al. 1977; Zorin et al. 2014). In the late 1st-early 2nd centuries CE Alans – one of the Sarmatian tribes – gradually conquered all the other Sarmatian tribes. The basis of the Sarmatian economy was the breeding of cattle, sheep and horses. Sarmatians did not build settlements, in summer they wandered with their herds in steppe and in winter they went down to the river banks to winter pastures (Zorin et al. 2014).

Zarubyntsi archeological culture appeared in the Middle and Upper Dnieper around the 2nd century BCE. In the 2nd century CE the descendants of the Zarubyntsi culture reached Kharkiv region in Ukraine and Kursk region in Russia. They cultivated fertile light forest soils and podzolized chernozems for growing millet, rye, wheat and barley, grazed cattle in the meadows of river floodplains, manually made simple pots from clay, and smelted iron from swamp ores (Zorin et al. 2014).

In the 3rd-5th centuries CE the Chernyakhiv archeological culture was spread on the territories from the lower Danube in the west to the Siverskyi Donets River in the east including our study area (Lyubichev 2019). The Chernyakhiv population was highly developed in economic, technological, and social terms as reflected by numerous and diverse archaeological finds. This differs from the previous cultures. The basis of the subsistence economy was agriculture, and the population actively used the black soil (chernozem) of the region. The people of the Chernyakhiv culture used plows pulled by horses or oxen. They grew mainly wheat and barley but also millet and rye (Zorin et al. 2014). During the first half of the 5th century the settlements of the Chernyakhiv culture ceased to exist. The reasons for this are still not fully understood and controversially discussed (Lyubichev 2019; Oblomskiy 2017).

During the Migration period the Huns came from beyond the Volga River at the end of the 4th century CE moving forward to enter the decaying Roman Empire in the west. Early Slavic sites of the Penkivka archaeological culture were dated to the 5th-7th century CE in the Kharkiv region (Shramko et al. 1977). The Penkivka culture was replaced by the Romny culture that is thought to be connected with the Slavic Severian tribe (8-10 centuries CE). Slavic tribes had developed agriculture and pastoralism as well as crafts and trade. The Severian territory became part of Kievan Rus in the 10th century. The Saltovo-Mayaki culture was also spread in the Kharkiv region in the 8th-10th centuries and was closely associated with the Khazar Khaganate. There were several variants of the Saltovo-Mayaki culture representing different social-economic lifestyles from nomadism to semi-sedentary agropastoralism (Kiyashko 2016; Pletniova 1967). In the 10th century Kievan Rus defeated Khazar Khaganate and the forest-steppe part of the region was united under the Kievan Rus rule (Shramko et al. 1977). Following the Mongol-Tatar invasion, the study area was conquered by the Golden Horde in the 13th-14th centuries. We attribute the following evens to modern history in this study.

Materials and methods

Sediment core and loss-on-ignition

The sediment core was obtained from a peatbog ~3 km south and west from the Siverskyi Donets River channel, in 2013. Two sister cores "Omelchenki I" (0-150 cm) and "Omelchenki II" (25-175 cm) were taken next to each other with a Russian corer. The sediment description was carried out directly after obtaining the cores (Table 3.1). LOI analysis followed Heiri et al. (2001) and included drying the samples at 105 °C for 24 hours, burning at 550 °C for 4 hours and at 950 °C for 2 hours.

Chronology

Radiocarbon dating was carried out at the AMS Radiocarbon Laboratories in Poznan, Poland and Institute of Physics of the University of Erlangen Nuremberg, Germany. The radiocarbon ages were calibrated and the age-depth model was built using the R package 'bacon' based on Bayesian statistics (Blaauw and Christen 2011) with the IntCal20 calibration curve for Northern Hemisphere (Reimer et al. 2020).

Pollen and NPP

In total, we analysed 52 samples for pollen and non-pollen palynomorphs in 3 cm resolution. The processing technique followed Faegri and Iversen (1989) and included the treatment with 10 % HCl, 48 % HF and acetolysis for 3 minutes. The samples were sieved through 200 µm metallic mesh and 5 µm nylon mesh using ultrasound bath for less than 1 minute. To calculate the pollen concentration and influx, 1 *Lycopodium* spores' tablet was added per sample (batch number 1031, 20848 ± 1546 spores per tablet) prior to the chemical treatment.

The samples were counted up to at least 500 terrestrial pollen grains per sample under 400× to 1000× magnification. Four pollen samples with the low pollen concentration of 885-1472 grains/cm^3 were counted up to 300 pollen grains. Eight samples with the pollen concentration less than 520 grains/cm^3 were calculated up to at least 100 pollen grains when possible. Four pollen samples were excluded from the pollen diagram due to the insufficient pollen counts.

The percentages of the pollen and NPP were calculated relative to the pollen sum of terrestrial plants excluding Cyperaceae and aquatics. Cyperaceae pollen was excluded from the sum due to the origin of the core in a Cyperaceae mire and the persistent local presence of sedges according to the pollen and macro-remains data. To identify the pollen types, we used Beug (2004) and Göttingen University reference collection, and for NPP – NPP Image Database (Shumilovskikh et al. 2022). Local Pollen Zones (LPZ) were defined using CONISS (Grimm 1987). The number of LPZ was determined by the broken stick model (Bennett 1996) and visually based on the changes in dominant and indicator taxa. The NPP zones were defined based on the changes in NPP composition.

To explore the variation in the pollen data, we applied Principal Component Analysis (PCA) using R package 'vegan' version 2.6-2 (Oksanen et al. 2022) and 'ellipse' version 0.4.3 (Murdoch and Chow 2022) for correlations with 95 % confidence intervals. We excluded rare pollen types occurring less than 4 times from the dataset and performed square root transformation to reduce the effect of extreme values.

Forest cover reconstruction

The reconstructions of forest cover were performed using modern analogue technique (MAT) based on matching analogues between modern and fossil pollen assemblages (Overpeck et al. 1985). The data set of modern analogues consists of 726 modern pollen samples from a wide variety of landscapes in Eastern Europe and Siberia (Novenko et al. 2014a), combined with estimates of forest cover 20 km around the site from MODIS satellite images (Hansen et al. 2003). Calculations were carried out using the 'analogue' package (Simpson 2007). We used squared-chord distances (SCD) as the measure of similarity between pollen assemblages and weighted mean of the k-closest analogues. The number of the nearest analogues (k) was defined automatically using the lowest root mean square error of prediction (RMSEP) for the leave-one-out errors (Fig. S3.2).

Charcoal

To track the fire history of the area, the core was studied for macro-charcoal in 1 cm resolution. 159 samples of 1 cm^3 each were treated following Stevenson and Haberle (2005): 10 % KOH, 6 % H_2O_2 and sieved through 125 µm metallic mesh. The charcoal was counted under 100× magnification. The results were processed in CharAnalysis version 0.9 (Higuera 2009). We used log transformation and calculated the peaks as residuals with the locally defined threshold over 250-year fire return interval for the last 2000 years, over 1000 years for the period 2000-5000 cal. yrs BP and over 2000 years for the rest of the record. Microscopic charcoal was processed and calculated simultaneously with pollen and NPP in 3 cm resolution.

Macro-remains

15 samples were processed for macro-remains including seeds, parts of plants, algae, animal remains, eggs and charcoal to track the changes in local vegetation. The entire 1-cm thick core section was sieved through 250 µm metallic mesh. Remained sediment was studied under 40× to 100× magnification. We used Cappers et al. (2006) and Göttingen University reference collection to identify the seeds. The number of Local Macro-remains' Zones (LMZ) was determined based on the changes in macro-remains' composition.

Results

Lithological characteristics and LOI

The sediment changes from the organic rich (up to 88 %) blackish brown upper part of the core to the organic-poor (2 %) sediment of clay and sand at the bottom (Table 3.1, Fig. 3.3). Visible plant remains occur in the upper and middle parts of the core. Based on the LOI results we combined the upper 25 cm of the core "Omelchenki I" with the core "Omelchenki II" to obtain a continuous record of Omelchenki (Fig. 3.3).

Table 3.1 – Sediment description and LOI values of the composite core Omelchenki

CORE	DEPTH	DESCRIPTION	LOI (ORGANIC PART, %)
OMELCHENKI I	0-25 cm	Loose, brownish black, poor decomposed organic mud with visible plant remains	32-43

OMELCHENKI II	25-37 cm	Blackish brown, middle/well decomposed peat with visible plant remains	33-44
	37-55 cm	Brown, middle decomposed peat	78-83
	55-67 cm	Brown, poor decomposed peat	51-88
	67-75 cm	Blackish brown, middle-well decomposed, compact peat	29-35
	75-97 cm	Greyish black minerogenic silty clay	10-18
	97-116 cm	Blackish brown, well decomposed peat with plant remains	22-42
	116-125 cm	Minerogenic silty clay with organic, blackish grey plant remains	5-14
	125-140 cm	Bluish grey silty clay	4-10
	140-171 cm	Transition from bluish grey to turquoise grey silty clay	2-5
	171-175 cm	Turquoise grey sand	2

Radiocarbon dating and age-depth model

According to the age-depth model (Table 3.2, Fig. 3.3), the core Omelchenki covers the last ~9.8 cal. kyr BP. Two of the nine provided dates (Poz-147105 at 83 cm and Poz-147046 at 138 cm) show inversions and have been statistically discarded. Mineral-rich lower part of the core had a slow sedimentation rate unlike the more organic middle and upper parts. All the ages provided in the paper are given in calibrated years BP (before present is related to 1950).

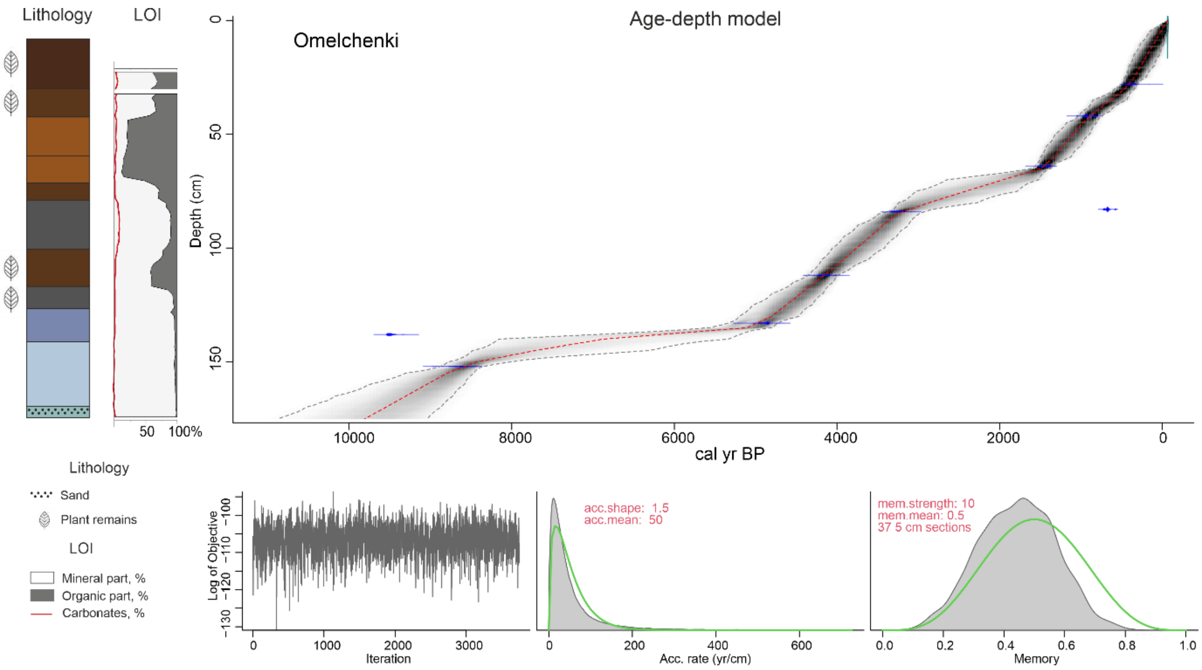

Fig. 3.3. Age-depth model, LOI results and lithology of the core Omelchenki: brown colour represents peat, dark grey – silty clay with organics, light blue/grey – bluish-grey silty clay and sand (see Table 3.1 for details)

Table 3.2 – Radiocarbon and calibrated dates of the core Omelchenki

DEPTH, CM	**DATED MATERIAL**	**LAB. CODE**	**^{14}C AGE, YRS BP**	**AGE RANGE, CAL. YRS BP**	**MEDIAN AGE, CAL. YRS BP**	**MEAN AGE, CAL. YRS BP**
28**	Charcoal and *Sphagnum* leaves	Poz-147104	320 ± 35	312 - 495	419	414
40-45 (42)**	Pollen	Erl-18679	1021±40	754 - 1023	887	882
64**	Bulk (0 % of carbonates)	Poz-146496	1555 ± 30	1349 - 1530	1449	1445
83**	Roots	Poz-147105	735 ± 35 *	-	-	-
83-85 (84)**	*Alisma* seeds and a *Lythrum* seed	Poz-157397	3060 ± 40	2841 - 3484	3211	3194
112**	Charcoal	Poz-83082	3775 ± 40	3902 - 4377	4143	4142
132-134 (133)**	Charcoal, *Alisma*	Poz-157398	4300 ± 40	4685 - 5417	4938	4983

	seeds and *Carex bicarpillata* seeds					
138**	Bulk (0.32 % of carbonates)	Poz-147046	8490 ± 50 *	-	-	-
150-155 (152)**	Pollen	Erl-18680	7836 ± 66	8434 - 9091	8687	8719

* - dates excluded from the age-depth model

** - depths used when constructing the age-depth model

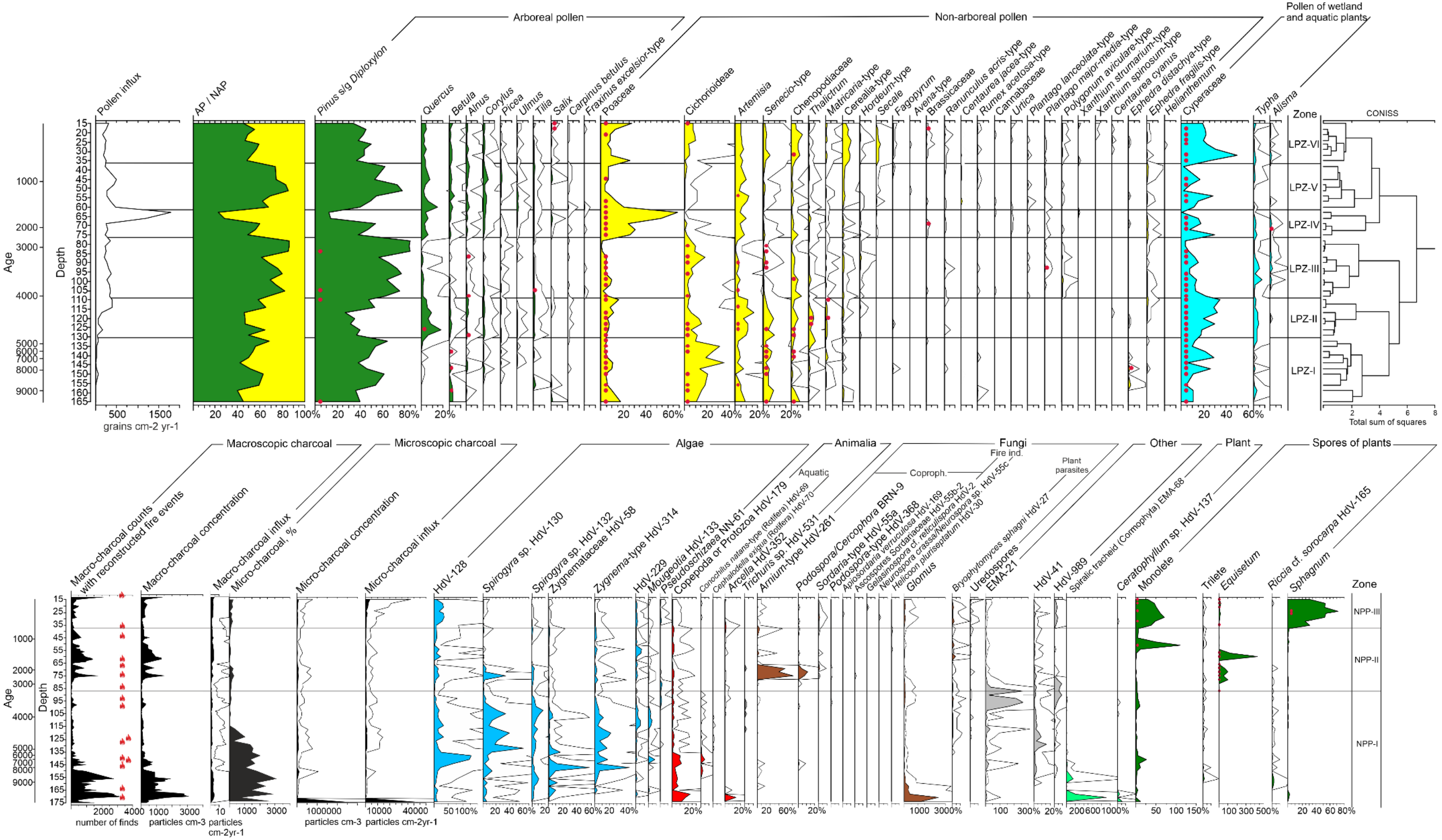

Fig. 3.4. Pollen, NPP and charcoal records of the Omelchenki core. Red dots on the pollen and NPP diagrams mark pollen or spores' clumps (local presence of the plant), fire symbols on the charcoal diagram mark reconstructed fire events

Pollen

The lowermost samples of the Omelchenki core have insufficient counts due to the very low pollen concentration and thus were excluded from the pollen diagram. The pollen diagram starts with the sample at 165 cm with the corresponding age of ~9.3 kyr BP. Temporal resolution between the samples in the lowermost part of the core is ~150 yrs. Starting from ~8.4 kyr BP, it decreases to ~500 yrs between the samples reaching ~1000 years between 6.1 and 5.1 kyr BP. After 5.1 kyr BP the resolution increases to ~100 yrs between the samples. In the upper part of the core, it varies from ~200 yrs to ~50 yrs between the uppermost samples.

In total, we identified 86 terrestrial taxa and 15 wetland and aquatic taxa (including Cyperaceae). The pollen record was divided into 6 local pollen zones (LPZ) based on the changes in terrestrial taxa (Fig. 3.4). The LPZ-I (165-131 cm, 9.3-4.9 kyr BP) is dominated by *Pinus* s/g *Diploxylon* (36-65 %). Arboreal pollen (AP) varies within the range 40-69 % increasing towards the end of the zone. Broadleaf taxa (*Quercus, Ulmus, Corylus, Tilia, Carpinus betulus*) increase in the end of the period up to 2 % as well as *Picea* (up to 1 %) and *Alnus* (up to 2 %). Among NAP, Poaceae (4-18 %), Cichorioideae (10-35 %), *Artemisia* (1-9 %), *Senecio*-type (2-10%) and Chenopodiaceae (up to 7 %) dominate.

The LPZ-II (131-109 cm, 4.9-4.0 kyr BP) is characterized by the maximum of *Quercus* (19 %) and a slight increase in other broadleaf taxa. *Pinus* s/g *Diploxylon* decreases to 27-48 % as well as AP (46-65 %). Among NAP, Poaceae (4-16 %), Cichorioideae (3-15 %), *Artemisia* (8-17 %), *Senecio*-type (3-11 %), Chenopodiaceae (2-6 %) and *Thalictrum* (up to 5 %) dominate. There's a clear increase in Cerealia- and *Hordeum*-types (both up to 1 %) in the second half of the zone.

During the LPZ-III (109-76 cm, 4.0-2.5 kyr BP), AP increases significantly (62-86 %). *Pinus* s/g *Diploxylon* dominates (57-85 %). Broadleaf taxa decrease to 0-4 %. Poaceae (1-10 %), Cichorioideae (3-19 %), *Artemisia* (1-4 %), *Senecio*-type (up to 2 %) and Chenopodiaceae (0.4-9 %) dominate among NAP. Cerealia- and *Hordeum*-types increase further up to 1.3 % and 2 %, respectively. Ruderal *Plantago major-media*-type*, P. lanceolata*-type*, Polygonum aviculare*-type, Cannabaceae, *Rumex acetosa*-type and Brassicaceae also increase.

The LPZ-IV (76-61 cm, 2.5-1.4 kyr BP) has the lowest AP values (23-60 %) for the record. Pine pollen reaches the minimum of 12 %, broadleaf taxa increase to 5-9 %. NAP varies within 40-77 %. Poaceae dominates the record (25-69 %). *Secale* (0.2 %) joins Cerelia-type (2 %) and *Hordeum*-type (1 %) among the cultivated crops. Brassicaceae, *Rumex acetosa*-type, Cannabaceae, *Urtica*, *Centaurea jacea*-type, *Plantago major-media*-type and *P. lanceolata*-type are also abundant.

During the LPZ-V (61-36 cm, 1.4-0.7 kyr BP), AP increases to 62-86 % while NAP decrease to 14-38 %. *Pinus* s/g *Diploxylon* dominates the spectrum (40-79 %), broadleaf taxa reach 4-20 %. Poaceae (4-21 %) and *Artemisia* (4-12 %) dominate among the herbs. *Fagopyrum* (0.2 %) and *Avena*-type (0.2 %) appear in the spectrum. Cerealia-type (0.2-2 %), *Hordeum*-type (up to 0.4 %) and *Secale* (up to 1 %) as well as Brassicaceae, *Ranunculus acris*-type, *Centaurea jacea*-type, *Rumex acetosa*-type, Cannabaceae, *Urtica*, *Plantago major-media*-type, *P. lanceolata*-type and *Polygonum aviculare*-type are present.

In the LPZ-VI (36-15 cm, ~700-170 yrs BP), AP varies within 45-59 %, NAP – 41-55 %. *Pinus* s/g *Diploxylon* dominates among AP (34-50 %) while the broadleaf taxa have 3-7 %. Poaceae (6-28 %), *Artemisia* (5-7 %), Cichorioideae (1-10 %), Chenopodiaceae (4-10 %) and

Cerealia-type (3-8 %) dominate among NAP. *Senecio*-type, *Matricaria*-type, *Hordeum*-type, *Secale*, Brassiacaceae, *Ranunculus acris*-type, *Centaurea jacea*-type and *Polygonum aviculare*-type are abundant. *Fagopyrum*, *Avena*-type, *Rumex acetosa*-type, Cannabaceae, *Urtica*, *Plantago major-media*-type and *P. lanceolata*-type, *Xanthium strumarium*-type and *X. spinosum*-type, *Centaurea cyanus* and *Helianthemum* occur and most of them have their maximum.

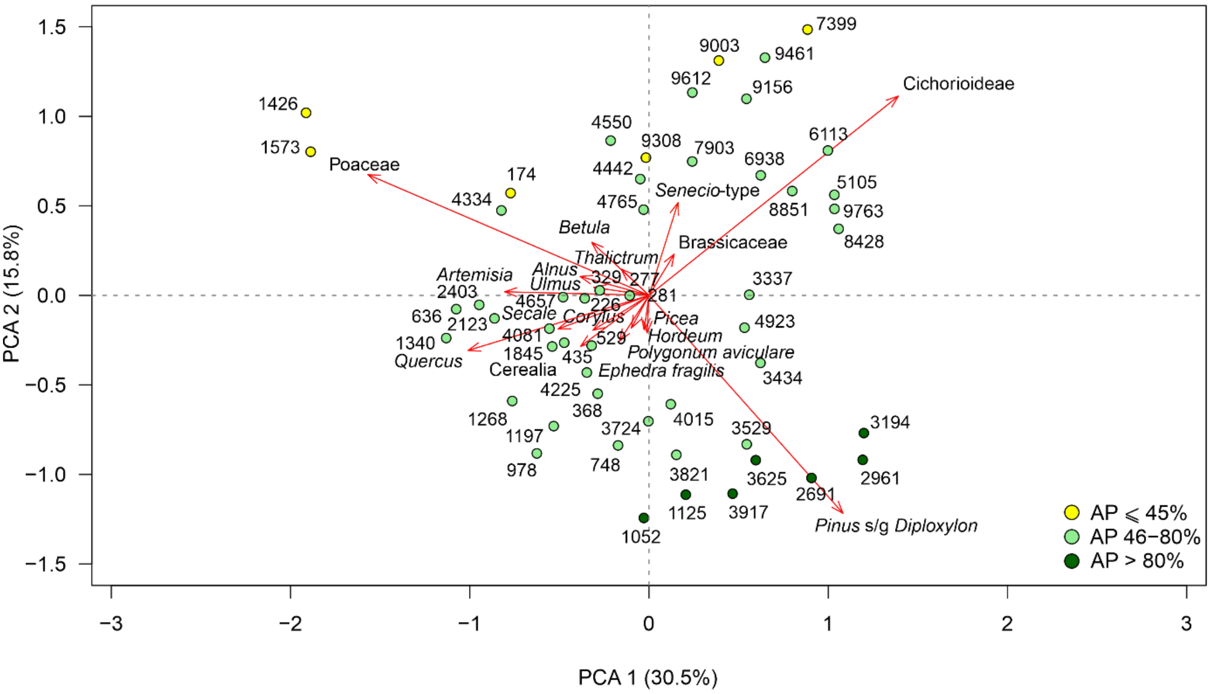

Fig. 3.5. PCA of the Omelchenki core pollen data. The numbers next to the dots show the ages of the samples

PCA (Fig. 3.5) shows variation in the pollen data. The first axis of the PCA explains 30.5 % of variance and is likely connected to the anthropogenically caused deforestation together with agricultural activities. Taxa related to human activity including *Secale*, Cerealia-type, *Hordeum*-type, *Polygonum aviculare*-type, etc. are located in the left part of the graph together with the broadleaf taxa and Poaceae. Two of the most deforested samples of the Omelchenki spectra corresponding to the ages of 1426 and 1573 yrs BP are located left-most. Early Holocene samples and the samples from the later stages of the Holocene with restored forest cover values are to the right of the graph. The second axis explains 15.8 % of variance and is strongly associated with the environmental gradient between the first and the second halves of the Holocene. The samples corresponding to the beginning of the Holocene and more steppe conditions are at the top of the graph with Cichorioideae as the longest vector associated with the second axis up while more forested Late Holocene samples are located down with the dominant tree taxon of *Pinus* s/g *Diploxylon* as the longest vector.

Non-pollen palynomorphs

54 NPP types were identified including algae, fungi, animals' and plants' remains, as well as spores of ferns, mosses and *Equisetum*, and other. The NPP record was also divided into three NPP zones according to the changes in the NPP composition (Fig. 3.4).

NPP-I zone (174-87 cm, 9.8-3.3 kyr BP) is characterized by the abundance of algae up to 162 % (HdV-128, *Spirogyra* HdV-130 and HdV-132, *Zygnema*-type HdV-314, Zygnemataceae HdV-58, *Mougeotia* HdV-133 and HdV-134, *Pseudoschizaea* NN-61, Desmidiaceae or *Closterium idiosporum*-type HdV-60, and HdV-229), aquatic animals up to 17 % (Copepoda or Protozoa HdV-179, rotifers *Conochilus natans*-type HdV-69 and *Cephalodella exigua* HdV-70), spores of *Riccia* cf. *sorocarpa* HdV-165 up to 2 % and some spores of *Equisetum* and Monolete and Trilete ferns. Some other NPP including EMA-21, HdV-41 and HdV-989 also occurred. In the beginning of the zone, *Arcella* HdV-352, *Glomus*-type, spiralic tracheids of cormophytes EMA-68 and *Ceratophyllum* remains were found. During the second half of the zone, eggs of parasitic worm *Trichuris* sp. HdV-531, *Bryophytomyces sphagnii* HdV-27 and few *Sphagnum* spores appeared.

During the NPP-II zone (87-38 cm, 3.3-0.75 kyr BP), the amount of algae significantly decreased to 2-58 %, as well as the amount of aquatic animals' remains (to 3 %). Among other animal remains', *Arcella* HdV-352 and *Trichuris* sp. HdV-531 were present up to 1 % and 0.2 % respectively. Coprophilous fungi reached 90 % during the zone. Monolete fern and *Equisetum* spores increased to 110 % and 422 %. *Bryophytomyces sphagnii* HdV-27 and some *Sphagnum* spores were present.

NPP-III zone (38-15 cm, ~750-170 yrs BP) is characterized by high amounts of *Sphagnum* (1-70 %), monolete fern (7-70 %) and *Equisetum* (2-19 %) spores. Algae and aquatic animals continued to decrease to 12-38 % and 1-2.5 %. Coprophilous fungi reached 1-6 %, *Glomus*-type increased to 16-107 %. Fire indicators *Neurospora crassa*/*Neurospora* sp. HdV-55c and *Gelasinospora* cf. *reticulispora* HdV-2 occurred.

Macro-remains

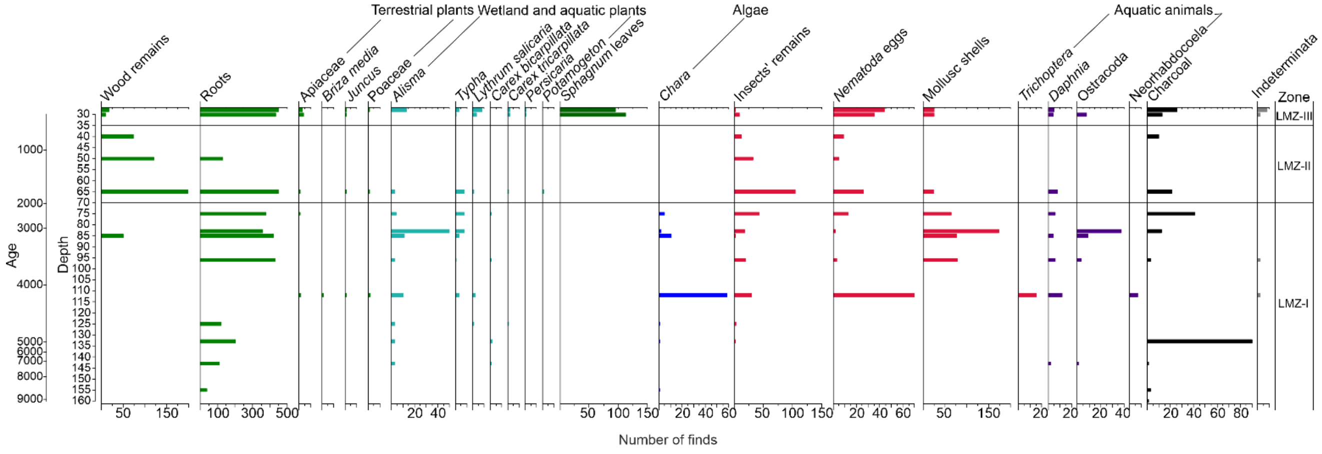

Fig. 3.6. Macro-remains' diagram of the Omelchenki core

We identified 28 types of macro-remains including seeds of plants, wood, roots' and leaves' remains, algae, eggs and parts of animals and charcoal (Fig. 3.6). Three Local Macro-remains' Zones (LMZ) were distinguished.

LMZ-I (174-70 cm, 9.8-1.9 kyr BP, 10 samples) contains the seeds of mostly wetland and aquatic plants including *Alisma*, *Typha*, *Lythrum salicaria*, *Carex bicarpillata* and *C. tricarpillata*. Some seeds of terrestrial plants (Apiaceae, *Briza media*, *Juncus* and Poaceae) occurred in the sample from ~4.2 kyr BP. *Chara*, *Daphnia*, Ostracoda and Neorhabdocoela remains were found as well as *Nematoda* eggs and insects' remains. At lot of charcoal particles were found in a sample from ~5 kyr BP.

LMZ-II (70-35 cm, 1.9-0.6 kyr BP, 3 samples) contains a lot of wooden particles. Among the aquatic plants, seeds of *Alisma*, *Typha*, *Lythrum salicaria*, *Carex tricarpillata* and *Potamogeton* were found. Terrestrial plants' seeds included Apiaceae, *Juncus* and Poaceae. *Chara* and Neorhabdocoela remains disappeared. *Daphnia* eggs occurred just in the lowermost sample.

In LMZ-III (35-28 cm, 0.6-0.4 kyr BP, 2 samples) *Sphagnum* leaves were found as well as seeds of Apiaceae, *Juncus,* Poaceae, *Alisma*, *Typha*, *Lythrum salicaria*, *Carex tricarpillata* and *Persicaria.* Eggs of *Daphnia* and Ostracoda remains occurred.

Charcoal

The macro-charcoal record covers the period from 9.8 kyr BP to ~140 yrs BP (175-13 cm) while the micro-charcoal record corresponds to the ages of 9.8 kyr BP to ~170 yrs BP (174-15 cm). The two records demonstrate a similar trend with the highest amount of charcoal in the beginning, lower amount of charcoal in the middle and some increase towards the end of the records.

For the macro-charcoal record, the maximum of charcoal particles (up to 3275 particles/cm^3) occurred during the period of 9.8-8.4 kyr BP. Less charcoal was found in the samples of 8.3-5.1 kyr BP (87-968 particles/cm^3). Low charcoal concentration (20-191 particles/cm^3) was in the samples from 5.0-2.6 kyr BP with a slight increase in charcoal ~4.7 kyr BP (up to 229 particles/cm^3) and ~3.7 kyr BP (up to 389 particles/cm^3). During 2.5-1.0 kyr BP the amount of charcoal rose up to 1737 particles/cm^3 decreasing to 58-196 particles/cm^3 for ~900-460 yrs BP. After ~440 yrs BP the number of particles increased again reaching 2131 particles/cm^3 ~140 yrs BP. Sixteen local fire events were reconstructed: in ~9.7, 9.3, 7.7, 7.4, 7.1, 4.8, 4.7, 3.8, 3.6, 3.3, 2.5, 1.7-1.8, 1.4, 1 kyr BP, 700 and 140 yrs BP.

The micro-charcoal counts were the highest (up to 3112 %) during ~9.8-7.9 kyr BP deceasing to 320-2064 % during ~7.9-4.3 kyr BP and did not exceed 328 % for the rest of the record (Fig. 3.4). However, the high percentages of micro-charcoal in the beginning of the record are likely connected to the low pollen concentration and influx (Fig. 3.4). Micro-charcoal concentration and influx show a different trend. At the bottom of the record ~9.8 kyr BP micro-charcoal concentration reaches 2,574,728 particles/cm^3 and influx reaches 51,154 particles/cm^2 yr. Between 9.6 and 8.9 kyr BP micro-charcoal concentration and influx drop to 1450-9700 particles/cm^3 and 29-172 particles/cm^2 yr respectively. Local peak occurred ~8.4 kyr BP with the concentration of 105,599 particles/cm^3 and influx of 1003 particles/cm^2 yr after which micro-charcoal values decreased to 10,888 particles/cm^3 and 63 particles/cm^2 yr ~7.9 kyr BP. The next increases in micro-charcoal concentration and influx occurred ~4.9-4.3 kyr BP (41,552-77,772 particles/cm^3 and 1154-1714 particles/cm^2 yr respectively), ~3.6-3.5 kyr BP (36,977-37,288 particles/cm^3 and 1138-1171 particles/cm^2 yr), ~2.7-1.8 kyr BP (47,928-70,794 particles/cm^3 and 515-748 particles/cm^2 yr), in 1.3 kyr BP (28,162 particles/cm^3 and 1182 particles/cm^2 yr) and after ~600 yrs BP reaching 77,555 particles/cm^3 and 4474 particles/cm^2 yr by ~170 yrs BP.

Interpretation and discussion

Local wetland development

The study site represented a lake already by ~9.8 kyr BP. Freshwater conditions are supported by the findings of algae including *Spyrogira* sp., Zygnemataceae, *Mougeotia*, HdV-128 and HdV-229, as well as remains of *Daphnia*, ostracods and Copepoda or Protozoa HdV-179 (Geel et al. 1983). The occurrence of *Ceratophyllum* remains together with *Chara* (Fig. 3.4 and 3.6) suggests good light and oxygen availability, high water transparency with a higher pH and carbonates and a high species diversity in the lake (Pełechaty et al. 2014). Findings of *Arcella*, *Sphagnum* spores and *Sparganium* pollen point to shallow fens around the lake. The abundance of *Glomus*-type spores in the beginning of the record might be either due to the presence of roots of locally growing plants (Fig. 3.4 and 3.6, e.g. locally present Cyperaceae), the presence of which is also supported by the findings of spiralic tracheids of Cormophyta (Fig. 3.4), or soil erosion. Spores of liverwort *Riccia* indicate bare soils alongside the lake (Geel et al. 1983). After ~7.9 kyr BP the increase in algae and disappearance of *Arcella* and *Sphagnum* might imply some expansion of the lake.

Significant reduction of algae and increase in *Arcella* and *Sparganium* by ~3.3 kyr BP indicate the process of lake overgrowing and peat development. Increased *Glomus*-type indicates the presence of plant roots. ~600 yrs BP the study site transformed into a mire and was overgrown by *Sphagnum*. The process could have been triggered by a total deforestation and the following soil erosion in the study area which occurred in the same time period (Fig. 3.4, 3.7).

Human-environment interactions

The reconstructed forest cover estimates of the Omelchenki core allow us to estimate the southern treeline dynamics. However, due to the no-analogue situation and high SCD values before ~4 kyr BP (Fig. S3.2), the reconstruction before ~4 kyr BP should be interpreted with caution. Furthermore, the forest cover is overestimated in the steppe areas due to the long-distance transport of some AP (Novenko et al. 2014a). Here, we consider 15 % of the reconstructed forest cover to be the steppe – forest-steppe boundary whereas ~30 % – a boundary between forest and forest-steppe (Ershov 2007).

Mesolithic hunters and gatherers in the early Holocene

Controlled by the North Atlantic, forests started to spread in the region around 11.7 kyr BP with the rise in temperatures in the beginning of the Holocene (Lukanina et al. 2022). Forest composition, however, varied along the latitudinal gradient of the extensive East-European forest-steppe. While mixed pine-broadleaf open forests with *Pinus*, *Betula*, *Quercus*, *Corylus* and *Ulmus* developed in the wetter and less continental western part of the ecotone already by ~11.5 kyr BP (Fig. 3.1 – records of Pukiv and Yunashkiv) (Hájková et al. 2022), the area eastwards was still represented by meadow steppe with pioneer birch and pine forest patches along the rivers (Fig. 3.1 – records of SV-8 and Zamostye) (Borisova et al. 2006; Lukanina et al. 2022). First, ~10.3 kyr BP open pine forests with *Quercus*, *Ulmus*, *Corylus* and *Tilia* established at Zamostye and continued to spread southwards reaching Omelchenki site ~9 kyr BP (Fig. 3.7).

According to the forest cover reconstruction (Fig. 3.7), ~9.3 kyr BP Omelchenki area was likely represented by steppe with a predominance of Poaceae, Cichorioideae, *Artemisia*, *Senecio*-type and Chenopodiaceae. Some pine, birch, willow and alder trees grew along the rivers. By ~9 kyr BP the increasing amount of moisture led to the spread of pine forests turning Omelchenki into a forest-steppe. The development of its broadleaf component started around 8.9-8.4 kyr BP, when the presence of *Quercus*, *Corylus* and *Tilia* pollen became constant and increasing. Moisture-demanding *Picea* appeared in the record around the same time while *Ulmus* and *Carpinus betulus* pollen – ~7.9-7.4 kyr BP. During the early Holocene available moisture was slowly increasing eastwards and southwards inducing forest spread further east and south in the region.

In the early Holocene Mesolithic hunting and gathering societies inhabited East-European forest-steppe. From the early Mesolithic our study area was populated by people of Zimovniky archaeological culture (Fedyunin 2015; Zalyznyak 2020). Its territorial borders is thought to stretch from the north-eastern Azov Sea region to the Don-Volga interfluve (Fedyunin 2015). Zimovniky is described as a forest-steppe culture (Fedyunin 2015; Zalyznyak 2020). However, Omelchenki pollen record obtained to the north from the known Zimovniky archaeological sites (Zalyznyak 2020), showed that the area was likely represented by steppe, although it is located in a river valley with the best hydrological conditions for a forest development. A considerable change in environment might have led to the change in cultures ~9 kyr BP (~7 kyr BCE) due the people migrations or changes in objects of hunting followed by changes in hunting tools, etc. Thus, the Dniepr-Donets culture might have replaced Zimovniky following the forest spread. However, the transition from Zimovniky to the Dniepr-Donets culture is very poorly dated and it is not yet clear how true the coincidence with the natural changes is.

Donets culture was formed under the influence of the descendants of the north-western Janislawice culture of forest hunters and fishers and a neighbouring Kurkek culture (Fedyunin 2015; Zalyznyak 2020), which existed south from the study area between ~9.9 and 8.4 kyr BP (~7.9 and 6.4 kyr BCE) (Kiosak et al. 2022). The forest cover estimates for the Mesolithic stage of the Donets culture are within 18-29 % representing a forest-steppe environment with forests likely spread in the river valleys where the Donets archaeological sites were found (Zalyznyak 2020).

Spread of agriculture in the middle Holocene

Many researches link climate change namely the Holocene thermal maximum to the Neolithic revolution as one of its driving forces (Ashraf and Michalopoulos 2010; Bar-Yosef 1998). A period of warm climate in the first half of the Holocene (IPCC 2007; Wanner et al. 2008) mostly recorded in the middle and high latitudes of the Northern Hemisphere (IPCC 2007; Renssen et al. 2009), the Holocene thermal maximum is associated with the orbitally forced summer insolation maximum (Berger and Loutre 1991; Kaufman 2004). However, even within the European continent it was reflected differently (Davis et al. 2003).

Holocene climate reconstructions for Central Europe show the beginning of the warm period around 8 kyr BP, with the highest annual temperature close to 6 kyr BP (Davis et al. 2003). Rising winter and summer temperatures are observed for the records from the western part of the East-European forest-steppe and forest zones through a substantial increase in broadleaf taxa and a decline in pine (Hájková et al. 2022; Kremenetski 1995; Schwörer et al. 2021). Milder climate conditions could have favoured the adoption of agriculture in the west of the ecotone by ~7.3 kyr BP (Motuzaitė Matuzevičiūtė and Telizhenko 2016).

In more continental eastern part of forest-steppe and in the Mid-Russian Upland, a significant broadleaf forest expansion occurred not earlier than ~7 kyr BP (including records SV-8, Zamostye, Klukva, Fig. 3.1) (Borisova et al. 2006; Lukanina et al. 2022; Novenko et al. 2015; Novenko et al. 2016a). Omelchenki record also had a slight increase in the broadleaf taxa ~6.9 kyr BP. Sufficient moisture of the forest-steppe ecotone at that time (19 % of the reconstructed forest cover) together with favourable higher summer and winter temperatures might have provided proper conditions for the start of agriculture in more continental areas of the ecotone. A thousand years difference between the establishment of a milder climate in the west and the east might explain the gap in the adoption of agriculture by the Donets culture foragers compare to the agricultural societies of western Ukraine (Anthony 1995).

Meadow steppes of the forest-steppe ecotone were attractive for the development of stock breeding as a basis of subsistence economy for the Copper Age cultures at Omelchenki (Pashkevich 2000; Shramko et al. 1977). The decrease in forest cover ~4.8 kyr BP might be explained by the spread of copper following the arrival of the Yamnaya culture, and the existence of the nearby Donetsk copper mines (Chernykh 1976). The increase in charcoal and local fire events could mark deforestation and fires for the copper production. Furthermore, the increase in the broadleaf taxa during the same time period might indicate the use of pine and possibly the spread of broadleaf trees following the beginning of the forests spread indicated for other forest-steppe study sites (Lukanina et al. 2022; Shumilovskikh et al. 2018).

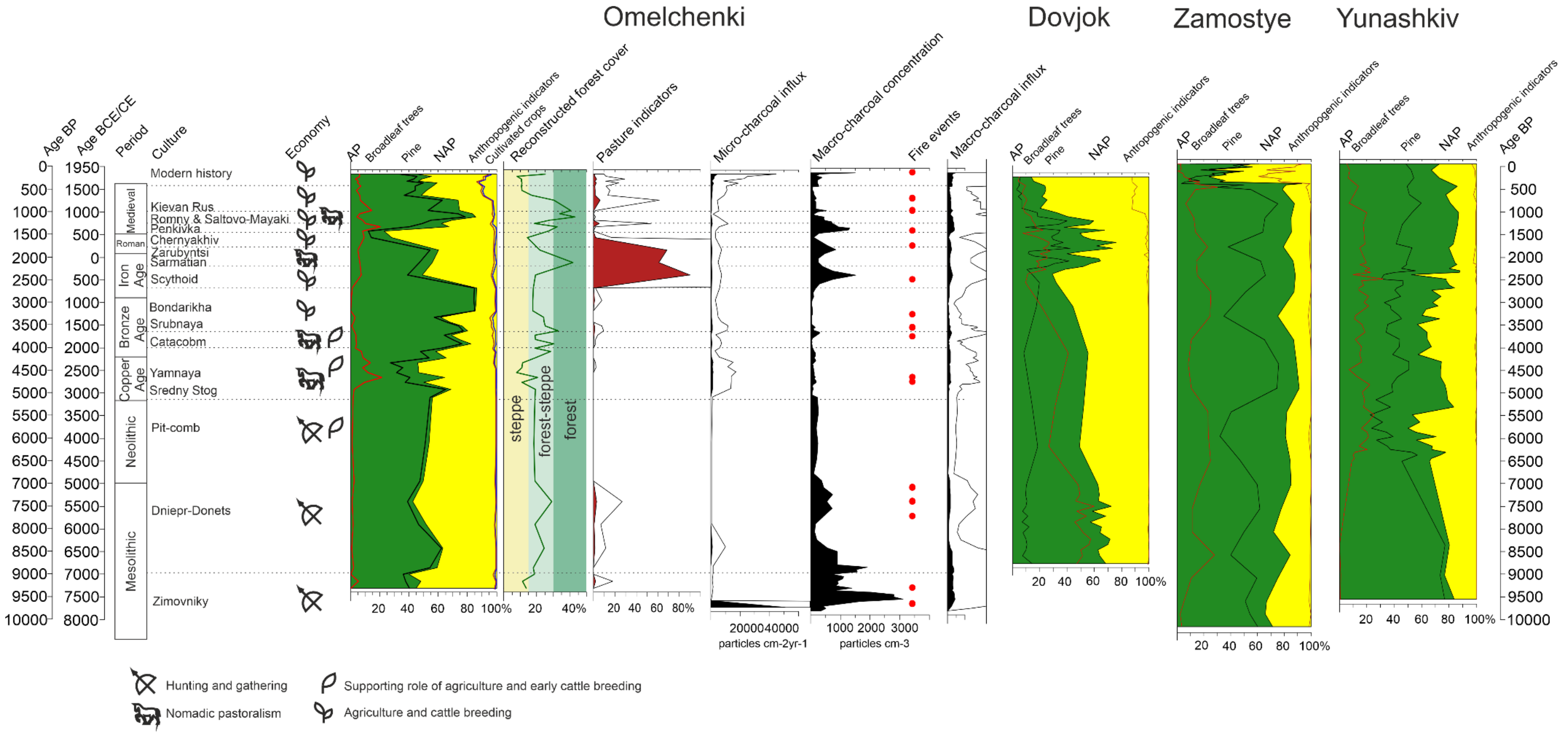

Fig. 3.7. Summary diagram of the archaeological data from the study area (after Shramko et al., 1977; Zalyznyak, 2020), pollen, NPP, charcoal records and the reconstructed forest cover of the Omelchenki core (steppe, forest-steppe and forest values after Ershov (2007) and Novenko et al. (2014)) and published pollen records from the East-European forest-steppe ecotone: Dovjok (Kremenetski, 1995), Zamostye (Lukanina et al., 2022) and Yunashkiv (Hájková et al., 2022).

By ~4.2 kyr BP, the forest cover estimates reached 19 % increasing further to 33 % by ~3.6 kyr BP indicating the development of forests. Many other records from the ecotone have a similar trend with Omelchenki: ~4.5 kyr BP the forest cover at Podkosmovo site has risen from ~12 to ~31 % (Fig. 3.1) (Novenko et al. 2014a) and at Zamostye – from 34 to 42 % (Lukanina et al. 2022). In the western part of the forest-steppe ecotone, e.g. at the Oltina Lake site and Durankulak, the tree cover also reached its maximum after ~4.2 kyr BP (Feurdean et al. 2021; Marinova and Atanassova 2006). Coinciding with the decreasing summer insolation (Berger and Loutre 1991) lower temperatures of the second half of the Holocene (Davis et al. 2003; Svensson et al. 2008; Wanner et al. 2008) lowered evapotranspiration and induced the shift of the southern treeline southwards in Eastern Europe (Kremenetski 1995; Lukanina et al. 2022; Marinova and Atanassova 2006; Novenko et al. 2014a; Novenko et al. 2016b; Shumilovskikh et al. 2018; Spiridonova 1991).

The change in moisture balance was beneficial for agriculture and supported the switch of the main activities of the Bronze Age cultures from nomadism to farming. Thus, agriculturally developed Srubnaya and Bondarikha cultures (Khazanov 1984) spread in the area of the previous semi-nomadic Catacomb culture (Fig. 3.2). From this time ~3.5 kyr BP (~1.5 kyr BCE), the area experienced deforestation reflected as a decrease of arboreal pollen and the forest cover associated with the increase of agricultural and ruderal markers. Reconstructed forest cover values were within 30-33 % when the anthropogenic indicators including the crops' pollen did not exceed 1-1.5 %. During the periods of increasing anthropogenic pressure the forest cover estimates were decreasing to 18-25 %. Corresponding with the decline in the forest cover, local fire events might indicate land clearance for farming or the use of slash-and-burn agriculture (Fig. 3.7).

Interestingly, the forests were expanding mostly due to the spread of pine. The question if it was natural or the spread of broadleaf trees was inhibited due to their active use is quite important for understanding of climate dynamics in the region. Between ~3.5 and 2.7 kyr BP (~1.5-0.7 kyr BCE), the percentage of broadleaf taxa at Omelchenki was very low – similar to their amount of the early to mid-Holocene forests ~9-6 kyr BP. However, the climate conditions were unlikely to be the same.

The most probable explanation for such a low percentage of the broadleaf taxa was given by Krasnov (1971). In his opinion, animal husbandry could have affected broadleaf forests of Eastern Europe more than slash-and-burn agriculture due to the preparation for the winter of woody fodder for livestock (predominantly *Ulmus*, *Tilia*, *Fraxinus* and *Acer*). *Ulmus* and *Corylus* almost completely disappeared for the time period ~4-2.7 kyr BP from the Omelchenki record. Grazing by possibly domestic animals is suggested from an increase in coprophilous fungal spores at Omelchenki. Some other records from the East-European forest-steppe also display some reduction in the broadleaf taxa. At Dovjok (Fig. 3.1 and 3.7), they decreased from 40 % in the beginning of the period to 10 % at the end coinciding with the increase in anthropogenic markers (Kremenetski 1995). However, other records from the ecotone and the broadleaf forest zone didn't show any remarkable decline in broadleaf taxa (e.g. Podkosmovo, Klukva, Selikhovo, Istochek, Zamostye, Yunashkiv, Fig. 3.1) highlighting heterogeneity in land use and its impact on the vegetation (Hájková et al. 2022; Lukanina et al. 2022; Novenko et al. 2014a; Novenko et al. 2015; Novenko et al. 2016b; Novenko et al. 2017).

Human-driven vegetation changes since the Iron Age

In the last 3000 years the forest cover kept increasing reaching its maximum of 41-43 % for the Holocene. Especially strong increase in the forest cover occurred during the dominance of nomadic Sarmatian tribes in the beginning of the second millennium BP (first millennium CE) inhabiting the forest-steppe and steppe areas of the Siverskyi Donets River. A drastic increase in coprophilous fungi between ~2.4 and 1.8 kyr BP (5th century BCE and early 2nd century CE) (Fig. 3.4 and 3.7) which could be pasture indicators corresponds with the Scythoid and Sarmatian periods. The lake shore might have been used for grazing. This is also supported by a finding of an egg of *Trichuris* – a parasitic worm infecting domestic animals and people (Fig. 3.4).

Later forest maxima are related to the Migration period after the disappearance of Chernyakhiv culture ~1.5 kyr BP (5th century CE) and the confrontation between Slavic tribes and the Khazar Khaganate ~1.1 kyr BP (9th century CE) (Fig. 3.7). This allows us to conclude that climatic conditions would have allowed a wider distribution of forests over the past 2000 years without constant agricultural activities. Many other pollen records, e.g. Zamostye, Dovjok, Yunashkiv, demonstrate a similar trend – the highest values of arboreal pollen in the last 2000 years decreasing proportionally to the increasing anthropogenic and agricultural markers (Fig. 3.7).

Two remarkable deforestation events occurred in the study area within this time period. The first one is attributed to the Chernyakhiv archaeological culture from the 3-5th centuries CE. Arboreal pollen percentage of 23 % of this time period was the lowest for the whole record. The forest cover estimates dropped to 14 % correspondingly. Locally present trees around the lake indicated by wooden particles in macro-remains were cut and burned as shown by the abundance of charcoal (Fig. 3.6, 3.7). Active deforestation and fires were either indicative of slash-and-burn agriculture or the land clearance for arable farming. Chernyakhiv culture, with highly developed economy, agriculture and technologies (Zorin et al. 2014), had a major impact on the environment of the study area in the second quarter of the second millennium BP (first millennium CE) (Fig. 3.2). A sharp increase of the reconstructed forest cover to 27-32 % after the 5th century suggests economic degradation and partial abandonment of the land.

The second major deforestation event started after the defeat of the Khazar Khaganate by Kievan Rus in the 10th century CE (Shramko et al. 1977). The forest cover was declining since then while the crops' pollen was within of 8-12 % indicating constant use of the land for agriculture. A total deforestation of the area occurred ~600 yrs BP when the forest cover estimates decreased first to 17 and then to 8-10 % transforming the area into a treeless environment by the 15th century. Many of the Kievan Rus cities were destroyed due to the Golden Horde attack in the 13th century. However, some of them kept functioning until the 17th century according to historical data (Shramko et al. 1977) explaining agricultural activities in the area. The record ends in the 18th century due to peat degradation because of its draining in the 20th century.

All the available records from the East-European forest-steppe show a total deforestation in the last 1000 years. In some areas – e.g. at Dovjok (Fig. 3.1 and 3.7) arboreal pollen dropped to 30 % in the 10th century decreasing further to ~20 % in the 11th and to 14 % in the 18th century (Kremenetski 1995). In the records from the northern forest-steppe, e.g. Podkosmovo, Zamostye and Sudzha, a total deforestation took place later in the 17th century

(Lukanina et al. 2022; Novenko et al. 2014a; Shumilovskikh et al. 2019a). Our data highlight a high sensitivity of forests in their southern limits to anthropogenic pressure, which emphasizes the possibility of their potential spread further south. However, considering the current global warming the southern tree line is likely to shift northwards bringing the area to the mid-Holocene conditions increasing risks for agriculture.

The results from the Omelchenki study site strongly suggest that the Holocene climate changes had a high impact on the changes in the subsistence economy of the Holocene archaeological cultures. In the first half of the Holocene the fluctuations of the southern tree line correspond with the changes of the cultures with forager economies. A late adoption of agriculture in the more continental eastern part of the ecotone might be explained by the difference in establishment of favourable climate conditions between the western and eastern parts of the forest-steppe. The mid-Holocene spread of steppe promoted stock breeding as a basis of the Copper Age cultures' economy. The late Holocene increase in available moisture and the following forest spread contributed to the establishment of farming communities. They had in turn a major impact on vegetation controlling the forest spread by fire and active deforestation. Therefore, forests were spread in the area during the periods of decreasing anthropogenic pressure.

Fire history

Dry climate conditions together with sufficient fuel provided by the forest-steppe vegetation induced its high flammability in the early Holocene (Feurdean et al. 2020; Pausas and Ribeiro 2013). Furthermore, pine trees dominating the forest-steppe at the time are more prone to ignition than temperate broadleaf deciduous trees due to lower leaf moisture, volatile compounds and resins, retention of dead biomass in the crown, ladder fuels and slower litter decomposition (Feurdean et al. 2020). Early Holocene fires are known for the records from Central and Eastern Europe (Feurdean et al. 2012; Feurdean et al. 2013; Florescu et al. 2018; Lukanina et al. 2022). Feurdean et al. (2020) provide the time period of ~10.5-8 kyr BP as the time with the highest biomass burning in the early Holocene. The Omelchenki record is in line with the trend. Drier conditions at the southern limits of the forest-steppe ecotone promoted more severe wildfires compare to the its central and northern parts. Thus at Zamostye (Fig. 3.1), macro-charcoal influx and concentration reached 2.4 particles/cm^{2}yr and 365 particles/cm^3 respectively (Lukanina et al. 2022) while at Omelchenki – 4.1 particles/cm^{2}yr and 3113 particles/cm^3 in the early Holocene. The fires' intensity decreased after ~7 kyr BP simultaneously with the reduction of forest cover and, consequently, the amount of fuel and some expansion of the broadleaf trees with positive effects on fuel moisture and a dampening effect on biomass burning compare to the pine forest-steppe (Feurdean et al. 2020). The fire events after that might have had anthropogenic nature.

The amount of background charcoal decreased further ~5-4 kyr BP and was low in the second half of the Holocene. We suggest it is connected with the increased moisture availability for the region (Lukanina et al. 2022; Shumilovskikh et al. 2018) and a further spread of the broadleaf trees. Micro-charcoal, on the other hand, somewhat increased due to the human-induced deforestation likely following the development of metallurgy (Chernykh 1976) and a better particles transport indicating regional fires (Fig. 3.7).

Further development of forests by ~4.2 kyr BP and decreased summer insolation (Berger and Loutre 1991) allow us to assume that the late Holocene fire dynamics was strongly connected with the human activities. Detected fire events strongly correlate with the periods of low arboreal pollen content and forest cover together with a higher content of crops' pollen implying burning of wood after land clearance or the use of slash-and-burn agriculture. Such fire events occurred during the periods of Catacomb and Srubnaya cultures ~3.8-3.6 and ~3.3 kyr BP (~18/19th-16/17th and ~14th centuries BCE), Scythoid ~2.5 kyr BP (~6th century BCE), Chernyakhiv ~1.7-1.8 kyr BP (~3rd century CE), and Penkivka ~1.4 kyr BP (~6th century CE). Later fire events belong to the Kievan Rus period (10th and 13th centuries CE) and to the early 19th century.

Local fires related to the sedentary cultures of the late Holocene were evidenced by the macro-remains' record from Omelchenki (Fig. 3.6). The samples from ~3.1, ~2.4, ~1.5 kyr BP and after 800 yrs BP (~12th, 5th centuries BCE, 5th century CE and after the 12th century CE) contain big charcoal particles implying the use of fire by Srubnaya or/and Bondarikha, Scythoid and Chernyakhiv cultures and since the establishment of Kievan Rus. A sample from ~1.1 kyr BP containing no charcoal particles corresponds with a maximum of the reconstructed forest cover of 43 % and evidences a decrease in anthropogenic pressure following the location of the site between the Slavic tribes and the Saltovo-Mayaki culture associated with Khazar Khaganate (Shramko et al. 1977).

Conclusions

Environmental changes affected the cultures and supported the changes in subsistence bases throughout the Holocene. Thus, the spread of forests in the early Holocene steppe ~9 kyr BP (~7 kyr BCE) might have triggered the spread of the Dniepr-Donets culture in the territory of the previous Zimovniky culture.

The mid-Holocene climate warming led to the reduction of the forest cover and some spread of broadleaf trees ~6.9 kyr BP (~4.9 kyr BCE). Sufficient moisture of the forest-steppe ecotone together with favourable higher summer and winter temperatures might have provided proper conditions for the start of agriculture in more continental areas of the forest-steppe. A thousand years difference between the establishment of mild climate in the west and the east corresponds with the gap in the adoption of agriculture by the Donets culture foragers compared to the agricultural societies of western Ukraine.

Meadow steppes of the forest-steppe ecotone were attractive for the development of stock breeding as a basis of subsistence economy for the Copper Age cultures at Omelchenki. The decrease in forest cover ~4.8 kyr BP (~2.8 kyr BCE) and the increase in charcoal might be explained by the development of metallurgy in the region following the arrival of the Yamnaya culture, and the existence of the nearby Donetsk copper mines.

The increase in humidity led to the spread of forests in the study area by ~4.2 kyr BP (2.2 kyr BCE), providing more favourable climatic conditions for agriculture, which likely contributed to the switch of the main activities of the Bronze Age cultures from nomadism to farming. Since the Late Bronze Age human impact on the environment increased strongly. First significant signs of land clearance occurred ~3.5 kyr BP (~1.5 kyr BCE) due to the agricultural activities of the Srubnaya culture. Remarkable deforestation events were attributed to the Chernyakhiv archaeological culture from the 3-5th centuries CE when the forest cover estimates dropped to 14 %, and since the 10th century CE after the defeat of the Khazar Khaganate by Kievan Rus. A total deforestation of the area occurred ~600 yrs BP.

In the last 2000 years the forest cover kept increasing reaching its maximum of 41-43 % for the Holocene. Increases in the forest cover correspond with the uncalm periods or the dominance of nomadic tribes. This allows us to conclude that climatic conditions would have allowed a wider distribution of forests over the past 2000 years without constant anthropogenic pressure. Our data highlight a high sensitivity of forests in their southern limits to anthropogenic pressure. Considering the current global warming the southern tree line is likely to shift northwards bringing the area to the mid-Holocene conditions increasing risks for agriculture.

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Data availability

The data obtained in the present study has been submitted to PANGAEA Data Publisher for Earth & Environmental Science https://www.pangaea.de/.

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Supplementary material

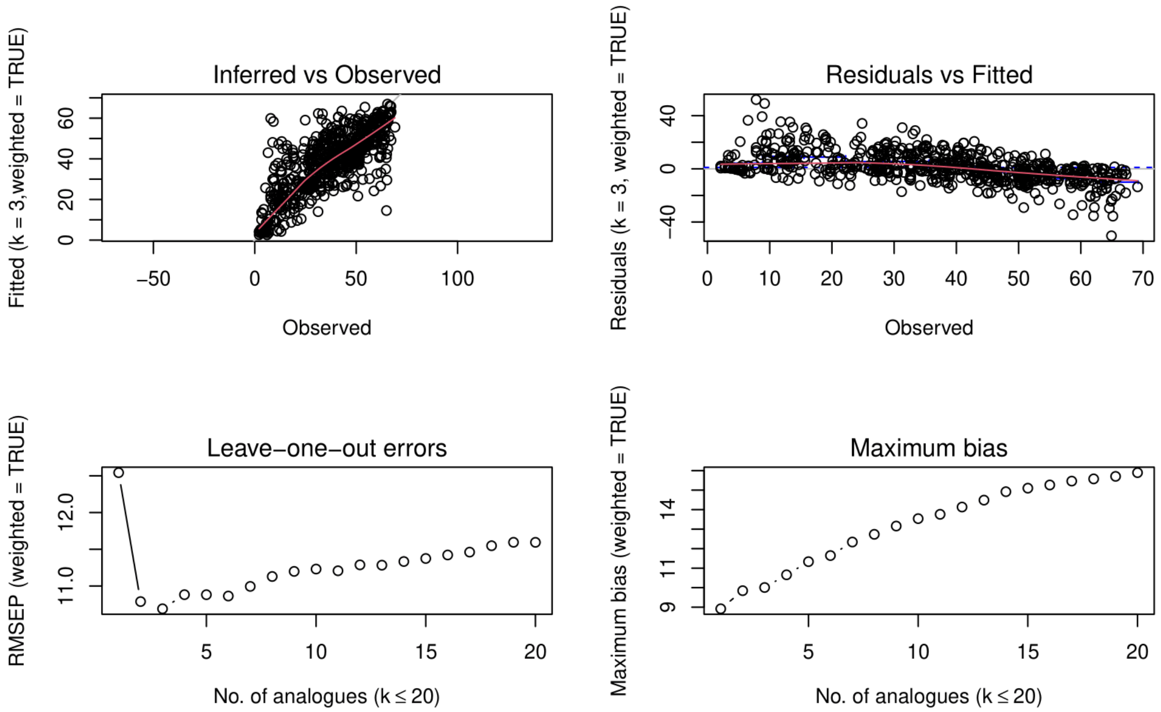

Fig. S3.1. Modern analogue technique applied to the Omelchenki pollen record to reconstruct forest cover

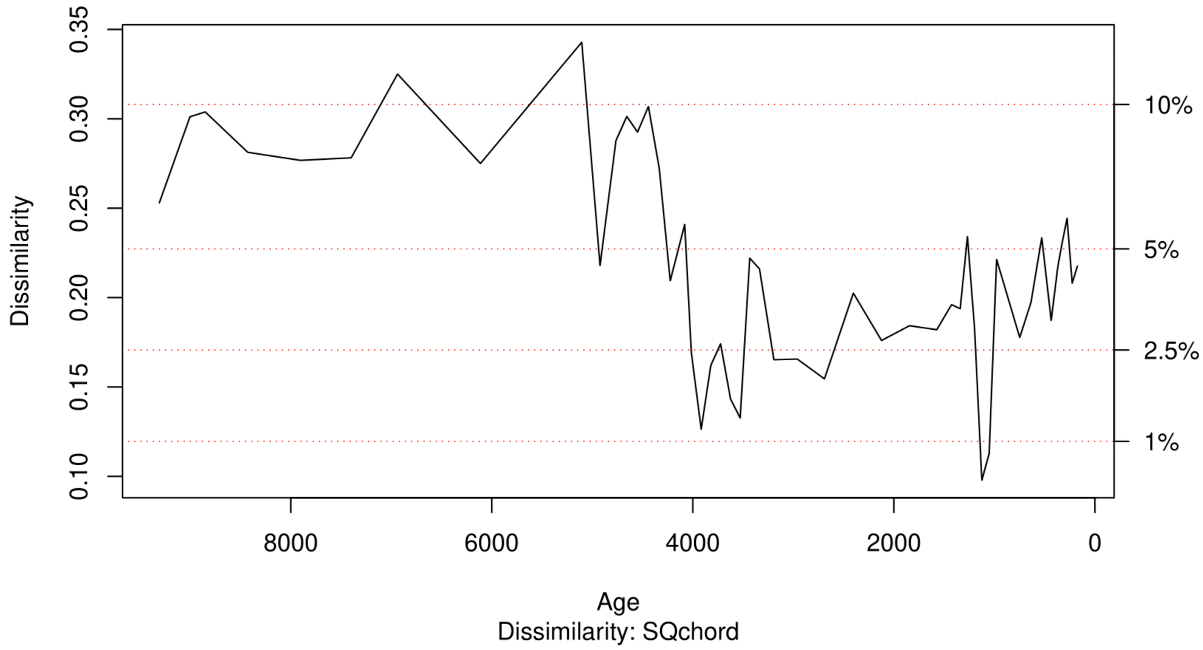

Fig. S3.2. SCD values of the Omelchenki forest cover reconstruction

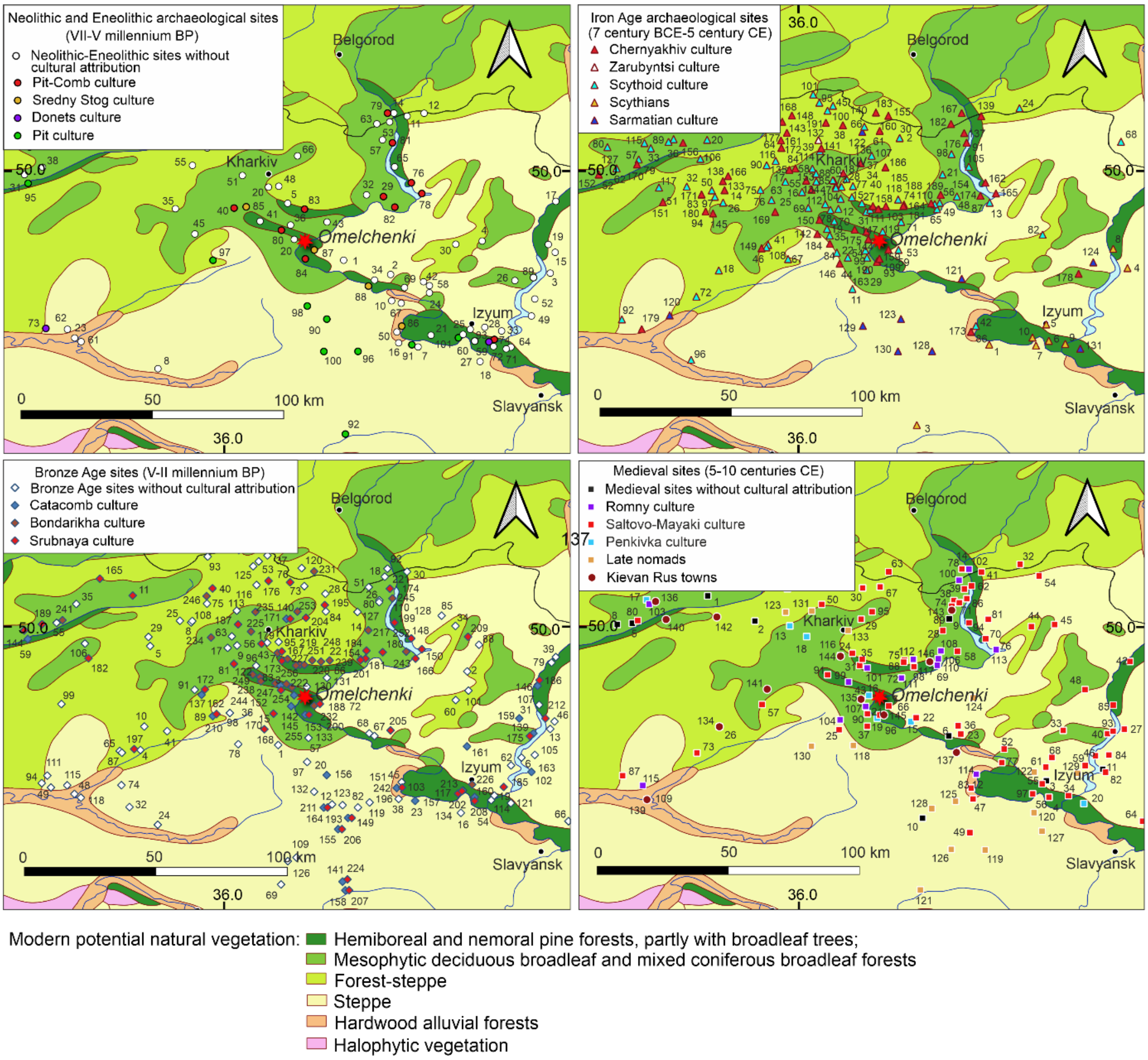

Fig. S3.3. Archaeological sites of the study area (after Shramko et al., 1977)

Table S3.1 – Archaeological sites of the study area (Shramko et al. 1977)

#	Site	Culture	Type
		Neolithic and Eneolithic sites	
1	Andreevka	without cultural attribution	
2	Balakleya	without cultural attribution	
3	Boguslavka	without cultural attribution	
4	Borovskoy	without cultural attribution	
5	Vasischevo	without cultural attribution	
6	Bukino	without cultural attribution	
7	Velikaya Kamyshevakha	without cultural attribution	
8	Velikiye Buchki	without cultural attribution	
9	Vishnevy sad	without cultural attribution	
10	Volobuevka	without cultural attribution	
11	Volchansk	without cultural attribution	

12	Volchanskiye Khutora	without cultural attribution
13	Garazhevka	without cultural attribution
14	Gatische	without cultural attribution
15	Glushkovka	without cultural attribution
16	Grushevakha	without cultural attribution
17	Gryanikovka	without cultural attribution
1	Dolgen'koye	without cultural attribution
19	Zhivotovka	without cultural attribution
20	Zhikhor'	without cultural attribution
21	Zavody	without cultural attribution
22	Zadonetskoye	without cultural attribution
23	Zaymanka	without cultural attribution
24	Zaliman	without cultural attribution
25	Izyum	without cultural attribution
26	Kalinovoye	without cultural attribution
27	Kamenka	without cultural attribution
28	Kapitolovka	without cultural attribution
29	Kitsevka	without cultural attribution
30	Kolesnikovka	without cultural attribution
31	Kolontaev	without cultural attribution
32	Kochetok	without cultural attribution
33	Krasny Oskol	without cultural attribution
34	Kreydyanka	without cultural attribution
35	Kruglyanka	without cultural attribution
36	Levkovka	without cultural attribution
37	Liman	without cultural attribution
38	Lyubovka	without cultural attribution
39	Malaya Rogozyanka	without cultural attribution
40	Merefa	without cultural attribution
41	Mirgorody	without cultural attribution
42	Morozovka	without cultural attribution
43	Mokhnach	without cultural attribution
44	Novokomsomol'skoye	without cultural attribution
45	Novoselovka	without cultural attribution
46	Naddonetsky	without cultural attribution
47	Ogurtsovo	without cultural attribution
48	Osnova	without cultural attribution
49	Peski Rad'kovskiye	without cultural attribution
50	Petrovskoye	without cultural attribution
51	Podvorki	without cultural attribution
52	Podliman	without cultural attribution
53	Prilipka	without cultural attribution
54	Proletarskoye	without cultural attribution
55	Protopopovka	without cultural attribution
56	Revolutsyonnoye	without cultural attribution
57	Rubezhnoye	without cultural attribution

58	Savintsy	without cultural attribution	
59	Sinicheno	without cultural attribution	
60	Snezhkovka	without cultural attribution	
61	Somovka	without cultural attribution	
62	Skalonovka	without cultural attribution	
63	Staritsa	without cultural attribution	
64	Studenok	without cultural attribution	
65	Khotomlya	without cultural attribution	
66	Tsyrkuny	without cultural attribution	
67	Chepel'	without cultural attribution	
68	Cherkassky Bishkin	without cultural attribution	
69	Schurovka	without cultural attribution	
70	Yanokhino	without cultural attribution	
71	Yaremovka	without cultural attribution	
72	Bukino	Dnieper-Donets	
73	Maly Orchik	Dnieper-Donets	
74	Bukino	Pit-Comb	
75	Kitsevka	Pit-Comb	
76	Martovoye	Pit-Comb	
77	Merefa	Pit-Comb	
78	Novokomsomol'skoye	Pit-Comb	
79	Ogurtsovo	Pit-Comb	
80	Proletarskoye	Pit-Comb	
81	Revolutsyonnoye	Pit-Comb	
82	Taganka	Pit-Comb	
83	Khmarovka	Pit-Comb	
84	Cherkassky Bishkin	Pit-Comb	
85	Aleksandrovka	Sredny Stog	
86	Zavrogodneye	Sredny Stog	
87	Liman	Sredny Stog	
88	Yanokhino	Sredny Stog	
89	Vishnevy sad	Pit	settlement
90	Bunakovo	Pit	cemetry
91	Velikaya Kamyshevakha	Pit	cemetry
92	Verkhniaya Samara	Pit	cemetry
93	Kamenka	Pit	cemetry
94	Knyazevo	Pit	cemetry
95	Kovalevka	Pit	cemetry
96	Mechebilovo	Pit	cemetry
97	Nikolaevka	Pit	cemetry
98	Otradovo	Pit	cemetry
99	Parkhomovka	Pit	cemetry
100	Rozhdestvenka	Pit	cemetry
101	Shpakovka	Pit	cemetry
		Bronze Age sites	
1	Alekseevka	without cultural attribution	

2	Arkadievka	without cultural attribution
3	Artyukhovka	without cultural attribution
4	Balki	without cultural attribution
5	Baranovo	without cultural attribution
6	Bakhtin	without cultural attribution
7	Bezlyudovka	without cultural attribution
8	Bezruki	without cultural attribution
9	Berezovka	without cultural attribution
10	Berestoven'ka	without cultural attribution
11	Bogodukhov	without cultural attribution
12	Bogomolvka	without cultural attribution
13	Boguslavka	without cultural attribution
14	Bolshaya Babka	without cultural attribution
15	Bolshaya Gomol'sha	without cultural attribution
16	Brazhkovka	without cultural attribution
17	Budy	without cultural attribution
18	Bugrovatka	without cultural attribution
19	Bukino	without cultural attribution
20	Bunakovo	without cultural attribution
21	Vasischevo	without cultural attribution
22	Vvedenka	without cultural attribution
23	Velikaya Kamyshevakha	without cultural attribution
24	Velikie Buchki	without cultural attribution
25	Vertievka	without cultural attribution
26	Verkhny Saltov	without cultural attribution
27	Verkhniaya Pisarevka	without cultural attribution
28	Veseloye	without cultural attribution
29	Voytenki	without cultural attribution
30	Volchansk	without cultural attribution
31	Vorontsovka	without cultural attribution
32	Vtoraya Dudovka	without cultural attribution
33	Garazhevka	without cultural attribution
34	Gnilitsa	without cultural attribution
35	Gorodneye	without cultural attribution
36	Gotval'dov	without cultural attribution
37	Granov	without cultural attribution
38	Grushevakha	without cultural attribution
39	Gryanikovka	without cultural attribution
40	Dovzhik	without cultural attribution
41	Dyachkovka	without cultural attribution
42	Zhivotovka	without cultural attribution
43	Zhikhor'	without cultural attribution
44	Zhukovo	without cultural attribution
45	Zavgorodneye	without cultural attribution
46	Zagrizovo	without cultural attribution
47	Zadonetskoye	without cultural attribution

48	Zaymanka	without cultural attribution
49	Zalineynoye	without cultural attribution
50	Zapaden'ka	without cultural attribution
51	Izbitskoye	without cultural attribution
52	Izyum	without cultural attribution
53	Kozachya Lopan'	without cultural attribution
54	Kamenka	without cultural attribution
55	Karaykozovka	without cultural attribution
56	Karachevka	without cultural attribution
57	Kiseli	without cultural attribution
58	Knyazevo	without cultural attribution
59	Kovalevka	without cultural attribution
60	Kolesnikovka	without cultural attribution
61	Kolontaev	without cultural attribution
62	Komarovka	without cultural attribution
63	Korotich	without cultural attribution
64	Kochetok	without cultural attribution
65	Krasnograd	without cultural attribution
66	Krasny Liman	without cultural attribution
67	Kreydyanka	without cultural attribution
68	Krinichnoye	without cultural attribution
69	Kryshtopovka	without cultural attribution
70	Kunye	without cultural attribution
71	Lageri	without cultural attribution
72	Liman	without cultural attribution
73	Liptsy	without cultural attribution
74	Lukashovka	without cultural attribution
75	Malaya Rogozyanka	without cultural attribution
76	Malye Prokhody	without cultural attribution
77	Martovoye	without cultural attribution
78	Maryevka	without cultural attribution
79	Masyutovka	without cultural attribution
80	Metallovka	without cultural attribution
81	Merefa	without cultural attribution
82	Mechebilovo	without cultural attribution
83	Mirgorody	without cultural attribution
84	Mikhaylovka	without cultural attribution
85	Moskalevka	without cultural attribution
86	Mokhnach	without cultural attribution
87	Natalyino	without cultural attribution
88	Nesterovka	without cultural attribution
89	Nikolayevka	without cultural attribution
90	Novokomsomol'skoye	without cultural attribution
91	Novoselovka	without cultural attribution
92	Ogurtsovo	without cultural attribution
93	Odnorobovka	without cultural attribution

94	Orchik	without cultural attribution	
95	Osnova	without cultural attribution	
96	Ostroverkhovka	without cultural attribution	
97	Otradovo	without cultural attribution	
98	Okhoche	without cultural attribution	
99	Pavlovschina	without cultural attribution	
100	Pavlyukovka	without cultural attribution	
101	Pervomayskoye	without cultural attribution	
102	Peski Rad'kovskiye	without cultural attribution	
103	Petrovskoye	without cultural attribution	
104	Pechenegi	without cultural attribution	
105	Podliman	without cultural attribution	
106	Pokrovka	without cultural attribution	
107	Pristen	without cultural attribution	
108	Protopopovka	without cultural attribution	
109	Razdolovka	without cultural attribution	
110	Revolyutsyonnoye	without cultural attribution	
111	Runovschina	without cultural attribution	
112	Savchinskoye	without cultural attribution	
113	Semenovka	without cultural attribution	
114	Sinicheno	without cultural attribution	
115	Skalonovka	without cultural attribution	
116	Slatino	without cultural attribution	
117	Snezhkovka	without cultural attribution	
118	Somovka	without cultural attribution	
119	Staraya Semenovka	without cultural attribution	
120	Strelechye	without cultural attribution	
121	Studenok	without cultural attribution	
122	Timchenki	without cultural attribution	
123	Tikhopolye	without cultural attribution	
124	Topoli	without cultural attribution	
125	Turovo	without cultural attribution	
126	Uplatnoye	without cultural attribution	
127	Fedorovka	without cultural attribution	
128	Khotomlya	without cultural attribution	
129	Tsyrkuny	without cultural attribution	
130	Chemuzhevka	without cultural attribution	
131	Cheremushnoye	without cultural attribution	
132	Chernokamenka	without cultural attribution	
133	Cherkassky Bishkin	without cultural attribution	
134	Shpakovka	without cultural attribution	
135	Yalta	without cultural attribution	
136	Bolshaya Danilovka	Catacomb	settlement
137	Brazhniki	Catacomb	settlement
138	Varenychevka	Catacomb	settlement
139	Vishnevy sad	Catacomb	settlement

140	Dal'nyaya Danilovka	Catacomb	settlement
141	Dobrovolye	Catacomb	settlement
142	Zadonetskoye	Catacomb	settlement
143	Kovalevka	Catacomb	settlement
144	Kolontaev	Catacomb	settlement
145	Koropovo	Catacomb	settlement
146	Kupyansk	Catacomb	settlement
147	Lyubovka	Catacomb	settlement
148	Martovoye	Catacomb	settlement
149	Novaya Mechebilovka	Catacomb	settlement
150	Novokomsomol'skoye	Catacomb	settlement
151	Petrovskoye	Catacomb	settlement
152	Proletarskoye	Catacomb	settlement
153	Cherkassky Bishkin	Catacomb	settlement
154	Chuguyev	Catacomb	settlement
155	Bogdanovka	Catacomb	cemetery
156	Bunakovo	Catacomb	cemetery
157	Velikaya Kamyshevakha	Catacomb	cemetery
158	Verkhniaya Samara	Catacomb	cemetery
159	Vorontsovka	Catacomb	cemetery
160	Kamenka	Catacomb	cemetery
161	Kunye	Catacomb	cemetery
162	Nikolayevka	Catacomb	cemetery
163	Peski Rad'kovskiye	Catacomb	cemetery
164	Rozhdestvenka	Catacomb	cemetery
165	Babaki	Srubnaya	settlement
166	Bazaleevka	Srubnaya	settlement
167	Bezlyudovka	Srubnaya	settlement
168	Bereka	Srubnaya	settlement
169	Bogodukhov	Srubnaya	settlement
170	Bolshaya Gomol'sha	Srubnaya	settlement
171	Bolshaya Danilovka	Srubnaya	settlement
172	Brazhniki	Srubnaya	settlement
173	Vasischevo	Srubnaya	settlement
174	Verkhniaya Pisarevka	Srubnaya	settlement
175	Vishnevy sad	Srubnaya	settlement
176	Dementyevka	Srubnaya	settlement
177	Dobrovolye	Srubnaya	settlement
178	Dovzhik	Srubnaya	settlement
179	Karachevka	Srubnaya	settlement
180	Kitsevka	Srubnaya	settlement
181	Klugino-Bashkirovka	Srubnaya	settlement
182	Kolomak	Srubnaya	settlement
183	Kolontaev	Srubnaya	settlement
184	Kochetok	Srubnaya	settlement
185	Krasny Oskol	Srubnaya	settlement

186	Kupyansk	Srubnaya	settlement
187	Kuryazhanka	Srubnaya	settlement
188	Liman	Srubnaya	settlement
189	Lyubovka	Srubnaya	settlement
190	Malye Prokhody	Srubnaya	settlement
191	Martovoye	Srubnaya	settlement
192	Merefa	Srubnaya	settlement
193	Novaya Mechebilovka	Srubnaya	settlement
194	Novokomsomol'skoye	Srubnaya	settlement
195	Petrovka	Srubnaya	settlement
196	Petrovskoye	Srubnaya	settlement
197	Popovka	Srubnaya	settlement
198	Proletarskoye	Srubnaya	settlement
199	Khotomlya	Srubnaya	settlement
200	Cherkassky Bishkin	Srubnaya	settlement
201	Chuguev	Srubnaya	settlement
202	Shpakovka	Srubnaya	settlement
203	Yanokhino	Srubnaya	settlement
204	Bayrak	Srubnaya	cemetery
205	Balakleya	Srubnaya	cemetery
206	Bogdanovka	Srubnaya	cemetery
207	Verkhniaya Samara	Srubnaya	cemetery
208	Kamenka	Srubnaya	cemetery
209	Kurul'ka	Srubnaya	cemetery
210	Nikolayevka	Srubnaya	cemetery
211	Rozhdestvenka	Srubnaya	cemetery
212	Sen'kovo	Srubnaya	cemetery
213	Snezhkovka	Srubnaya	cemetery
214	Artyukhovka	Bondarikha	settlement
215	Bazaleevka	Bondarikha	settlement
216	Bezlyudovka	Bondarikha	settlement
217	Bolshaya Babka	Bondarikha	settlement
218	Bolshaya Danilovka	Bondarikha	settlement
219	Vasischevo	Bondarikha	settlement
220	Vvedenka	Bondarikha	settlement
221	Verkhniaya Pisarevka	Bondarikha	settlement
222	Gotval'dov	Bondarikha	settlement
223	Dementyevka	Bondarikha	settlement
224	Dobrovolye	Bondarikha	settlement
225	Zalyutino	Bondarikha	settlement
226	Izyum	Bondarikha	settlement
227	Kirsanovo	Bondarikha	settlement
228	Kitsevka	Bondarikha	settlement
229	Klugino-Bashkirovka	Bondarikha	settlement
230	Kolontaev	Bondarikha	settlement
231	Krasnoye	Bondarikha	settlement

232	Liman	Bondarikha	settlement
233	Lyubovka	Bondarikha	settlement
234	Lyubotin	Bondarikha	settlement
235	Malaya Danilovka	Bondarikha	settlement
236	Martovoye	Bondarikha	settlement
237	Merefa	Bondarikha	settlement
238	Mirgorody	Bondarikha	settlement
239	Novaya Pokrovka	Bondarikha	settlement
240	Novokomsomol'skoye	Bondarikha	settlement
241	Pavlyukovka	Bondarikha	settlement
242	Petrovskoye	Bondarikha	settlement
243	Pechenegi	Bondarikha	settlement
244	Proletarskoye	Bondarikha	settlement
245	Revolyutsyonnoye	Bondarikha	settlement
246	Rodnoy Kray	Bondarikha	settlement
247	Sokolovo	Bondarikha	settlement
248	Ternovaya	Bondarikha	settlement
249	Timchenki	Bondarikha	settlement
250	Udy	Bondarikha	settlement
251	Khmarovka	Bondarikha	settlement
252	Khotomlya	Bondarikha	settlement
253	Tsyrkuny	Bondarikha	settlement
254	Chemuzhevka	Bondarikha	settlement
255	Cherkassky Bishkin	Bondarikha	settlement
256	Shubino	Bondarikha	settlement
		Iron Age sites	
1	Velikaya Kamyshevakha	Scythians (steppe)	settlement
2	Veseloye	Scythians (steppe)	settlement
3	Dobrovolye	Scythians (steppe)	settlement
4	Zigrizovo	Scythians (steppe)	settlement
5	Izyum	Scythians (steppe)	settlement
6	Kamenka	Scythians (steppe)	settlement
7	Malaya Kamyshevakha	Scythians (steppe)	settlement
8	Pristen	Scythians (steppe)	settlement
9	Sinicheno	Scythians (steppe)	settlement
10	Shpakovka	Scythians (steppe)	settlement
11	Alekseevka	Scythoid (forest-steppe)	settlement
12	Aksyutovka	Scythoid (forest-steppe)	settlement
13	Bazaleevka	Scythoid (forest-steppe)	settlement
14	Baranovo	Scythoid (forest-steppe)	settlement
15	Bezlyudovka	Scythoid (forest-steppe)	settlement
16	Berezovka	Scythoid (forest-steppe)	settlement
17	Berezovskoye	Scythoid (forest-steppe)	settlement
18	Berestoven'ka	Scythoid (forest-steppe)	settlement
19	Birochok	Scythoid (forest-steppe)	settlement
20	Bogodukhov	Scythoid (forest-steppe)	settlement

21	Bolshaya Babka	Scythoid (forest-steppe)	settlement
22	Bolshaya Gomol'sha	Scythoid (forest-steppe)	settlement
23	Bolshaya Danilovka	Scythoid (forest-steppe)	settlement
24	Bochkovo	Scythoid (forest-steppe)	settlement
25	Budy	Scythoid (forest-steppe)	settlement
26	Valki	Scythoid (forest-steppe)	settlement
27	Vasischevo	Scythoid (forest-steppe)	settlement
28	Vereschakovka	Scythoid (forest-steppe)	settlement
29	Verkhny Bishkin	Scythoid (forest-steppe)	settlement
30	Veseloye	Scythoid (forest-steppe)	settlement
31	Vodyanoe	Scythoid (forest-steppe)	settlement
32	Vysokopolye	Scythoid (forest-steppe)	settlement
33	Gorodneye	Scythoid (forest-steppe)	settlement
34	Gorodische	Scythoid (forest-steppe)	settlement
35	Grishkovka	Scythoid (forest-steppe)	settlement
36	Gubarovka	Scythoid (forest-steppe)	settlement
37	Dal'nyaya Danilovka	Scythoid (forest-steppe)	settlement
38	Dementyevka	Scythoid (forest-steppe)	settlement
39	Dergachi	Scythoid (forest-steppe)	settlement
40	Zhikhor'	Scythoid (forest-steppe)	settlement
41	Zavadovka	Scythoid (forest-steppe)	settlement
42	Zavgorodneye	Scythoid (forest-steppe)	settlement
43	Zadonetskoye	Scythoid (forest-steppe)	settlement
44	Zapaden'ka	Scythoid (forest-steppe)	settlement
45	Kozachya Lopan'	Scythoid (forest-steppe)	settlement
46	Karavan	Scythoid (forest-steppe)	settlement
47	Karachevka	Scythoid (forest-steppe)	settlement
48	Kitsevka	Scythoid (forest-steppe)	settlement
49	Klugino-Bashkirovka	Scythoid (forest-steppe)	settlement
50	Kovyagi	Scythoid (forest-steppe)	settlement
51	Kolomak	Scythoid (forest-steppe)	settlement
52	Kolontaev	Scythoid (forest-steppe)	settlement
53	Komsomol'sky	Scythoid (forest-steppe)	settlement
54	Koropovo	Scythoid (forest-steppe)	settlement
55	Korotich	Scythoid (forest-steppe)	settlement
56	Kochetok	Scythoid (forest-steppe)	settlement
57	Krasnokutsk	Scythoid (forest-steppe)	settlement
58	Kuryazhanka	Scythoid (forest-steppe)	settlement
59	Liman	Scythoid (forest-steppe)	settlement
60	Lipovaya Roscha	Scythoid (forest-steppe)	settlement
61	Liptsy	Scythoid (forest-steppe)	settlement
62	Lyubovka	Scythoid (forest-steppe)	settlement
63	Lyubotin	Scythoid (forest-steppe)	settlement
64	Malaya Rogozyanka	Scythoid (forest-steppe)	settlement
65	Malinovka	Scythoid (forest-steppe)	settlement
66	Malye Prokhody	Scythoid (forest-steppe)	settlement

67	Melikhovka	Scythoid (forest-steppe)	settlement
68	Melovoye	Scythoid (forest-steppe)	settlement
69	Merefa	Scythoid (forest-steppe)	settlement
70	Mirgorody	Scythoid (forest-steppe)	settlement
71	Mokhnach	Scythoid (forest-steppe)	settlement
72	Natalyino	Scythoid (forest-steppe)	settlement
73	Novaya Bavaria	Scythoid (forest-steppe)	settlement
74	Novaya Pokrovka	Scythoid (forest-steppe)	settlement
75	Ogul'tsy	Scythoid (forest-steppe)	settlement
76	Odrinka	Scythoid (forest-steppe)	settlement
77	Osnova	Scythoid (forest-steppe)	settlement
78	Ostroverkhovka	Scythoid (forest-steppe)	settlement
79	Pavlyukovka	Scythoid (forest-steppe)	settlement
80	Parkhomovka	Scythoid (forest-steppe)	settlement
81	Paseki	Scythoid (forest-steppe)	settlement
82	Pervomayskoye	Scythoid (forest-steppe)	settlement
83	Perekop	Scythoid (forest-steppe)	settlement
84	Peresechnoye	Scythoid (forest-steppe)	settlement
85	Pesochin	Scythoid (forest-steppe)	settlement
86	Petrovskoye	Scythoid (forest-steppe)	settlement
87	Pechenegi	Scythoid (forest-steppe)	settlement
88	Podvorki	Scythoid (forest-steppe)	settlement
89	Polkovaya Nikitovka	Scythoid (forest-steppe)	settlement
90	Protopopovka	Scythoid (forest-steppe)	settlement
91	Revolyutsyonnoye	Scythoid (forest-steppe)	settlement
92	Runovschina	Scythoid (forest-steppe)	settlement
93	Russky Bishkin	Scythoid (forest-steppe)	settlement
94	Snezhkovo	Scythoid (forest-steppe)	settlement
95	Sosnovka	Scythoid (forest-steppe)	settlement
96	Staroye Mazharovo	Scythoid (forest-steppe)	settlement
97	Starye Valki	Scythoid (forest-steppe)	settlement
98	Stary Saltov	Scythoid (forest-steppe)	settlement
99	Sukhaya Gomol'sha	Scythoid (forest-steppe)	settlement
100	Turovo	Scythoid (forest-steppe)	settlement
101	Udy	Scythoid (forest-steppe)	settlement
102	Kharki	Scythoid (forest-steppe)	settlement
103	Khraovka	Scythoid (forest-steppe)	settlement
104	Khoroshevo	Scythoid (forest-steppe)	settlement
105	Khotomlya	Scythoid (forest-steppe)	settlement
106	Khruschevaya Nikitovka	Scythoid (forest-steppe)	settlement
107	Tsyrkuny	Scythoid (forest-steppe)	settlement
108	Chervonosovo	Scythoid (forest-steppe)	settlement
109	Cherkassky Bishkin	Scythoid (forest-steppe)	settlement
110	Chuguev	Scythoid (forest-steppe)	settlement
111	Shubino	Scythoid (forest-steppe)	settlement
112	Yakovlevka	Scythoid (forest-steppe)	settlement

113	Bolshaya Danilovka	Scythoid (forest-steppe)	cemetery
114	Dergachi	Scythoid (forest-steppe)	cemetery
115	Kozievka	Scythoid (forest-steppe)	cemetery
116	Ol'shany	Scythoid (forest-steppe)	cemetery
117	Pokrovka	Scythoid (forest-steppe)	cemetery
118	Razdol'noye	Scythoid (forest-steppe)	cemetery
119	Cheremushnoye	Scythoid (forest-steppe)	cemetery
120	Abazovka	Sarmatians	
121	Balakleya	Sarmatians	
122	Bolshiye Prokhody	Sarmatians	
123	Bunakovo	Sarmatians	
124	Vorontsovka	Sarmatians	
125	Voskresenovka	Sarmatians	
126	Kolki	Sarmatians	
127	Lyubovka	Sarmatians	
128	Mechebilovo	Sarmatians	
129	Razdolye	Sarmatians	
130	Rozhdestvenka	Sarmatians	
131	Yaremovka	Sarmatians	
132	Shelkoplyasy	Zarubyntsi	
133	Baranovo	Chernyakhiv	
134	Berezovka	Chernyakhiv	
135	Berezovskoye	Chernyakhiv	
136	Bol'shaya Danilovka	Chernyakhiv	
137	Verkhnyaya Pisarevka	Chernyakhiv	
138	Voytenki	Chernyakhiv	
139	Volchansk	Chernyakhiv	
140	Dementyevka	Chernyakhiv	
141	Dergachi	Chernyakhiv	
142	Dzhgun	Chernyakhiv	
143	Dovzhik	Chernyakhiv	
144	Zadonetskoye	Chernyakhiv	
145	Zamoskoye	Chernyakhiv	
146	Zapaden'ka	Chernyakhiv	
147	Gotval'dov	Chernyakhiv	
148	Zolochev	Chernyakhiv	
149	Karavan	Chernyakhiv	
150	Kolesniki	Chernyakhiv	
151	Kolomak	Chernyakhiv	
152	Kolontaev	Chernyakhiv	
153	Korotich	Chernyakhiv	
154	Kochetok	Chernyakhiv	
155	Krasnoye	Chernyakhiv	
156	Kruchik	Chernyakhiv	
157	Kuliki	Chernyakhiv	
158	Lizogubovka	Chernyakhiv	

159	Liman	Chernyakhiv
160	Liptsy	Chernyakhiv
161	Malaya Rogozyanka	Chernyakhiv
162	Martovoye	Chernyakhiv
163	Nizhny Bishkin	Chernyakhiv
164	Novaya Pokrovka	Chernyakhiv
165	Novokomsomol'skoye	Chernyakhiv
166	Novy Merchik	Chernyakhiv
167	Ogurtsovo	Chernyakhiv
168	Oreshanka	Chernyakhiv
169	Pavlovka	Chernyakhiv
170	Pavlyukovka	Chernyakhiv
171	Perekop	Chernyakhiv
172	Peresechnoye	Chernyakhiv
173	Petrovskoye	Chernyakhiv
174	Pechenegi	Chernyakhiv
175	Proletarskoye	Chernyakhiv
176	Revolyutsyonnoye	Chernyakhiv
177	Rodnoy Kray	Chernyakhiv
178	Rossokhovatoye	Chernyakhiv
179	Skalonovka	Chernyakhiv
180	Snezhkovo	Chernyakhiv
181	Staraya Pokrovka	Chernyakhiv
182	Staritsa	Chernyakhiv
183	Strelechye	Chernyakhiv
184	Taranovka	Chernyakhiv
185	Ternovaya	Chernyakhiv
186	Frunze	Chernyakhiv
187	Kharkiv	Chernyakhiv
188	Khmarovka	Chernyakhiv
189	Chuguev	Chernyakhiv
190	Cherkassky Bishkin	Chernyakhiv
191	Shapovalovka	Chernyakhiv
		Medieval sites
1	Bogodukhov	without culturalattribution
2	Vertievka	without cultural attribution
3	Izyum	without cultural attribution
4	Kamenka	without cultural attribution
5	Karaykozovka	without cultural attribution
6	Kreydyanka	without cultural attribution
7	Liman	without cultural attribution
8	Lyubovka	without cultural attribution
9	Molodovaya	without cultural attribution
10	Novaya Mechebilovka	without cultural attribution
11	Peski Rad'kovskiye	without cultural attribution
12	Petrovskoye	without cultural attribution

13	Berezovskoye	Penkivka
14	Dementyevka	Penkivka
15	Donets	Penkivka
16	Zadonetskoye	Penkivka
17	Kozievka	Penkivka
18	Korotich	Penkivka
19	Nizhny Bishkin	Penkivka
20	Studenok	Penkivka
21	Cherkassky Bishkin	Penkivka
22	Andreevka	Saltovo-Mayaki
23	Bakaleya	Saltovo-Mayaki
24	Bezlyudovka	Saltovo-Mayaki
25	Bereka	Saltovo-Mayaki
26	Berestoven'ka	Saltovo-Mayaki
27	Boguslavka	Saltovo-Mayaki
28	Bolshaya Babka	Saltovo-Mayaki
29	Bolshaya Danilovka	Saltovo-Mayaki
30	Bolshiye Prokhody	Saltovo-Mayaki
31	Borovaya	Saltovo-Mayaki
32	Bochkovo	Saltovo-Mayaki
33	Bugayevka	Saltovo-Mayaki
34	Bukino	Saltovo-Mayaki
35	Vasischevo	Saltovo-Mayaki
36	Verbovka	Saltovo-Mayaki
37	Verkhny Bishkin	Saltovo-Mayaki
38	Verkhny Saltov	Saltovo-Mayaki
39	Verkhnyaya Pisarevka	Saltovo-Mayaki
40	Vishnevy Sad	Saltovo-Mayaki
41	Volchansk	Saltovo-Mayaki
42	Vorobyevka	Saltovo-Mayaki
43	Gaydary	Saltovo-Mayaki
44	Gnilitsa	Saltovo-Mayaki
45	Golubovka	Saltovo-Mayaki
46	Gorokhovatka	Saltovo-Mayaki
47	Grushevakha	Saltovo-Mayaki
48	Grushevka	Saltovo-Mayaki
49	Danilovka	Saltovo-Mayaki
50	Dergachi	Saltovo-Mayaki
51	Dovzhik	Saltovo-Mayaki
52	Zaliman	Saltovo-Mayaki
53	Zapaden'ka	Saltovo-Mayaki
54	Zakharovka	Saltovo-Mayaki
55	Izyum	Saltovo-Mayaki
56	Kamenka	Saltovo-Mayaki
57	Karavan	Saltovo-Mayaki
58	Kitsevka	Saltovo-Mayaki

59	Komarovka	Saltovo-Mayaki
60	Koropovo	Saltovo-Mayaki
61	Kramarovka	Saltovo-Mayaki
62	Krasnoarmeyskoye	Saltovo-Mayaki
63	Krasnoye	Saltovo-Mayaki
64	Krasny Liman	Saltovo-Mayaki
65	Lageri	Saltovo-Mayaki
66	Liman	Saltovo-Mayaki
67	Liptsy	Saltovo-Mayaki
68	Lipchanovka	Saltovo-Mayaki
69	Malinovka	Saltovo-Mayaki
70	Martovoye	Saltovo-Mayaki
71	Metallovka	Saltovo-Mayaki
72	Mokhnach	Saltovo-Mayaki
73	Natalyino	Saltovo-Mayaki
74	Netaylovka	Saltovo-Mayaki
75	Novaya Pokrovka	Saltovo-Mayaki
76	Novokomsomol'skoye	Saltovo-Mayaki
77	Nortsovka	Saltovo-Mayaki
78	Ogurtsovo	Saltovo-Mayaki
79	Odnorobovka	Saltovo-Mayaki
80	Pavlyukovka	Saltovo-Mayaki
81	Pervoye Maya	Saltovo-Mayaki
82	Peski Rad'kovskiye	Saltovo-Mayaki
83	Petrovskoye	Saltovo-Mayaki
84	Podliman	Saltovo-Mayaki
85	Pristen	Saltovo-Mayaki
86	Revolyutsionnoye	Saltovo-Mayaki
87	Runivschina	Saltovo-Mayaki
88	Staraya Pokrovka	Saltovo-Mayaki
89	Stary Saltov	Saltovo-Mayaki
90	Sukhaya Gomol'sha	Saltovo-Mayaki
91	Timchenki	Saltovo-Mayaki
92	Topoli	Saltovo-Mayaki
93	Fominoye	Saltovo-Mayaki
94	Khotomlya	Saltovo-Mayaki
95	Tsirkuny	Saltovo-Mayaki
96	Cherkassky Bishkin	Saltovo-Mayaki
97	Shpakovka	Saltovo-Mayaki
98	Eskhar	Saltovo-Mayaki
99	Artyukhovka	Romny
100	Bugrovatka	Romny
101	Vodyanoye	Romny
102	Gatische	Romny
103	Gorodnoye	Romny
104	Zapaden'ka	Romny

105	Karachevka	Romny
106	Klugino-Bashkirovka	Romny
107	Koropovo	Romny
108	Kochetok	Romny
109	Limanovka	Romny
110	Malinovka	Romny
111	Mokhnach	Romny
112	Novaya Pokrovka	Romny
113	Novokomsomol'sky	Romny
114	Protopopovka	Romny
115	Skalonovka	Romny
116	Khoroshevo	Romny
117	Chuguev	Romny
118	Alekseevka	Late nomads
119	Bogodarovo	Late nomads
120	Brazhkovka	Late nomads
121	Verkhnyaya Samara	Late nomads
122	Glinskoye	Late nomads
123	Grigoryevka	Late nomads
124	Ivanovka	Late nomads
125	Knyagin Liman	Late nomads
126	Kovalevka	Late nomads
127	Kurul'ka	Late nomads
128	Mechebilovo	Late nomads
129	Nikolaevka	Late nomads
130	Sekretarovka	Late nomads
131	Semenovka	Late nomads
132	Topoli	Late nomads
133	Kharkiv	Late nomads
134	Berestoven'ka	Kievan Rus town
135	Gaydary	Kievan Rus town
136	Gorodnoye	Kievan Rus town
137	Gusarovka	Kievan Rus town
138	Karachevka	Kievan Rus town
139	Limanovka	Kievan Rus town
140	Murafa	Kievan Rus town
141	Novoselovka	Kievan Rus town
142	Tsavlovo	Kievan Rus town
143	Stary Saltov	Kievan Rus town
144	Khoroshego	Kievan Rus town
145	Cherkassky Bishkin	Kievan Rus town
146	Chuguev	Kievan Rus town

Chapter IV – Manuscript 3

1,100-years history of transformation of the East European forest-steppe into arable land: Case study from Kursk region (Russia)

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Abstract

Nowadays, large parts of the East European forest-steppe are covered by agricultural and pastoral landscapes with decreasing proportions of semi-natural meadow steppes and fragments of semi-natural woodland. Although numerous palynological records indicate that total deforestation occurred in the last 500 years, the details of this transformation are still lacking. Here we focus on the vegetation and fire history at the northern edge of the forest-steppe in the Kursk region (Russia), in order to reconstruct the transformation process from natural vegetation into an agrarian landscape in its historical context. New pollen, non-pollen palynomorphs and charcoal records with decennial to centennial resolution obtained from the Seim River region enable a comprehensive reconstruction of the local and regional landscape history over the last 1,100 years. The palynological records provide unique insights into the vegetation cover of microregions and evidence spatial asynchronous deforestation and crop field creation. Significant forest reduction started already in the 13th (the Kievan Rus), subsequent deforestations followed in the 15th (the Grand Duchy of Lithuania) and 17th century when the Belgorod defence line of the Tsardom of Russia protected the fertile chernozem region against invaders from the south. This gradual deforestation contrasts to pollen data from the Psel River region, showing low human impact on vegetation before the 17th century and rapid deforestation after. In both regions, formation of agro-pastoral landscapes with small remaining forest patches of today occurred already within the 17th century CE.

Introduction

The question to the natural extension of forests versus tree-less landscapes is crucial for nature conservation and estimates of climate change consequences. One in this context worldwide unique ecotone is the East European forest-steppe, which extends from the Carpathian to the Ural Mountains (Fig. 4.1a). While botanical investigations suggest a natural vegetation with open meadow steppes and deciduous woodland patches, large areas are covered nowadays by cropland and pastures (Bohn et al. 2003; Fig. 4.1). An increasing number of palaeoecological studies from the East European forest-steppe reveals transformation of the naturally forested regions into agro-pastoral landscapes and show that this process was asynchronous across the region and related to local cultural processes. In the Danube forest-steppe, strong human impact started at ~ 2500 yrs BP (Feurdean et al. 2021), in Psel region (middle Dniepr) – after 3200 yrs BP (Lukanina et al. 2022), at the Upper Don – 2400 yrs BP (Novenko et al. 2014), and in Kungur forest-steppe at the Ural Mountains – at 3800 yrs BP (Shumilovskikh et al. 2021b). The majority of the studies exhibit phases of forest recovery after intense use. The current nearly total deforestation took place over the last 400-500 years (Serebryannaya 1981; Khotinsky 1984, 1993; Serebryannaya 1992; Spiridonova 1991; Novenko et al. 2009, 2012, 2014, 2015, 2016; Chendev et al. 2016, 2017; Shumilovskikh et al. 2018, 2019; Lukanina et al. 2022). Although the last millennium is a period of rapid increase in human activities with destructive influence, details on the transformation of the East European forest-steppe into an agro-pastoral landscape are rare.

To close this gap, we carried out investigations in the Seim River area at the middle Dniepr (Kursk region, Russia). In terms of vegetation, the study region is located at the turn from deciduous forests to forest-steppe (Fig. 4.1). In terms of archaeology and historical records, this area is unique, because of continuous presence of sedentary cultures and nomads, so called ‘dikoe pole’ (Russian ‘wild field’) in the last two thousand years (Kashkin 2000). Detailed analyses of pollen, non-pollen palynomorphs (NPP), micro- and macrocharcoal and loss-on-ignition were carried out on sites Peny and Razdolye. We compare the results with published pollen record Sudzha (Shumilovskikh et al. 2019) and Zamostye (Lukanina et al. 2022) from Psel River area (middle Dniepr; Fig. 4.1) as well as historical and archaeological data for more precise estimations of the extent of human activities that shaped the today East European forest-steppe ecotone. We aim to reconstruct exact timing of forest-steppe transformation into agrarian land and synchronise them with historical events.

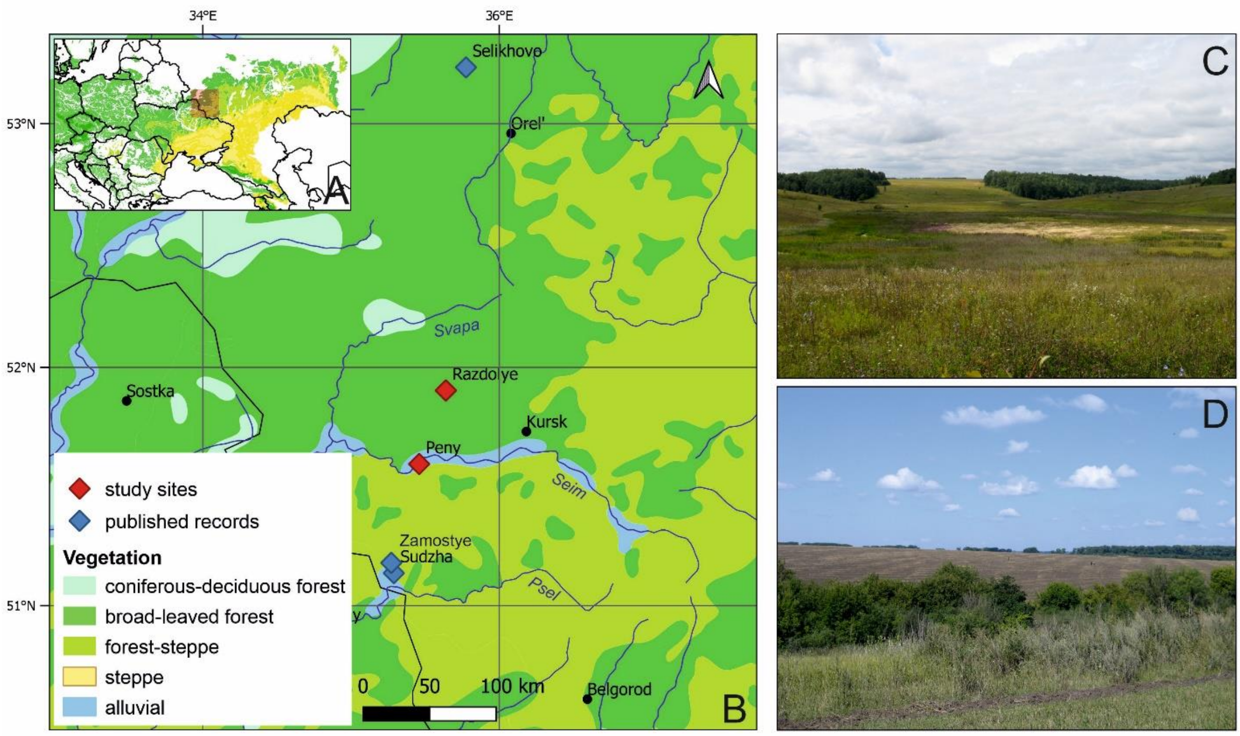


Fig. 4.1. Study area: a) Map of East European forest-steppe zone and adjacent deciduous forests and steppe zones (based on Bohn et al. 2003); b) map of the potential vegetation in the Psel-Seim (middle Dniepr) region with location of study sites of Razdolye and Peny and published records of Sudzha (Shumilovskikh et al. 2019) and Selikhovo (Novenko et al. 2016); c) study site of Razdolye (picture by Frank Schlütz); d) study site of Peny (picture by Frank Schlütz)

Study area

Geographical setting

The two study sites Peny and Razdolye are located in the south of the Central Russian Upland, south and north of the Seim River, which drains via the Desna River, into the Dnieper River (Fig. 4.1). Soils are mainly alluvial soils and typical chernozems (Shoba 2011). The climate is temperate, in the Köppen-Geiger classification system humid continental with warm summers (Dfb). The mean annual temperature is about 6.1 °C with average temperature of January around -8.1 °C, of July 19.1 °C. The annual precipitation is 604 mm, with the lowest precipitation in February (32 mm) and the highest in July (78 mm) (Kurchatov, https://ru.climate-data.org/).

Nowadays, the study region is characterized by the prevalence of agro-pastoral landscapes (Fig. 4.1). The coring site Peny is located 2 km from the Seim River and represents a wetland covered by *Phragmites australis*, *Salix* sp., *Artemisia vulgaris* and Cyperaceae. It is located in the bed of temporary Penka River, southern tributary of the Seim. It is flooded during high melting water discharge in spring (Radyush 2010). Typical grass steppe vegetation dominated by Poaceae, *Lathyrus* sp., *Arctium tomentosum*, *Cichorium* sp. grow on the slopes. On the fields around cereals such as rye (*Secale cereale*) and barley (*Hordeum vulgare*) are cultivated.

The coring site Razdolye represents a temporarily flooded depression 40 km north of the Seim River. It is overgrown with *Equisetum sp.*, *Typha* sp., *Lythrum salicaria, Carex* sp. and Apiaceae. The slopes are covered with grassland and patches of willows (*Salix* sp.).

Historical and archaeological context

The investigated area has a long history of human occupation (Fig. 4.2; Supplementary Table 4.1). The oldest archaeological findings in the microregion Peny date back to the Late Stone Age (Kashkin 2000; Akhmetgaleeva 2015). Several Bronze Age settlements are known on the floodplain hillocks of the Seim River (Kashkin 2000). The Early Iron Age sites (7th-1st century BCE; Kudeyarova Gora, Lysaya Gora) are concentrated on the right bank of the Seim. They are attributed to the nomadic Scythian and Yukhnov cultures. Fortification remains are located on high promontories of the main river bank (Kashkin 1998). The best-known sites belong to the Roman period (1st-5th century CE). The period of the Chernyakhov culture at the end of the 3rd - third quarter of the 4th century in the upper Seim and Psel valley is represented by numerous settlements. They are characterized by significant occupation areas of 10 to 30 hectares, traces of handicraft production, big amount of wheel-thrown pottery, finds of amphoras, and Roman coins in hoards and as single finds. The settlement of Peny is one of the largest of the late Roman period (3rd – the first half of the 5th century CE) in the region. The cultural layer is up to 1,6-1,8 m thick. It is saturated with fragments of molded pottery, burnt plaster and bones (Radyush 2010). This indicates intensive settlement activities in this period, while there are very few known archaeological remains from the Migration Period (6th-7th century CE) on the left bank of the Seim River, whose context remains, moreover, unclear.

After Migration period, Volyntsevo (8th-9th century CE) and later Romen culture (9th-11th century CE) occur showing influence of Khazar Khaganate (Kashkin 1998). The main Fortified settlements of the Kievan Rus (11th-13th century CE) were located on the left bank of the Seim (Kashkin 1998, 2000) with unfortified settlements nested around. This period is characterized by a graduated settlement arrangement around fortified site. During the Mongol-Tatar invasion (13th-14th century CE) the population in the Seim valley decreased significantly. The nearest late medieval settlement (Dichnya) dated by a Tatar coin to the 14th century CE, was located near Kurchatov, ca. 20 km NE from study site Peny.

The further historical development of the Seim valley dates to the 17th century, when the Belgorod defence line, the so-called “Zasechnaya cherta”, was constructed. It allowed the colonisation of the southern territories by the Russian State. The village of Peny (today Karl Liebknecht), was founded in 1606. The historical village centre was located just three km east of the Peny study site near the Penka River. At the end of the 18th century, the plan of general land surveying shows the territory of the study site Peny as ploughed fields, without large forest areas. Also, the military topographic map of 1868-1919 (http://www.oldmap.org/map-kursk_trehverstovka/) exhibits no tree vegetation. On the map of the General Staff of the Red Army 1935-1941 (http://www.oldmap.org/map-rkka_m-37-a/), a peat bog is indicated on the floodplain of the Penka River. Just on the opposite, on the right bank of the Seim River, there was a small garden and a separate unsigned building closer to the road. In the post-war period, parts of the Roman Peny settlement along the right bank of the Seim River are covered by vegetable gardens and buildings. A deep ploughing of the stream’s right bank started only in the early 2000s. Previously, it was partially used for vegetable gardens, and parts were occupied by an orchard cut down in the 1960-1970s.

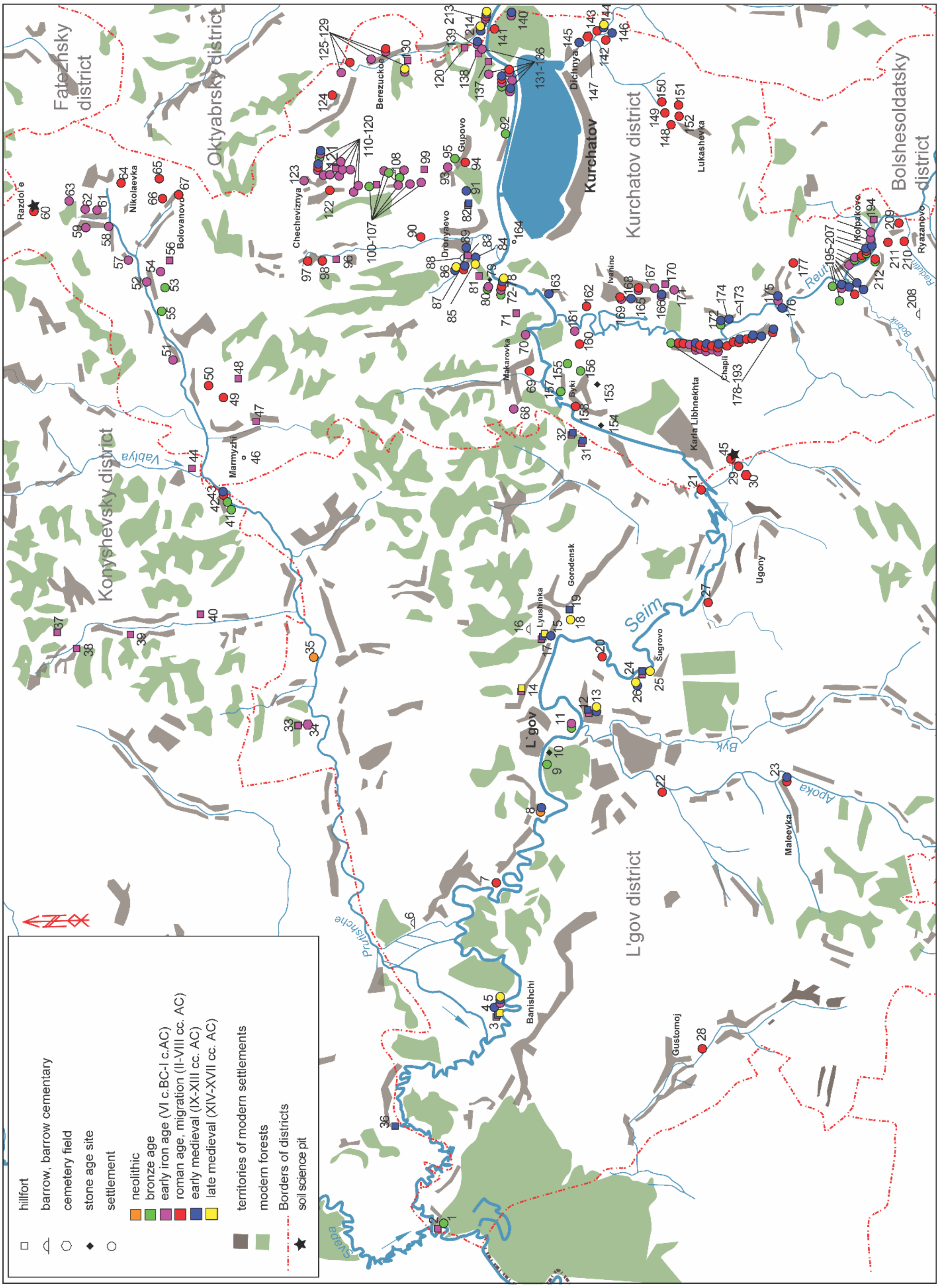


Fig. 4.2. Map of archaeological sites of the study region

Like Peny, the villages of Bunino and Razdolye started to develop in the 17th century. The area around the village of Bunino is notified in the Strelbickiy maps from 1865-1871 (http://www.oldmap.org/map-karta-strelbickogo/) as an open landscape desiccated by ravines. The village of Razdolye occurred on a map of the General Staff of the Red Army 1935-1941 (http://www.oldmap.org/map-rkka_m-36-b/), where the coring place is indicated as a wetland, while surrounding slopes are covered by trees. A nearby water reservoir near Bunino is notified on the Soviet Military Maps 1:200,000 from the 1970-1990s (http://www.oldmap.org/map-genshtab_m-36/).

Material and methods

Coring of both study sites Peny and Razdolye took place in 2009 using a Russian peat corer. The core Peny (51°35'48.10''N, 35°27'31.56''E, 152 m a.s.l.) was obtained from the small valley of the Penka River. It contains the two core sections: Peny I (0-110 cm) and Peny II (120-210 cm) (Fig. 4.3). The core section Peny II was not studied due to a very low and insufficient pollen content, further in the text we call Peny I as Peny. The core Razdolye was taken in a depression of the catchment of the Ruda River between the villages of Bunino and Razdolye (51°54'34.51"N, 35°38'28.88"E), 37 km north-east of Peny and 40 km north-west of Kursk. The Ruda River drains into the Seim River via the Usozha and the Svapa Rivers as a right tributary. The upper 30 cm of the Razdolye core consisted of very loose *Equisetum* peat, which could not be obtained by the Russian corer. The lithological descriptions for both cores were carried out in the field.

For an absolute chronology, bulk samples, macroremains and pollen were dated by the radiocarbon laboratories of Poznan (Poland) and Erlangen (Germany) (Table 4.1). The age-depth models for Peny and Razdolye were constructed using the IntCal20 and Postbomb calibration curves (Reimer et al. 2020) implemented in the Clam 2.3.4 package (Blaauw 2010) (Fig. 4.5). All ages further in text are given in calibrated years before present (BP, present = 1950) and/or in calendar years.

For palynological analysis, 1 cm^3 samples were taken at 4-cm intervals from the core Peny (22 samples) and at 2-cm intervals from the core Razdolye (26 samples). Samples were treated with cold 10% hydrochloric acid, cold 40% hydrofluoric acid (Peny overnight, Razdolye 72 hours), followed by acetolysis (Erdtman 1960). The samples were sieved through a 200 µm metallic mesh and 6 µm nylon mesh, using an ultrasound bath for less than one minute. To calculate pollen concentration, one tablet of *Lycopodium* spores (Batch numbers 1031 and 177745) was added to each sample (Stockmarr 1971). The prepared samples are stored in glycerine.

Pollen identification was conducted using Beug (2004, 2015), Kapp et al. (2000) and the database https://www.paldat.org/. NPPs were determined according to NPP-ID (Shumilovskikh et al. 2022a,b; https://non-pollen-palynomorphs.uni-goettingen.de/) and NPP database of Kiel University (https://www.wikis.uni-kiel.de/non_pollen_palynomorphs). The samples were counted up to at least 300 pollen grains of terrestrial plants under 400× to 1,000× magnification. Pollen and NPP data are presented as percentages of the sum of terrestrial pollen, excluding water and wetland plants. Due to low pollen concentration and poor preservation, counting in lowermost samples of Peny (96 cm and 104 cm) and Razdolye (75 cm) was conducted up to at least 100 pollen grains. The microcharcoal particles were counted for evaluation of the regional fire regime.

Macrocharcoal analysis and LOI were performed for both cores. For this, 1 cm^3 samples were obtained at 2 cm intervals for the core Peny (44 samples) and at 1 cm intervals for Razdolye (48 samples). For macrocharcoals, laboratory treatment included Sodium Hexametaphosphate and bleach, leaving overnight after each treatment and followed by sieving through a 125 µm mesh. Charcoal particles were counted under 10× to 15× magnification. For Peny, macrocharcoals were counted with minimal classification, while for Razdolye, types were identified following Enache and Cumming (2006). In order to determine macrocharcoal influx and fire episodes for the core Peny, charcoal concentrations and their modelled ages were computed using the software package CharAnalysis version 0.9 (Higuera 2009). LOI samples were oven-dried for 22 hours at 105 °C, for 4 hours at 550 °C and for 2 hours at 950 °C (Dean 1974; Heiri et al. 2001). LOI records are given as percentages, charcoals as concentrations. All data are illustrated with the C2 software version 1.7.7 (Juggins 2007).

Results

Lithology, sediment characteristics and chronology

The surface (0-7 cm) of the composite core Peny (Fig. 4.3) consists of grey low decomposed *Phragmites* peat. The sediment between 7 and 115 cm comprises dark highly decomposed Cyperaceae peat. At the depth of 66-72 cm there is a dark grey clay layer. From 72 to 115 cm the peat has a higher sand and clay content as well as leaf sheaths at 75, 82, 100 and 105 cm. From 115 to 124 cm the sediment is composed of black clay. In 124-135 cm is a transition from black to grey clay, and grey clay down to the base at 210 cm. White concretions were observed from 160 to 180 cm and black layer at 153-154 cm. The LOI results (Fig. 4.4a) show that organic matter in the lower part of the peat core (96-72 cm) increases upwards from 12 to 44%, followed by a maximum at 60-64 cm (up to 81%) and decrease upwards (48-16 cm; 19-8%). The carbonate content is <1% in the entire sediment core.

According to the radiocarbon dates (Table 4.1), the clay at 106-110 cm was deposited before the onset of the Holocene. The next dating at 92 cm depth reveal age of 1,100±123 C^{14} yrs (791-1274 CE), suggesting a hiatus between the layers, possibly due to dry Early and Middle Holocene climate. The constructed age-depth model for the last 1,100-year-old upper part of the Peny archive (Fig. 4.5) is close to linear with an accumulation rate of around 0.8 mm/year.

The top part (30-40 cm) of the sediment core Razdolye (Fig. 4.4b) consists of brown clayey loam with coarse plant remains and roots. Below 40 cm (40-80 cm), the core is composed uniformly of black-grey clayey loam. The organic content is about 6-7% below 40 cm, increasing to 8-15% to the top. Carbonate content is ~1% throughout. The lower radiocarbon date at 76 cm demonstrates a very young sedimentation started at about ~195±30 C^{14} yrs BP (1725-1785 CE). The age-depth model is close to linear with a high accumulation rate of 3.9 mm/year.

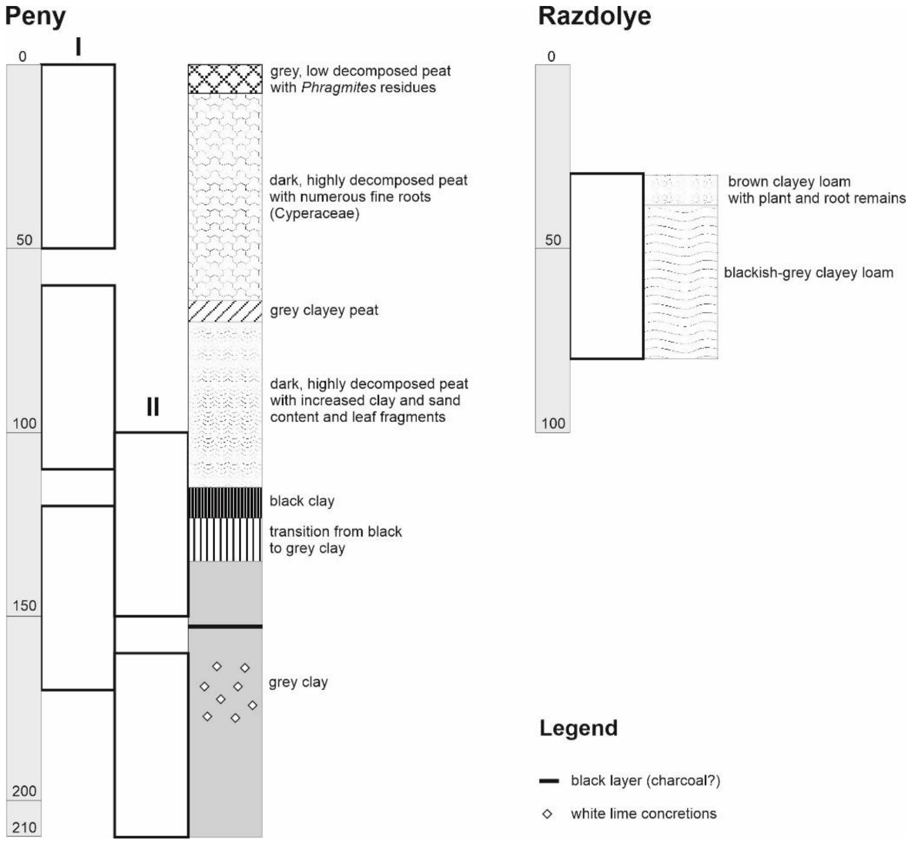


Fig. 4.3. Lithology of the composite core of Peny and a core of Razdolye

Table 4.1 – Radiocarbon dates for the archives of Peny and Razdolye.

Depth, cm	Lab. Code	Dated material	^{14}C age, years BP	Cal. Age, cal years BP (probability)
Peny I				
15	Poz-146907	bulk sample	109.64 ± 0.33 pMC	34-72 (33.1%) 79-83 (1.9%) 90-106 (6.4%) 113-138 (24%) 226-255 (29.6%)
45	Poz-83084	Vegetative grass remains; 1 seed of *Melica nutans*	410±30	430-518 (83%) 331-358 (12%)
92	Poz-122530	Cyperaceae peat	1,100±123	791-1274 (95%)
Peny II				
106-110	Erl-15329	Pollen	10,327±123	11,707-12,560 (94.8%) 11,654-11,660 (0.2%)
Razdolye				
53	Poz-147940	bulk sample	40 ± 30	34-72 (34.4%) 79-83 (1.2%)

				89-107 (4.4%) 112-138 (26.7%) 226-255 (28.2%)
76	Poz-83085	17 seeds of *Ranunculus repens*	195±30	1725 (54 %) 1646 (24.1 %)

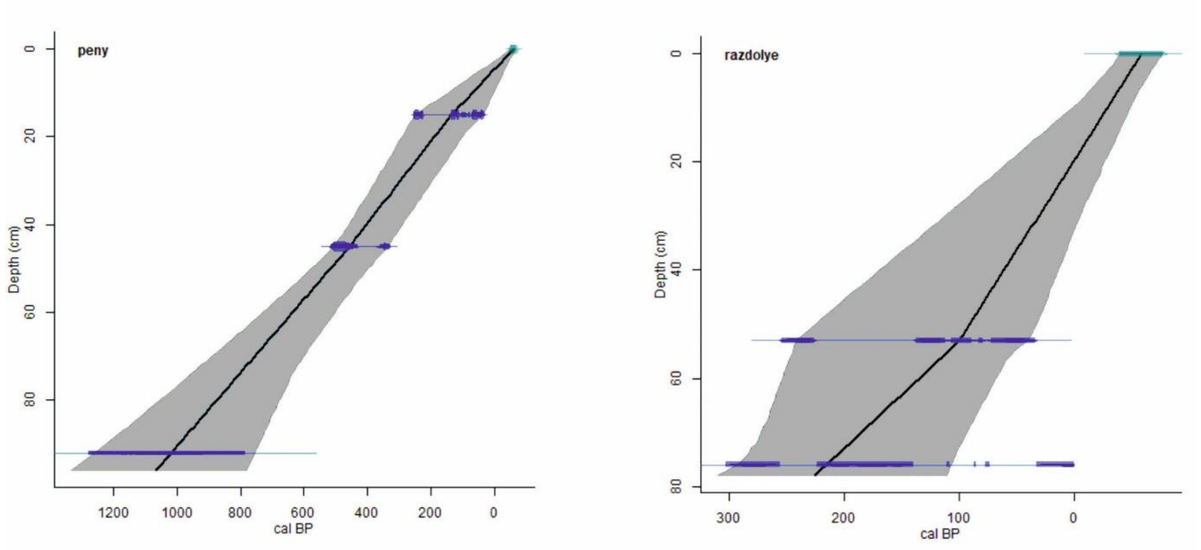


Fig. 4.4. Age-depth models of the sediment cores of Peny and Razdolye

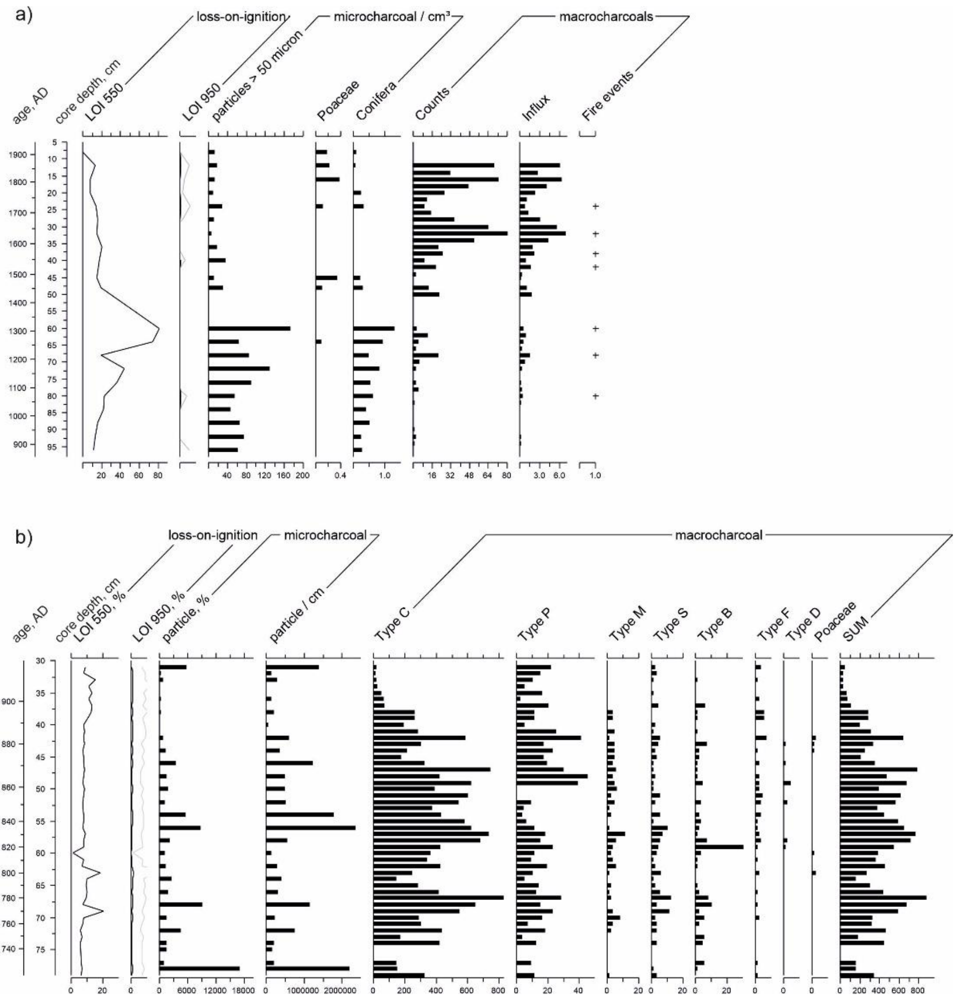


Fig. 4.5. LOI, micro- and macrocharcoal records of the sediment cores of Peny (a) and Razdolye (b)

Palynological data

Peny

For Peny, 82 pollen, 4 fern and moss spore and 61 NPP taxa are recorded (Fig. 4.6). Based on main changes in the pollen assemblages, the palynological diagram is divided into three local pollen zones (PN 1-3).

Due to low counts, the lower-most sample at 104 cm (Late Glacial/Early Holocene) is excluded from the diagram. Its spectrum is dominated by non-arboreal pollen (NAP, 73%) with Cichorioideae (29%), Asteraceae (13%), *Matricaria*-type (10%), *Cirsium*-type (5%), *Artemisia* (2%) and Poaceae (4%). Arboreal pollen (AP) is represented mainly by *Pinus diploxylon*-type (11%), *Quercus robur*-type (10%) and *Picea* (3%). NPP comprise HdV-128, shells of *Arcella*, spores of lignicolous fungus *Savoryella* cf. *lignicola*, uredospores of rust fungi and spores of the smut fungi *Thecaphora*.

PN-1 (97-70 cm, ~1,100-750 cal yrs BP; 850-1200 CE) is characterized by a dominance of AP (up to 72%) with *Pinus diploxylon*-type (41-61%), *Alnus* (1-18%) and *Quercus robur*-type

(2-16%). The NAP is dominated by Cichorioideae (8-20%) and Poaceae (12%). Common taxa are *Matricaria*-type, *Plantago lanceolata*-type, *Ranunculus acris*-type, Asteraceae and Rosaceae. Pollen of *Alnus*, Poaceae, *Matricaria*-type, *Ranunculus acris*-type and Cyperaceae occurs in clumps. Pollen concentrations vary between 3,000 and 13,000 pollen grains/cm^3. Wetland and water plants such as *Nymphaea*, *Potamogeton*, *Typha latifolia*-type, *Persicaria maculosa*-type are present, although in low quantity. Cyperaceae pollen, spores of arbuscular mycorrhizal fungi of the *Glomus*-type and algae remains HdV-184 reach their maxima. Fungi are represented by spores of HdV-200, coprophilous (*Podospora*, *Sordaria*, *Sporormiella*, *Coniochaeta*, *Chaetomium*), lignicolous (*Savoryella*, *Diporotheca*) and carbonicolous fungi (*Neurospora*, *Gelasinospora*) taxa. Spores of monolete ferns, *Equisetum* and *Sphagnum* occur in low quantity.

PN-2 (70-38 cm, ~ 750-380 cal yrs BP; 1200-1570 CE) is marked by the upwards reduction of AP from 79% to 30%, especially by a decrease of the *Pinus diploxylon*-type down to 13%. *Quercus robur*-type is quite common (7-16%), accompanied by *Alnus*, *Betula*, *Picea*, *Carpinus betulus*, *Corylus*, *Salix* and *Tilia*. *Ulmus*, *Fraxinus excelsior*-type and Ericaceae are present (up to 1%). Poaceae (12-28%) and Cerealia-type (up to 9%) increase. *Hordeum*-type, *Secale*, *Avena*-type and *Fagopyrum* appear for the first time. NAP consists of *Artemisia* (3-11%), Chenopodiaceae, Cichorioideae, Caryophyllaceae, *Plantago major/media*-type, *Plantago lanceolata*-type, Cannabaceae and Urticaceae. The pollen concentrations range from 11,000 to 36,000 pollen grains/cm^3. Wetland and water plants are represented by Cyperaceae, *Potamogeton*, *Typha latifolia*-type, *Persicaria maculosa*-type, *Lemna*-type and *Sparganium*-type. Pollen clumps of Poaceae, Caryophyllaceae and Cyperaceae occur. Monolete fern spores, HdV-128, HdV-200 and uredospores reach their maxima, while *Glomus*, HdV-184, coprophilous fungi and smut fungus *Thecaphora* strongly decrease.

PN-3 (38-0 cm, ~ 380 cal yrs BP to present; since 1570 CE) differs from the previous zones by the dominance of NAP (58-83%) with Poaceae (19-39 %) and less *Artemisia*, Chenopodiaceae, Cerealia-type, Cichorioideae and *Fagopyrum*, accompanied by the regular presence of Cannabaceae, *Plantago lanceolata*-type, *Plantago major/media*-type, Brassicaceae, *Ranunculus acris*-type and several Asteraceae taxa. The percentages of crops is accelerated (*Avena*-type, *Hordeum*-type, *Secale*, *Fagopyrum*) and the diversity increased by the appearance of the *Triticum*-type and *Zea mays*. AP is reduced with low values of *Pinus diploxylon*-type (5-12%), *Quercus robur*-type (2-7%) and *Alnus* (up to 3%) but an increased abundance of *Salix* (2-21%) and *Sambucus nigra*-type (up to 4%). *Juglans* appears sporadically. Pollen concentrations vary between 9,000-36,000 pollen grains/cm^3. Among the wetland and water plants, Cyperaceae decreases, while *Sparganium*-type, *Alisma*-type and *Typha latifolia*-type are constantly present. The NPP include an increased amount of *Pseudoschizaea* and *Mortierella chlamydospora*–type (PNY-1), while monolete fern spores, HdV-128, HdV-200 and uredospores decrease.

Razdolye

The palynological analysis of the core Razdolye (Fig. 4.7) revealed 86 pollen taxa, 7 spores of ferns and mosses, and 79 NPP types. The diagram is visually divided into 3 local pollen zones (RZ).

RZ-1 (78-57 cm; 230-120 cal yrs BP; 1720-1830 CE) is characterized by the lowest pollen concentrations (<13,000 pollen grains/cm^3). NAP dominates, major taxa are Cichorioideae (4-30%), Poaceae (5-20%), Cerealia-type (4-24%) and Chenopodiaceae (2-12%).

Cyperaceae occurs in high amounts (up to 73%). *Pinus, Betula, Quercus, Picea* and *Corylus* are the most abundant arboreal taxa. Cerealia-type, *Secale*, *Fagopyrum* appear frequently, they are accompanied by *Polygonum aviculare*-type, *Ranunculus acris*-type, *Plantago lanceolata*-type, *Rumex acetosa*-type, *Convolvulus arvensis* group, *Centaurea cyanus*, Caryophyllaceae, *Dianthus* and *Xanthium strumarium*-type. *Anthoceros* (RZD-5), *Riccia* and *Equisetum* have their maxima. Wetland and aquatic organisms such as testate amoeba and algae are common. Among fungi, *Glomus*-type, *Brachydesmiella caudata*-type (RZD-4), coprophilous fungi (*Sordaria*-type, *Podospora anserina*-type, *P. decipiens*-type, *Cercophora*) and two types of Neorhabdocoela oocytes (*Gieysztoria virgulifera* and *Gyratrix hermaphroditus* 1-A) occur.

RZ-2 (57-39 cm; 120-60 cal yrs BP; 1830-1890 CE) is marked by the highest Poaceae percentages reaching 61%, making up most of the dominant NAP (64-89 %). *Secale* and *Fagopyrum* decrease below <2%, while *Zea mays* occurs for the first time and Chenopodiaceae increases up to 17%. Cyperaceae strongly decreases to below 7%. AP is dominated by *Pinus* (9-32%), accompanied by *Betula*, *Quercus*, *Corylus, Picea* and *Sorbus* group. Pollen concentration increases up to 47,000 pollen grains /cm^3 at the top of the zone. Spores of *Equisetum* are constantly low (2-5%), while *Riccia* decreases (2-22%). Aquatic organisms occur less frequent.

RZ-3 (39-30 cm; 60-30 cal yrs BP; 1890-1920 CE) is characterised by the dominance of Cerealia-type (50%), *Senecio*-type (33%) and *Secale* (up to 8%). Poaceae decrease towards top from 22 to 5%. AP dominated by *Pinus* (6-31%) increase from 11 up to 55%. This increase is driven mainly by *Pinus*, *Betula* and *Quercus*. *Typha latifolia*-type has a major increase to its maximum of 130%. Pollen grains of perennial water plants *Myriophyllum spicatum*, *Sparganium*-type, *Saggitaria saggitifolia* appear more frequently. Spores of plants, *Glomus*-type*,* and coprophilous fungi are reduced. The percentages of aquatic taxa increase, HdV-128 and HdV-731 are present.

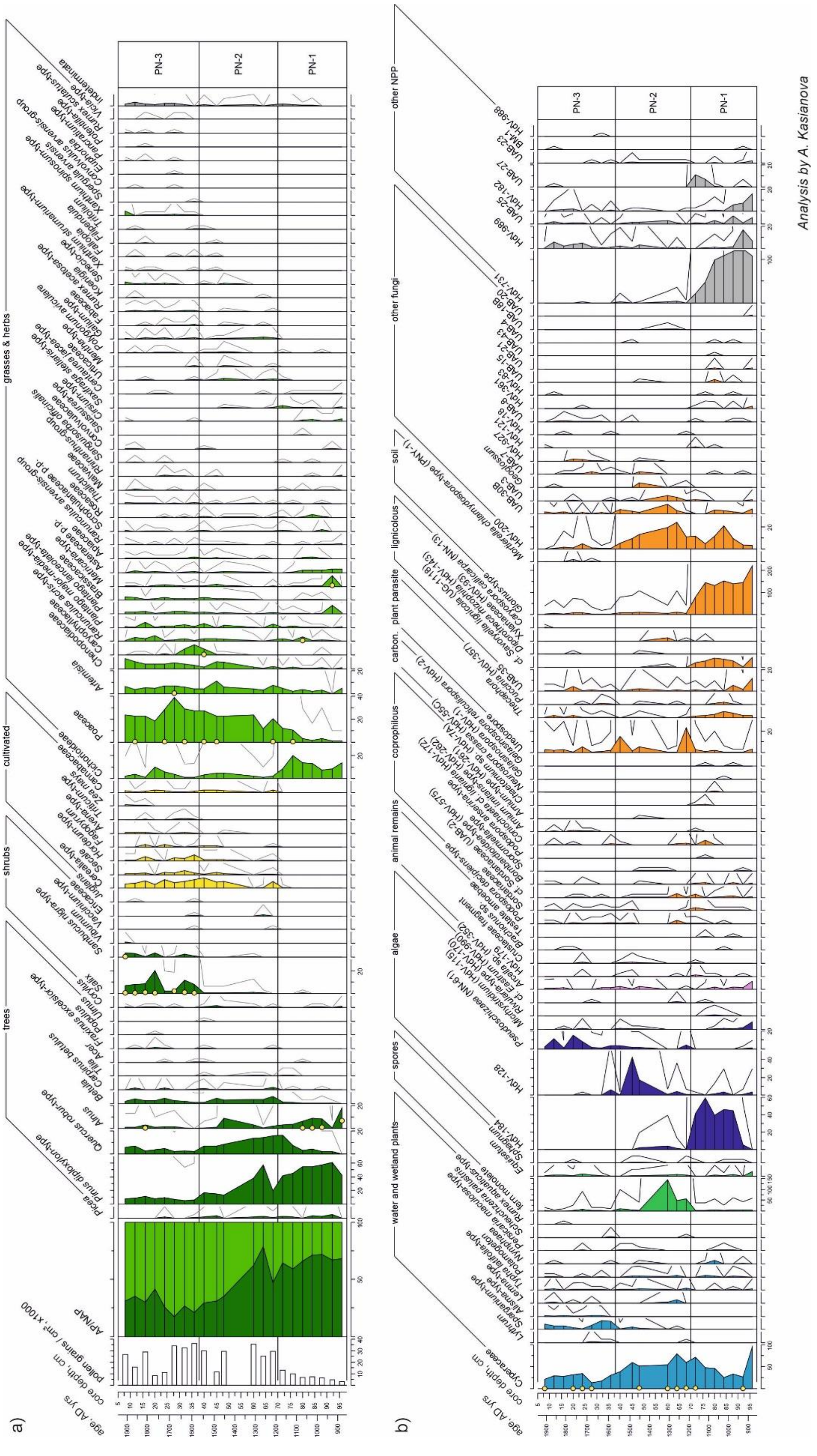
Description of new NPP types

We describe three new NPP types for Peny (PNY) and five for Razdolye (RZD).

PNY-1 (Plate 4.2: 11) is globose, dark brown, about 23-25 µm in diameter, exclusive 6-8 µm long hairy appendages, dark coloured thick-walled (ca. 2.5-3.5 µm). PNY-1 resembles the chlamydospores of *Mortierella chlamydospora* (Zygomycota) known from cultivated field soils and is therefore named *Mortierella chlamydospora*–type (Watanabe 2010). PNY-1 occurs in the upper part of the core Peny, indicating soil erosion.

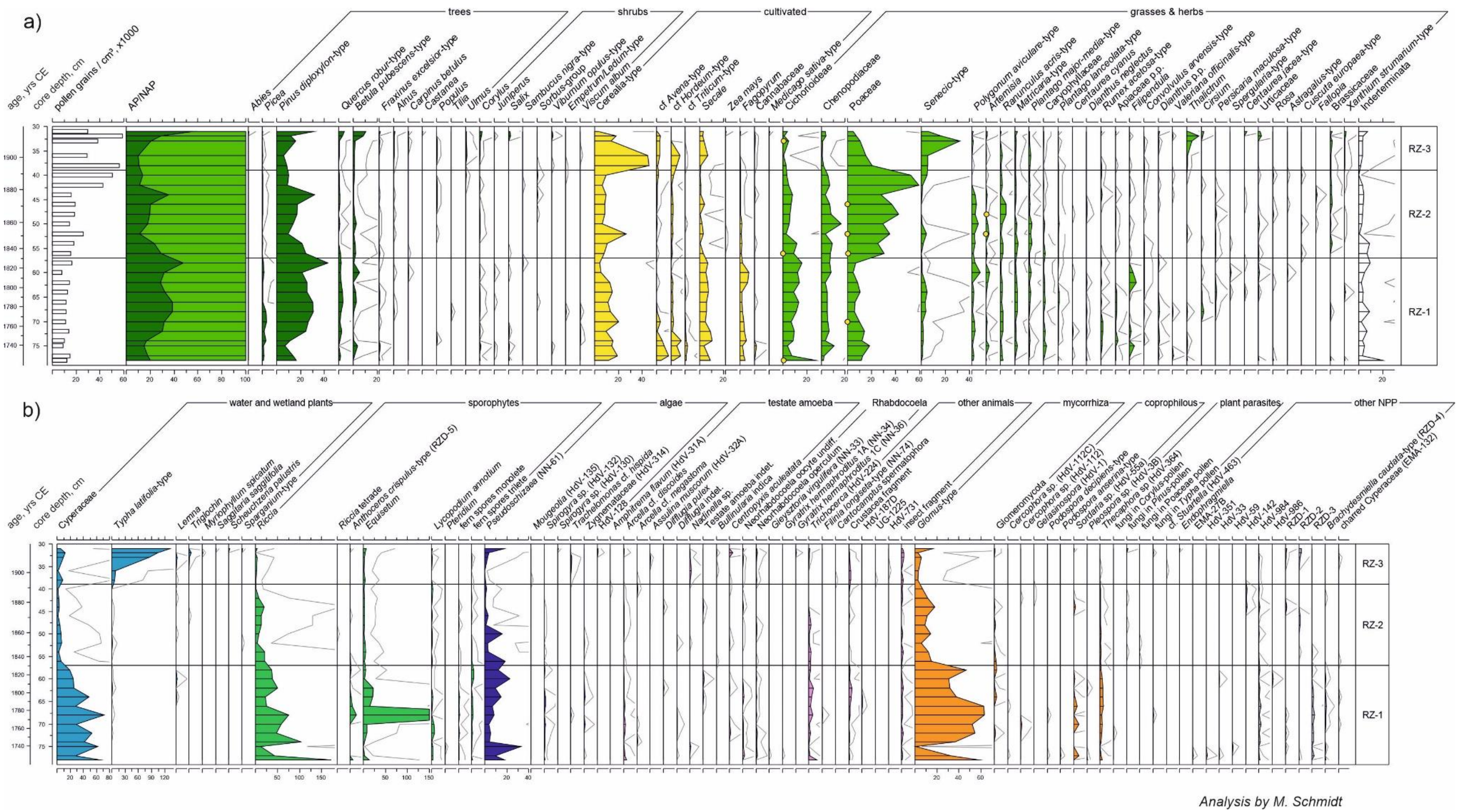
PNY-2 (Plate 4.2: 14a, b) is globose, pale yellowish, 18-21 µm in diameter, exclusive 1.5-2.5 µm long evenly spaced protuberances, thick-walled (ca. 2-3 µm). Origin of this microfossil is unknown. It occurred once in 12 cm depth in Peny.

PNY-3 (Plate 4.2: 15) bicellular fungal spore, brown to dark brown, 22-24 × 16-18 µm, with thick middle septum (ca. 3-4 µm), cells are slightly constricted at the septum, hyaline outer wall. Its origin is unknown. This spore was recorded only in the upper part of the core Peny in sample from 12 cm depth.



Analysis by A. Kasianova

Fig. 4.6. Palynological percentage diagram of the sediment core of Peny: a) arboreal (AP) and non-arboreal pollen (NAP); b) wetland and water plants; spores, algae, animal remains, fungal assemblages and other non-pollen palynomorphs (NPP). Yellow circles indicate the presence of pollen grains clumps



Analysis by M. Schmidt

Fig. 4.7. Palynological percentage diagram of the sediment core of Razdolye: a) Pollen; b) Non-pollen palynomorphs (NPP). Yellow circles indicate the presence of pollen grains clumps

RZD-1 (Plate 4.3: 1) represents a fungal fruiting body, very various in size (30-50 µm), circular, brown, constructing cells of irregular shape. Often attached to plant remains. It occurred sporadically in the lower and upper parts of the record Razdolye.

RZD-2 (Plate 4.3: 2) is circular, hyaline, ~21-24 µm in diameter with baculate appendages 3-4 µm long. Origin of the microfossil is unknown. It occurred in zones RZ-2 and RZ-3 of Razdolye.

RZD-3 (Plate 4.3: 3a, b) is circular, light brown of 70-80 × 50-60 µm in size, with evenly distributed thin hair-like hooks up to 5 µm. One apical side is covered by a smooth operculum of ~22-24 µm in diameter, surrounded by an anulus of 3-4 µm thickness. RZD-3 represent a resting stage. Its overall morphology reminds on eggs of *Diphyllobothrium* sp. or *Paragonimus* sp., both however, do not have hooks. It could origin also from free-living flatworms or other worms. In record Razdolye, it occurred often in the zone RZ-1.

RZD-4 (Plate 4.3: 4) is fungal spore, ~60 × 80 µm, 2 apical pores, 2 subapical septa, the middle cell is strongly curved outwards ("inflated") and dark brown, the remains of the two outer cells are lighter in colour. RZD-4 resembles the conidia of the lignicolous freshwater hyphomycetes *Brachydesmiella biseptata* and *B. caudata* (Jiang et al. 2008, Sivichai et al. 1998). Due to its strong inflation, we erect here the *Brachydesmiella caudata*-type for RZD-4. RZD-4 occurs several times in the zone RZ-1.

RZD-5 (Plate 4.3: 5) is a trilete spore, 40-45 µm, brown, subtriangular in polar view, flat proximal site with oval-shaped lumina, echinate distal site covered by spines with rounded-off top. It is identified as bryophyte spore of the hornwort *Anthoceros* sp. *Anthoceros* grows on moist soils rich in loam in fallow land, hills, in ditches, in damp hollows among rocks (Boros and Járai-Komlódi 1975; Schubert et al. 1994). RZD-5 is similar to *A. crispulus* (Mont.) Douin. However, other species can have the same spore morphology. Therefore, we name this palynomorph *Anthoceros crispulus*-type. RZD-5 is often in the zone RZ-1.

Charcoal data

For Peny, the depth 104 cm was again excluded from the diagram. However, it is worth to mention that charcoal concentration in this sample was relatively high (microcharcoals: 24,000 particles/cm^3, conifer microcharcoals: 1,725 particles/cm^3, macrocharcoals: 13 particles/cm^3).

The microcharcoal concentrations exceed 40,000 particles/cm^3 at 96-60 cm (~1,070-640 cal yrs BP) and remain below this value in the upper part of the core. The majority of conifer microcharcoals were recorded at the depths 96-60 cm with a decreasing trend upwards, whereas Poaceae microcharcoals appear in the upper part. In contrast, macrocharcoals show their maxima from 42 cm (~425 cal yrs BP; 1525 CE) upwards. Based on the macrocharcoal influx, several fire events were identified at 24 cm (~232 cal yrs BP; 1720 CE), 32 cm (~320 cal yrs BP; 1635 CE), 38 cm (~380 cal yrs BP; 1570 CE), 42 cm (~425 cal yrs BP; 1525 CE), 60 cm (~635 cal yrs BP; 1315 CE), 68 cm (~730 cal yrs BP; 1220 CE) and 80 cm (~875 cal yrs BP; 1075 CE).

Charcoal records of Razdolye are characterized by very high values of both micro- and macrocharcoals. Microcharcoal concentration vary between 50,000 and 2,000,000 particles/cm^3 with the lowest values in 36-40 cm. Macrocharcoal concentrations are very high in almost the entire core reaching 800 particles/cm^3 but strongly decrease to the top (37-30 cm) to less than 100 particles. Macrocharcoals are mainly presented by type C and P, just few Poaceae charcoals were found (Fig. 4.4b).

Plate 4.1. Selected pollen and spores from the core Peny: 1. *Pinus diploxylon*-type; 2. *Picea*; 3. *Rumex acetosa*-type; 4. *Tilia*; 5. *Alnus*; 6. *Betula*; 7. *Salix*; 8. *Artemisia*; 9. Caryophyllaceae; 10. Chenopodiaceae; 11. *Senecio*-type; 12. Cichorioideae; 13. *Convolvulus arvensis* group; 14. *Vicia*-type; 15. Apiaceae; 16. *Polygonum aviculare*; 17. *Plantago major/media*-type; 18. *Plantago lanceolata*-type; 19a, b. *Xanthium spinosum*-type; 20. Cannabaceae; 21. Poaceae; 22. *Zea mays*; 23. *Fagopyrum*; 24. *Alisma*-type; 25. Cyperaceae; 26. *Sparganium*-type; 27. *Typha latifolia*-type; 28. *Sphagnum* spore; 29. Monolete fern spore.

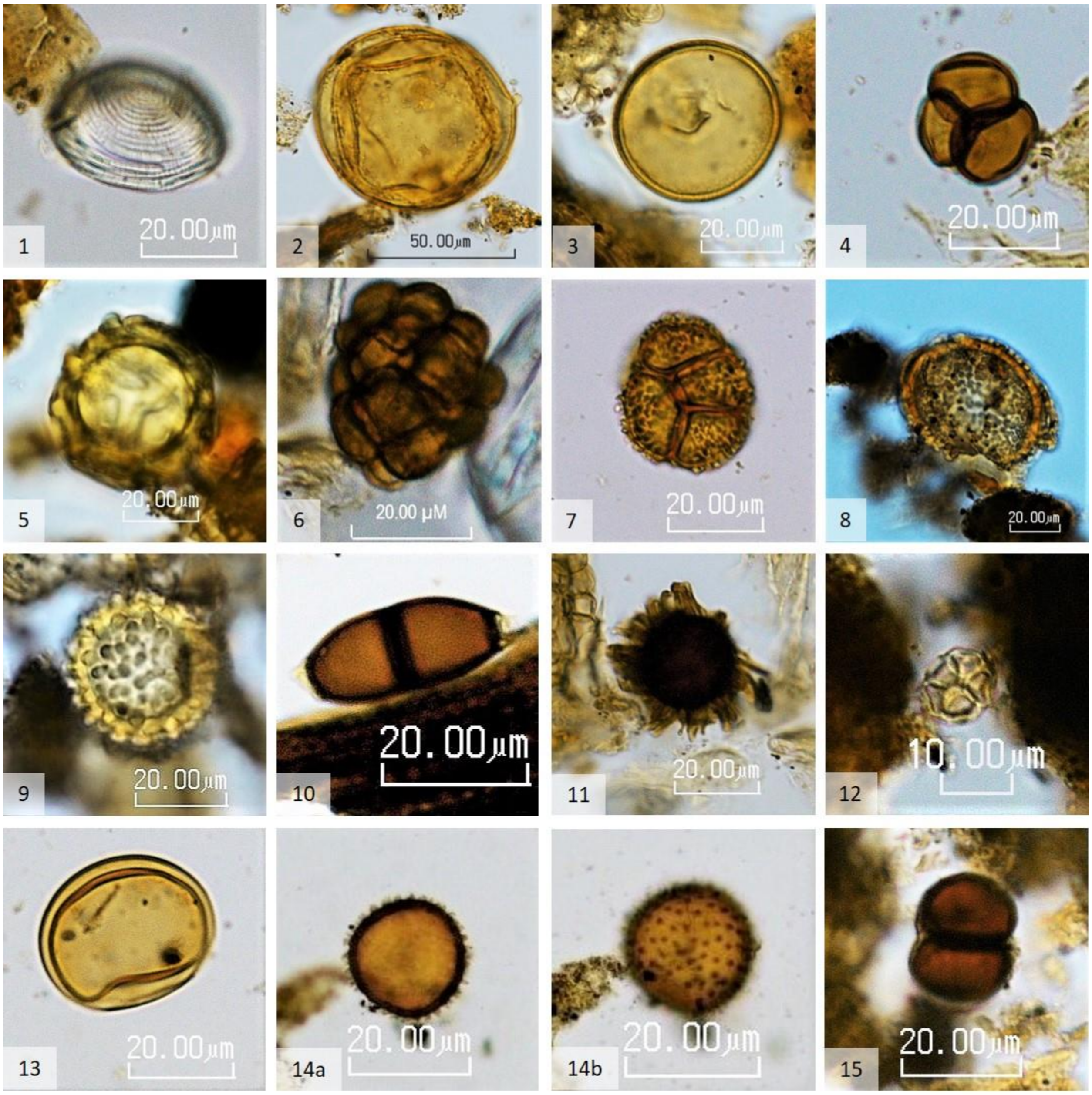


Plate 4.2. Some non-pollen palynomorphs from the core of Peny: 1. *Pseudoschizaea*; 2. *Glomus*-type; 3. HdV-731; 4. HdV-200; 5. HdV-989; 6. UAB-20; 7. *Thecaphora*; 8. UAB-27; 9. cf. *Euastrum ansatum/oblongum* (HdV-984); 10. *Savoryella lignicola* (UG-1118, UAB-35, IBB-16); 11. PNY-1; 12. HdV-184; 13. UAB-25; 14 a, b. PNY-2; 15. PNY-3.

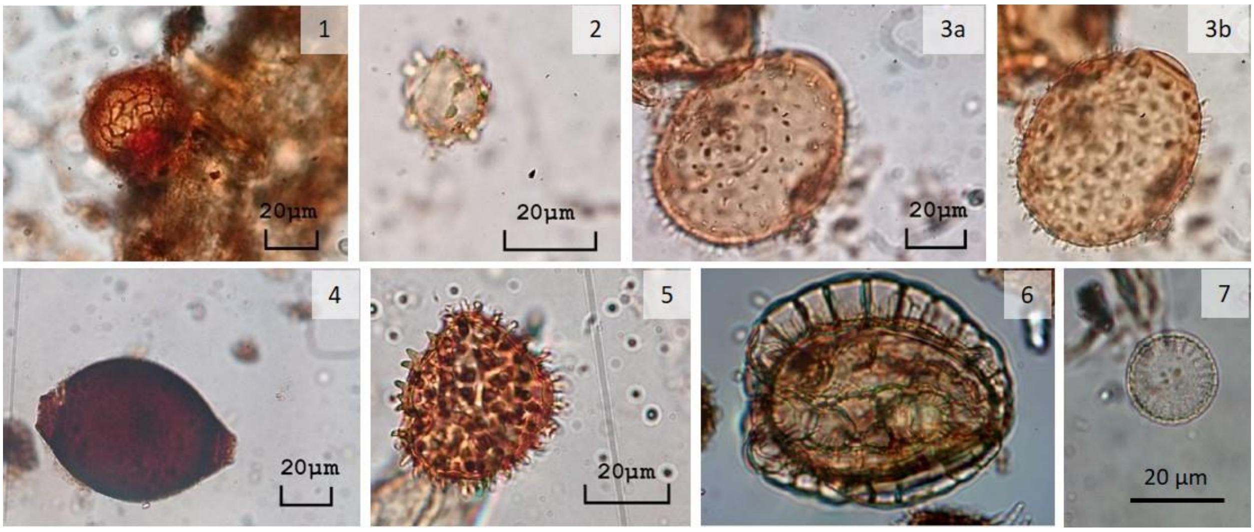


Plate 4.3. Selected non-pollen palynomorphs from the Razdolye core: 1. RZD-1; 2. RZD-2; 3a, b. RZD-3; 4. RZD-4; 5. *Anthoceros* spore (RZD-5); 6. *Filinia longiseta*-type (NN-74); 7. HdV-187D.

Discussion

Local conditions

Peny

At ~1,100 cal yrs BP (9th-10th century CE), increased local wetness led to the development of a Cyperaceae peat with *Equisetum* and ferns. Presence of the water plants *Potamogeton* and *Nymphaea* as well as the algae *Rivularia*-type and cf. *Eastrum* indicate the existence of stagnant open water at the site, while HdV-731 suggests meso- to eutrophic conditions (Bakker and van Smeerdijk 1982; van Smeerdijk 1989). High values has the algae HdV-184, which was described first from a black soil layer on sandy clay (van Geel et al. 1983). High percentages of HdV-200 indicate the presence of relatively dry microhabitats on the standing culms of helophytes or on plant remains in temporary desiccating bottoms of pools (van Geel et al. 1989; Kuhry 1997). The high values of *Glomus*-type spores may indicate the input of eroded soil material and coincides with a low organic matter content as well as a local growing of this endomycorrhizal fungus on roots of the local plants in moderately wet phases (Smith and Read 2008; Anderson et al. 1984; Kołaczek et al. 2013). The fungus *Savoryella lignicola* and the coinciding maximum of *Coniochaeta ligniaria* reflect the presence of decaying wood (Jones and Eaton 1969). Permanent presence of a wide variety of coprophilous fungal spores such as *Podospora anserina*-type, *Podospora decipiens*-type, *Bombardioidea*, Sordariaceae strongly suggest herbivore grazing throughout.

A mark changes in NPP assemblages occurred at ca. 750 cal yrs BP. The maximum in monolete fern spores indicates a local development of ferns in association with sedges. Pollen of water plants point out to the presence of stagnant open water. Also, the high values of algae HdV-128 reflect shallow eutrophic to mesotrophic fresh water conditions (Miola et al. 2006). Wetland communities with *Sparganium*, *Typha*, *Lythrum salicaria*, *Persicaria maculosa* and *Scheuchzeria palustris* developed. Xylariaceae (HdV-93) indicates the local presence of decaying wood.

About 380 cal yrs BP, the local site got overgrown by *Salix* and *Sambucus nigra*, indicated by presence of pollen clumps. This speaks for drier local conditions because *Sambucus nigra* prefers moderate humid soils avoiding water saturated soils. This vegetation type is present today at the study site. Wetland plant association is enriched with *Alisma* and *Rumex aquaticus*. Algal assemblage is dominated by *Pseudoschizaea*, green algae, which together with *Rivularia*-type, *Brachionus* eggs and pollen of *Lemna* and *Potamogeton* indicate shallow open water. The maximum of *Pseudoschizaea* may be explained by seasonal drying or longer summer drought (Carrión and Navarro 2002), as well as by increased soil erosion (Farrell et al. 2020), most likely connected to agricultural activity.

Razdolye

Locally wet conditions at ~1720 are indicated by the dominance of Cyperaceae. The presence of open water is indicated by *Lemna* and the algae *Spirogyra*, *Trachelomonas*, Zygnemataceae, *Pseudoschizaea* as well as HdV-187D. Bare soils in the surroundings are suggested by liverworts (*Riccia*) and hornworts (*Anthoceros*, RZD-5). Presence of lignicolous freshwater hyphomycetes *Brachydesmiella caudata*-type (RZD-4) suggest presence of decaying wood. During this period, spores of coprophilous fungi such as *Podospora decipiens*-type, *P. anserina*-type, *Cercophora* and *Sordaria*-type are common, indicating pastures or manuring of fields nearby. Frequent occurrence of RZD-3 points to herbivore faeces. The start of the archive falls into the beginning of strong anthropogenic influence and might be caused by related changes in the hydrology of the location.

At ~1830, Cyperaceae and *Riccia* are replaced by local Poaceae, reflected by their pollen clumps. This points to a denser vegetation layer under possibly dryer conditions. The decline of aquatic organisms such as algae, Neorhabdocoela, *Trichocerca* underlines dryer conditions. Coprophilous fungi decrease, suggesting a decline of dung or reduced inwash of spores due to the denser vegetation cover.

Subsequent rewetting and formation of a water body at ~1890 is evidenced by the increasing amount of *Typha latifolia*-type, Cyperaceae and in particular perennial aquatic plants, such as *Myriophyllum spicatum*, *Saggitaria saggitifolia* and *Sparganium*-type. Algae and Neorhabdocoela oocytes increase again, indicating the presence of open water body. This change could be attributed to the construction of an artificial water reservoir by Bunino.

Vegetation and fire history

According to the radiocarbon dates (Table 4.1) the oldest palynologically analysed part of Peny corresponds to the turn of the Late Pleistocene / Early Holocene. The pollen assemblages suggest that the Peny area was covered by mosaic vegetation of pine-broadleaf forests and grasslands. This correlates well with the palynological data of Borisova et al. (2006), Shumilovskikh et al. (2019) and Lukanina et al. (2022), illustrating the dominance of *Pinus* in the Seim and Psel areas at that time.

The upper part of Peny representing the last 1,100 years and Razdolye covering the last 300 years will be discussed in relation to the settlement history of the region (Fig. 4.8).

9th-13th century CE

Climatically the PN-1 corresponds to the medieval warm period (or medieval climate anomaly) that took place from the middle of the 9th to the middle of the 13th century CE (Mann et al. 2008). The studies of Bork et al. (1998) and Bork (2006) suggest that the medieval warming led to the intensive growth in human population, increase in village and town establishments and expansion of anthropogenic-made landscapes in central Europe (Poschlod 2015). Archaeologically, the first local pollen zone (PN-1) corresponds to the end of the Romen culture (8th-11th century CE), and the following expansion of the Kievan Rus (11th-13th century CE). During this period, the foundation of important towns in the broader Kursk region is mentioned by historical sources: Kursk in 1032, Lgov in 1152. The closest archaeological sites with presence of Romen culture are Pogorelovka 1, Pogorelovka 2 and Sugrovo (Fig. 4.2), which are located 7 to 10 km away from the Peny coring site. Vegetation was represented by mixed coniferous and broadleaf forests (*Pinus diploxylon*-type, *Quercus robur*-type) and herb meadow assemblages (Poaceae, Cichorioideae, *Matricaria*-type, *Cirsium*-type, *Centaurea jacea*-type). The presence of *Plantago lanceolata*-type and coprophilous fungi signals grazing activities in the region. These indicators do not allow to distinguish between domestic and wild animals (Shumilovskikh et al. 2021a). From archaeological view, animal husbandry of the Romen culture was based on pigs and less cattle and sheet/goats. However, hunting provided sufficient supplement of meat, indicating presence of wild animals in surroundings (Enukov 2007). The first phase of strong agricultural activities is visible in the 13th century by the appearance of Cerealia-type, *Hordeum*-type, *Secale*, *Fagopyrum* and Cannabaceae, which

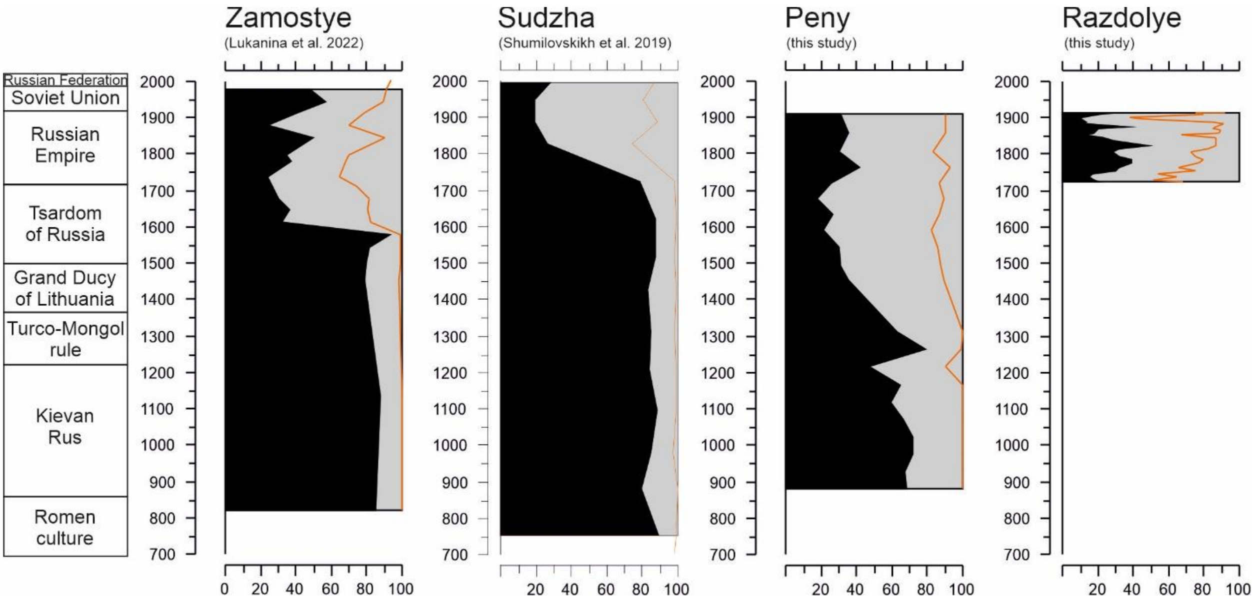


Fig. 4.8. Summary diagrams of the pollen records for the last 1,100 yrs in the region in relation to historical periods. Black fill – arboreal pollen, grey fill – non-arboreal pollen, orange line – sum of primary cultural indicators (cereals, maize, buckwheat, hemp, walnut). Zamostye and Sudzha adapted from Lukanina et al. (2022) and Shumilovskikh et al. (2019).

indicate the inception of noticeable agriculture including cereals, buckwheat and possibly hemp for fibre manufacturing (Zorin et al. 2014).

High microcharcoal values including coniferous particles correlate with carbonicolous fungi (*Neurospora*, *Gelasinospora*) and may reflect burning activities in forest around. Local fires are suggested around 1075 and 1220, starting after the establishment of towns and therefore possibly related to increased human activities. In terms of vegetation composition, increasing conifer charcoals around 1120 correlate well with decrease of pine pollen, strongly suggesting vast local pine burning. The pine habitats were possibly occupied by upcoming oaks, potentially anthropogenic promoted for forest pasture and acorn feeding.

13th - 16th century CE

In 1238, Kursk was destroyed by the Mongol army, and the entire territory was devastated. The related abandonment and general decrease in arable land in the Russian Plain (Khotinsky 1993; Shumilovskikh et al. 2019) is clearly reflected in the diagram of Peny by low presence of cereal pollen (Fig. 4.6). The decreased agricultural activities led to a recovery of pine and oak forests, indicated by increased *Pinus* and *Quercus robur*-type percentages. More frequent appearance of the pioneer birch (*Betula*) indicates early succession stages of forest recovery. Soil stabilization and lower erosion led to maximum in organic matter content. During the 13th-14th centuries, a mixed coniferous-broadleaf forest was established again.

The next period of increased human activities is related to the Grand Duchy of Lithuania, to which the Seim territory was integrated in 1392. After that, the amount of arboreal pollen strongly decreases by the middle of the 15th century CE, whereas an increase in ruderal taxa such as *Artemisia*, Chenopodiaceae, *Plantago major/media*-type and Urticaceae suggests that the landscape becomes more open. The increase in Cerealia-type, *Avena*, *Hordeum*, *Secale*, *Fagopyrum* and Cannabaceae are clearly indicative for enhanced agricultural activities. The significant decline in *Pinus* and *Quercus* and the spread of crop fields point to deforestation leading to enhanced soil erosion seen in increased inorganic content (Fig. 4.5a). Kursk was integrated to the Russian State in 1505, however, this is not reflected in the pollen diagram, indicating a continuity of settlements and agriculture. The reduction of woody plants and the presence of conifer and grass charcoals reflect fire activities in the vicinity of Peny. Although the percentage of macrocharcoals remains rather low, local fires around 1525 and 1570 are suggested by statistical analysis (Fig. 4.5a).

17th century - present

Since the 17th century (PN-3) the pollen composition changed significantly. The coniferous-broadleaf forest coverage is considerably reduced, accompanied by a relatively constant amount of birch. Opening of the landscape was accompanied by stronger agricultural activities (Cerealia-type, *Secale*, *Avena*-type, *Hordeum*-type, *Triticum*-type, *Fagopyrum*, Cannabaceae). Weeds were widespread as indicated by *Ranunculus acris*-type, *Fallopia*, *Convolvulus arvensis* group, *Spergula arvensis*. Ruderal habitats are indicated by Cichorioideae, *Rumex acetosa*-type, *Xanthium strumarium*-type, *Xanthium spinosum*-type. The establishment of new pastures is suggested from increases in *Cirsium*-type, *Plantago lanceolata*-type, *Euphorbia* and coprophilous fungal spores.

Start of these significant changes correlates well with the construction of the Belgorod defence line in 1635—1654 by the Tsardom of Russia for protection of the southern territories against slave raids of Crimean Khanate and Nogai Horde (Bagalei 1887). This protection encouraged the settlement of the fertile chernozem areas and led to flourishing of southern cities including Kursk. Many villages and towns, including Peny in 1606, were established in the region. This led to a strong deforestation and increase in crop fields. As a result of intensive deforestation, siltation started in many rivers in the 18th century (Bagalei 1887). Increased macrocharcoal concentrations (Fig. 4.4a) stand for local burning activities likely connected to nearby settlements.

Like Peny, the region around Razdolye was an open agricultural landscape in the 18th century. The woodland patches were also dominated by *Pinus*, *Betula* and *Quercus*. Higher frequency of *Picea* pollen can be explained by more northern location of the study site Razdolye and a possible presence of spruce in the forests. Similar to Peny, Cerealia-type, *Secale*, *Fagopyrum*, Cannabaceae, and *Zea mays* reflect cultivated fields. *Centaurea cyanus* may point to winter cereals, but can also grow in summer crops (Korsmo and Wollenweber 1930). This crop assemblage agrees with historical data of the 19th century listing rye, wheat, oat, buckwheat, barley, millet, potato, red beet, pea, sun flower, poppy, flax, hemp, and less common tobacco, anis, water melon, melon, pumpkin, cucumber, maize and even grapes cultivation (Bagalei 1887). In addition, Peny record evidence pollen of *Juglans* at the beginning of the 17th century, suggesting cultivation of walnut in the area. The noteworthy increase in *Senecio*-type in Razdolye (Fig. 4.7: RZ-3) might reflect the cultivation of sunflower (*Helianthus annuus*). Native in North Amerika sunflowers were first introduced to Russia in the 18th century by the tsar Peter the Great and was used as garden crops. In 1830-1840 sunflower seeds started to be used for oil production and became important agricultural crops in southern Russia and Ukraine (Zhukovskiy 1950; Zimmermann 1958). Already in 1854, 200,000 ton of sunflower oil was produced in Voronezh region, while in 1880, 150,000 ha of sunflowers were cultivated in Russia (Schuster and Marquard 2003).

Various anthropogenic indicators of trails and the compaction of soils as well as weeds (e.g. *Polygonum aviculare*-type, *Plantago major/media*-type, *P. lanceolata*-type) are continuously present highlighting ongoing strong human land use. The sharp decrease of spores of bryophytes colonising bare soils of for instance long fallow lying stubble fields (*Riccia*, *Anthoceros*) (Koelbloed and Kroeze 1965) prove a more intensified and mechanised cultivation of the fields, including early ploughing after harvest in the end of the 19th century (Porley 2000). Occasional occurrence of coprophilous fungi (e.g. *Sordaria*-type) indicates some pastures or manuring with animal dung (van Geel et al. 2003).

Vegetation mosaic and timing of transformation of forest-steppe to arable land

There is a substantial difference in the forest composition between and within studied microregions. In the Psel River region, the pollen record Sudzha (Shumilovskikh et al. 2019) and the charcoal data from neighbouring Kurilovka (Rodinkova et al. 2020) indicate the prevalence of oak broadleaf forests before the total deforestation. High amount of oaks is likely related to alluvial oak forests in the broad valley of Psel River. Located just five km to the north and in narrower valley of the Sudzha River, the pollen record Zamostye is dominated by pine with much lower contribution of broadleaf trees (Lukanina et al. 2022). In the Seim River region, pollen records Peny and Razdolye exhibit mixed pine-oak woodlands with only some hazel, elm and linden. The high percentages of *Pinus* at Peny coinciding with conifer microcharcoals, clearly indicate the local presence of pine forests. All pollen records concur well with the historical data from the 17th century, which report closed oak and pine forests on the right steep banks for most of the rivers in Kursk and Kharkov regions. The left banks are flat by nature and were covered by alder, hazel and willow, steppe was common in the uplands, ravines were covered by forests (Bagalei 1887). Pollen records provide unique details for the vegetation cover in microregions: the estuary of the Psel was covered by alluvial oak forests, high banks of the Sudzha River and the slopes of the Penka River were covered by pine forests and the depression of Razdolye – by mixed pine-oak forests with spruce.

Strong anthropogenic forest destruction in the southern Russian Plain is well documented since the 17th-18th century by numerous pollen records and broadly correlates to the Russian colonisation (Serebryannaya 1981; Khotinsky 1984, 1993; Serebryannaya 1992; Spiridonova 1991; Novenko et al. 2009, 2012, 2014, 2015, 2016; Chendev et al. 2016, 2017; Shumilovskikh et al. 2018, 2019; Lukanina et al. 2022). In the Kursk region these changes appear to be asynchronous (Fig. 4.8). In Seim River region, Peny reveals a continuous decrease of trees and increase in crops since already the 14th century with a maximum of deforestation in the 17th century. This contradicts to the Psel River region (Shumilovskikh et al. 2019; Lukanina et al. 2022; Fig. 4.1), which pollen records show rapid and strong deforestation and cultivation since the 17th century CE but no deep anthropogenic influence before (Fig. 4.8).

Pollen records Zamostye and Sudzha (Psel River region) are located only 50 km to the south of Seim River region (Fig. 4.1). Both catchment systems have divergent colonisation histories over the last millennium. Along the Seim River, several towns were founded already by the Kievan Rus. The in the Chronicles first mentioned Kursk in 1032 was followed by Lgov and Rylsk in 1152. The Seim territory came under Turco-Mongol control from 1234 to 1382, then under control of the Grand Duchy of Lithuania until 1505 and since the 16th century it has been part of the Tsardom of Russia. With protection by the Belgorod defence line in the 17th century, the chernozem territories became settled and deforested. The early transformation started already in the 16th century is exceptionally well reflected by the pollen record of Peny (Fig. 4.6). Timing of the colonization of the Psel catchment differs substantially. The foundation and construction of the oldest towns there like Sumy, Sudzha, Oboyan was forced by the Russian State to protect the territory against slave raids of Crimean Khanate and Nogai Horde at first in the 17th century (Bagalei 1887). Sudzha was built by the Cossacks over one or two years (Babin, 2015) using mainly oaks and some elms for construction of walls (Ozerov and Babin, 2015). During and after town Sudzha (1661) and satellite villages were founded, the forests around coring sites Zamostye and later Sudzha were intensively explored and destructed leading to a significant decrease of forest cover in the 18th century (Shumilovskikh et al. 2019; Lukanina et al. 2022). According to historical data, it was the 18th century when population strongly increased (Bagalei 1887) with all the need of wood for construction, heating, cooking, tar, potash, saltpeter and vodka production.

Conclusions

The palynological records Peny and Razdolye provide insights into the local and regional vegetation history of the northern part of the Kursk region within the last 1,100 years. In the 9th century CE, the territory around Peny was covered by mixed pine forest and patches of steppe. Anthropogenic influence by grazing and burning took place. The significant subsequent forest reductions were related to the spread of sedentary populations. Distribution of agriculture occurred in the 13th century CE during the Kievan Rus period, but was disrupted during the Tatar-Mongol invasions. New agricultural activities appeared in the 15th century under control of the Grand Duchy of Lithuania, while total deforestation took place in the 17th century CE when the Belgorod defence line protected the fertile chernozem soils of the forest-steppe against invaders. Openness of the territory also to the north is proved by the Razdolye record. The cultivation of regionally new introduced crops such as sunflower or walnut is evident by both cores. The gradual deforestation in the Seim River area is in contrast to pollen data from the Psel River region. They show low human impact on vegetation before the 17th century and rapid deforestation after. This asynchronous decrease of the forest cover and spread of the crop fields is strongly related to the settlement history of each region. All palynological data are in good general agreement with the historical sources, reporting the existence of pine and oak forests before first strong deforestations. The total deforestation and conversion of the forest-steppe into an agrarian landscape already at that time left over only very small patches of semi-natural vegetation today.

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Chapter V – Manuscript 4

Modern pollen spectra from the East-European forest-steppe reflect land use patterns rather than climate

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Abstract

Current global warming will highly likely change water balance in the region of the East-European forest-steppe affecting agricultural production. One of the ways to understand the effects of climate change on such systems is to look at how it affected vegetation in the past which can be reconstructed from fossil pollen data. To understand how pollen samples reflect the forest-steppe landscapes, and the potential of the palaeorecords to capture this variety as well as to provide a training set for quantitative pollen-climate reconstructions, we conducted a study of the surface samples from the East-European forest-steppe. 60 modern pollen samples were collected along the north-south latitudinal gradient of the East-European forest-steppe mostly from near-natural environments. The results show that the variability in the surface pollen spectra is connected firstly to the land use and secondly to the local conditions on site rather than to the latitudinal gradient. The minimum AP values for the sites with "near-natural" vegetation of the ecotone do not go under 33%. The majority of the pollen records from the East-European forest-steppe reflect the dominance of pine forests as the majority of the palynological archives are located in wetlands of the oxbow lakes and rivers where pine dominates. Open areas in such cases are also underrepresented. We conclude that pollen records from watersheds would potentially give a better insight into the vegetation dynamics.

Introduction

East-European forest-steppe is a region known as a breadbasket of Europe. Thus, Ukraine, located largely within this territory is one of the world's largest agricultural producers and exporters (2003-2018; Barrientos and Soria 2021-2023). For example, in 2018, it was the world's largest producer of sunflower seed, 3rd largest producer of buckwheat, 5th largest producer of maize, 8th largest producer of wheat, etc. (FAOSTAT 1961-2023). This is largely due to the fact that 30% of the territory of Ukraine is occupied by the most fertile black soils – chernozems (Voronina and et al. 1977), characteristic of the forest-steppes and steppes of Eastern Europe.

Climate is a key element defining the existence of forest-steppes. The current global warming will likely change the water balance in the region affecting agricultural production (World Resources Institute 2023). One of the ways to understand the effects of climate change on such systems is to look at how it affected vegetation in the past. Past climate conditions can be traced from vegetation changes which in their turn can be reconstructed from fossil pollen data (Birks and Birks 2005). Recently, several studies on the past vegetation dynamics of the East-European forest-steppe ecotone have been conducted (Feurdean et al. 2015; 2021; Hájková et al. 2022; Kasianova et al. 2023; Kremenetski 1995; Lukanina et al. 2022; 2023; Novenko et al. 2009; 2014; Shumilovskikh et al. 2018; 2019; 2021) which could be used for climate risks assessment as well as for conservation purposes.

As an ecotone, East-European forest-steppe has a variety of landscapes combining open vegetation types and forests (Erdős et al. 2019). Potential natural vegetation of the study area include mixed forests dominated by oak *Quercus robur* (Donita et al. 2004). This, however, is be problematic to trace in the pollen records. Most of the available records show pine dominating the pollen spectra throughout the Holocene (Borisova et al. 2006; Kasianova et al. 2023; Lukanina et al. 2022; 2023; Novenko et al. 2014; 2016), what is usually explained by a well-known long-distance transport of *Pinus* pollen (Dyakowska 1959). To understand how pollen samples reflect the mosaic vegetation, and the reliability of the vegetation reconstructions in the East-European forest-steppe, we conducted a study of the surface samples.

Another motivation of this study was to check the pollen spectra from the forest-steppe for their reliability for quantitative climate reconstructions. There have been several attempts to reconstruct the late glacial and Holocene climate dynamics on the European scale and more locally for individual regions based on the changes in vegetation (Bartlein et al. 2011; Davis et al. 2003; Herzschuh et al. 2023a; 2023b; Mauri et al. 2015; Seppä et al. 2009; Velichko et al. 2002). Continental-scale quantitative reconstructions focus on a broader scale and usually do not consider local differences especially if just few records per region are available (Mauri et al. 2015). Regional climate reconstructions in such cases can provide more reliable data but they require local surface pollen samples in the training set. The territory of the East-European forest-steppe have been used for agriculture since the Bronze Age (Lukanina et al. 2022; 2023) and completely deforested in the last 1000 years (Kasianova et al. 2023; Lukanina et al. 2022; 2023; Novenko et al. 2014; Shumilovskikh et al. 2018; 2019). The remaining woodland cover is estimated to be within 7% (Donita et al. 2004) or 9-30% (Bartalev et al. 2011). Due to the lack of natural vegetation within the ecotone, there are very few local modern pollen samples available for the training set for the East-European forest-steppe ecotone (Davis et al. 2020).

In this paper we study the surface samples from the variety of landscapes of the East-European forest-steppe. We aim to study: 1) how the regional vegetation is reflected in the pollen spectra; 2) the main trends in the distribution of pollen spectra and the main factors affecting it; 3) which surface samples can be used for quantitative pollen-climate reconstructions.

Study area

Located in the southern part of the Mid-Russian Upland, the study area belongs to the Dnieper and Don river basins between the Kursk (Russia) and Kharkiv (Ukraine) regions (Fig. 5.1). The landscapes represent undulating plateaus at an altitude of ~200-250 m above sea level dissected by river valleys. Parental rock for the soils are mainly loess sediments on which fertile chernozem soils have formed (Sycheva 2012; Velichko 2009).

Climate is a key element defining the existence of forest-steppes (Erdős et al. 2018; Walter and Breckle 1994). In the temperate zone, humid environments support forests while grasslands occupy more arid areas (Dengler et al. 2014). Transitional nature of the East-European forest-steppe ecotone (from semi-humid to semi-arid climate conditions) allows the coexistence the forest and steppe components and their distribution is defined by relief, microclimate and soil composition (Donita et al. 2004). Forests occur in valleys, gorges, hollows, on the northern slopes, hills and mountain tops while steppes occupy warm and dry southern slopes, plateaus with clay and silt-rich soils.

Located at the junction of two contrasting vegetation zones, East-European forest-steppe has an exceptionally high biodiversity (Donita et al. 2004; Erdős et al. 2018; Walter and Breckle 1994). Thus, the Central Black Soil Nature Reserve near Kursk noted 1287 species of vascular plants by the end of 2010 (Zolotukhin and Zolotukhina 2012-2023). Its meadow steppes rank amongst the most species-rich communities found anywhere (Donita et al. 2004) reaching 87 vascular plant species per m^2.

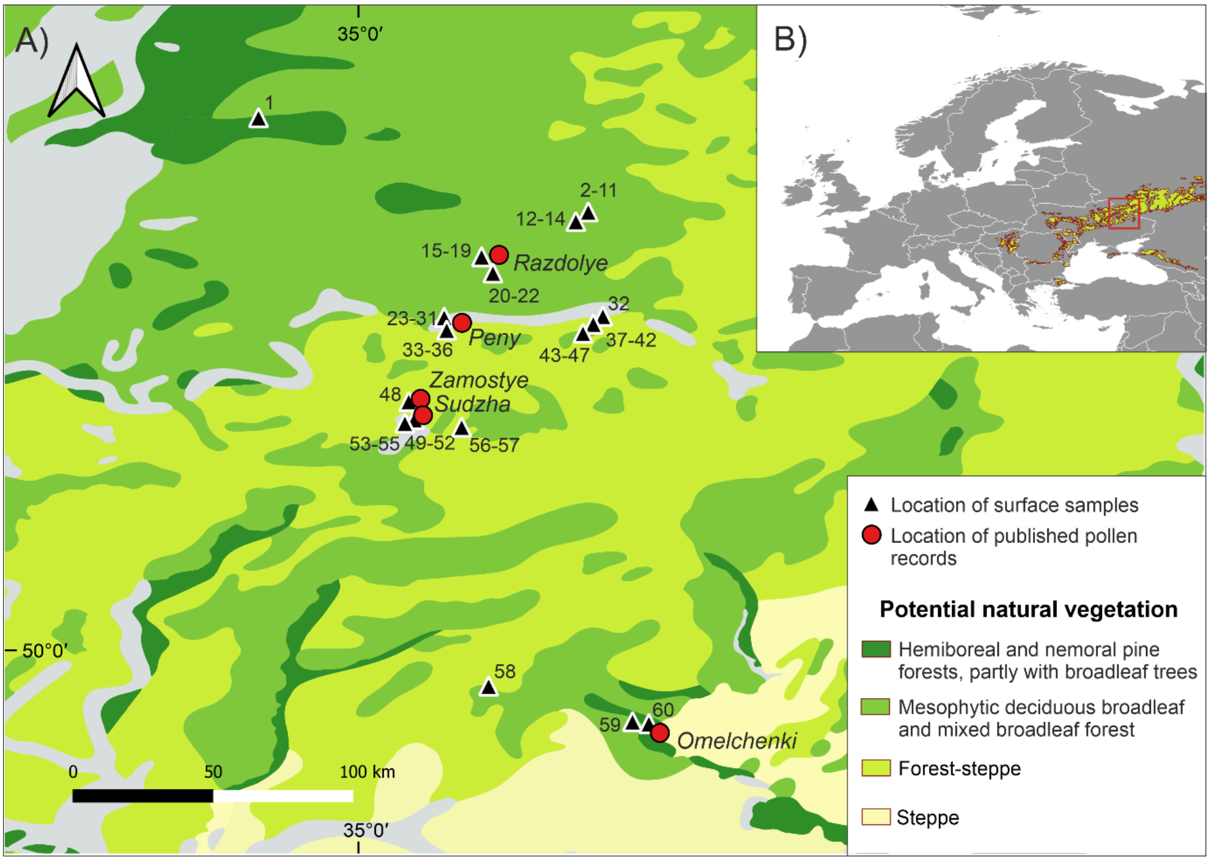

Fig. 5.4. a) Map of potential natural vegetation of the study area (Bohn et al. 2004) showing the location of the surface pollen samples and published pollen records; b) East-European forest-steppe on the map of Europe and the location of the study area

Table 5.1 – Published pollen records within the study area with references

Pollen record	N	E	Age, cal. yrs BP	Reference
Razdolye	51°54'34.51"	35°38'28.88"	~300	Kasianova et al. 2023
Peny	51°35'48.10''	35°27'31.56''	~1100	Kasianova et al. 2023
Zamostye	51°11'5.316"	35°16'47.568"	~14800	Lukanina et al. 2022
Sudzha	51°08’15”	35°17’17”	~2500	Shumilovskikh et al. 2019
Omelchenki	49°38'22.884"	36°25'0.372"	~9800	Lukanina et al. 2023

Potential natural vegetation represents a mosaic of forest patches and meadow steppes. In the mixed oak (*Quercus robur*) forests, some Central European species (*Acer plantanoides, Fraxinus excelsior, Corylus avellana, Tilia cordata*) occur (Bohn et al. 2004; Shahgedanova 2003). Pine and oak-pine forests (*Pinus sylvestris, Quercus robur*) are found on sandy soils together with *Prunus fruticosa, Genista tinctoria, Filipendula*. Hardwood alluvial forests (*Quercus robur, Ulmus laevis*) in combination with poplar and willow (*Populus nigra, Salix alba*) are typical for moist and wet sites (Bohn et al. 2004). The study area represents the eastern border of the *Carpinus betulus* areal and the southern border of *Picea abies* (Zerov 1950). The meadow steppes are dominated by *Stipa tirsa, S. pennata, Carex humilis, C. praecox, Filipendula vulgaris, Trifolium montanum, Onobrychis arenaria, Rhinanthus* *alectorolophus, Bunias orientalis, Bromus riparius, Festuca rupicola, Poa angustifolia* (Bohn et al. 2004).

Materials and Methods

In total, 60 modern pollen samples were collected along the north-south latitudinal gradient of the East-European forest-steppe to study the vegetation patterns and changes (Fig. 5.1, Table 5.2). Since most of the forest-steppe territory is anthropogenically changed and used for agriculture, the samples were mostly taken in near-natural environments, e.g. the Central Black Soil Nature Reserve. Established in 1935 to protect meadow steppe on virgin chernozems and spread over 6 sites with the total area of 5287 ha, the Nature Reserve territory, however, is not an anthropogenic impact-free environment. The steppe vegetation in modern absolutely reserved conditions, i.e. without human interference, gradually gives way to meadows and later tree and shrub species. Therefore, haymaking and livestock grazing with a moderate load is used (Filatova 2012-2022).

The samples were taken from various habitats including pine and broadleaf forests, peatbogs, lake shores, grasslands, fields and meadow steppe (Table 5.2). In order to dilute any local extremes in pollen deposition (Adam and Mehringer 1975), five subsamples of moss pollsters and litter were collected within 10 m^2 and mixed to one sample. The samples were stored in paper bags for drying and transported to the lab. For laboratory analysis, 1 cm^3 of mixed material was taken from each sample. The processing technique followed Faegri and Iversen (1989) and included the treatment with 10 % HCl, 10% KOH, 48 % HF and acetolysis for 3 minutes. The samples were sieved through 200 µm metallic mesh and 5 µm nylon mesh using ultrasound bath for less than 1 minute. To calculate the pollen concentration, 1 *Lycopodium* spores' tablet was added per sample (batch number 1031, 20848 ± 1546 spores per tablet) prior to the chemical treatment.

The samples were counted up to at least 500 terrestrial pollen grains per sample under 400× to 1000× magnification. A pollen sample #15 was excluded from the pollen diagram and further analysis due to the low pollen concentration and insufficient pollen counts. The percentages of the pollen were calculated relative to the pollen sum of terrestrial plants excluding Cyperaceae and aquatics due to their local presence at the peatbog sites. To identify the pollen types, we used Beug (2004) and Göttingen University reference collection.

Unconstrained cluster analysis was applied to the modern pollen data using CONISS (Grimm 1987). To explore the variation in the pollen data we applied a PCA using R package 'vegan' version 2.6-2 (Oksanen et al. 2022). We excluded rare pollen types occurring less than 4 times from the dataset and performed square root transformation to reduce the effect of extreme values.

Table 5.2 – List of the modern pollen samples from the East-European forest-steppe (* indicates samples collected in the area of the Streletskaya steppe of the Central Black Soil Nature Reserve; ** protected area of Melovoe).

#	**Sampling ID**	**Location**	**Dominant vegetation**	**Year of collection**	**N**	**E**	**Altitude**
1	116	*Pinus-Acer-Ulmus* forest	*Pinus sylvestris*, *Acer platanoides*, *Ulmus, Tilia, Corylus, Quercus robur, Aegopodium podagraria*, Lamiaceae, Poaceae, *Asarum europaeum, Thalictrum minus, Polygonatum*	2013	52.61175	34.51519	196 m
2	49.1	Lake shore at pasture	Surrounding: *Artemisia*, Asteraceae, Poaceae, *Cichorium, Rumex, Robinia*	2010	52.1278	36.1172	206 m
3	49.2	Cow pasture	*Achillea*, Asteraceae, *Artemisia*, Poaceae, *Cichorium*	2010	52.1278	36.1172	206 m
4	52.2	Lake shore at pasture	Surrounding: *Polygonum aviculare, Artemisia*	2010	52.1278	36.1167	209 m
5	46.2	Overgrazed cow pasture	*Artemisia*, Asteraceae, Poaceae, *Cichorium, Rumex, Robinia*	2010	52.1271	36.1203	206 m
6	45	Lake shore at pasture	Surrounding: *Typha*, Asteraceae, Poaceae, Cyperaceae, *Artemisia*, Apiaceae	2010	52.1270	36.1214	202 m
7	53	Grassland on slope (no grazing)	Poaceae, Apiaceae, *Artemisia, Galium, Equisetum, Agrimonia eupatoria, Bidens, Salix, Robinia*	2010	52.1234	36.1296	212 m
8	54	Grassland on slope (no grazing)	Poaceae, Asteraceae, *Artemisia, Eryngium, Achillea, Antennaria dioica, Equisetum, Agrimonia*, Caryophyllaceae	2010	52.1233	36.1296	216 m
9	55	Grassland on slope (no grazing)	Poaceae, *Agrimonia, Equisetum*, Apiaceae, Asteraceae, *Plantago lanceolata, Fragaria*	2010	52.1231	36.1295	217 m
10	57.1	Oak stand	Stripes of *Quercus, Sorbus, Populus tremula, Betula, Salix, Prunus, Urtica, Geranium, Fragaria*	2010	52.1224	36.1378	221 m

11	57.2	Oak stand	No trees near the collection point; *Malus*, Poaceae, Asteraceae, Apiaceae, *FragariaArctium, Hypericum, Cirsium, Agrimonia*	2010	52.1224	36.1378	221 m
12	57.2	Oak stand	*Quercus, Malus, Artemisia*, Fabaceae, Lamiaceae, Apiaceae, *Antennaria dioica*	2010	52.122389	36.137806	221 m
13	57.2	Oak stand	Inside the stand; *Quercus, Prunus, Fragaria*	2010	52.122389	36.137806	221 m
14	56	Grassland slope used by geese	*Artemisia*, Apiaceae, Fabaceae, *Convolvulus*, Asteraceae, Poaceae, *Rumex, Salix, Populus*	2010	52.0962	36.0658	204 m
15	56	Lake shore used by geese	Surrounding: *Artemisia*, Apiaceae, Fabaceae, *Convolvulus*, Asteraceae, Poaceae, *Rumex, Salix, Populus*	2010	52.096222	36.065778	203 m
16	79	Grassland on slope	*Galium verum, Achillea millefolium, Cichorium*, Fabaceae, *Hypericum, Convolvulus arvensis*, Asteraceae, Lamiaceae, *Agrimonia eupatoria, Poa, Artemisia, Salix*, Apiaceae	2009	51.9040865	35.63926	201 m
17	80	Grassland on slope	*Achillea millefolium*, Asteraceae, *Trifolium, Antennaria dioica*, Cichorioideae, Apiaceae, Fabaceae, *Equisetum, Poa, Betula, Salix*	2009	51.9040543	35.6399	205 m
18	77	Wetland of Razdolye (coring site)	*Equisetum, Epilobium, Urtica dioica*	2009	51.9038665	35.63899	199 m
19	77	Wetland of Razdolye	*Urtica dioica, Typha, Lythrum salicaria*, Apiaceae	2009	51.9038665	35.63899	199 m
20	69	Grassland slope at Nikolaevka wetland	*Cirsium, Urtica,* Lamiaceae*, Galium*, Poaceae, *Achillea*	2010	51.8564	35.6645	179 m

21	68	Wetland of Nikolaevka (coring site)	*Lemna*, Cyperaceae, *Achillea, Chamaenerion angustifolium, Bidens, Cirsium*, Apiaceae, Cyperaceae, *Typha, Salix,* Poaceae, Apiaceae, Asteraceae, *Betula, Rumex*	2010	51.8563	35.6651	179 m
22	70	Grassland slope at Nikolaevka wetland	Poaceae, Apiaceae, Asteraceae, Campanula, Galium, Plantago lanceolata, Fabaceae	2010	51.8560	35.6647	177 m
23	64	Wetland of Peny Usadba (coring site)	*Alisma*, Apiaceae, *Typha, Lythrum salicaria*	2010	51.6047	35.4538	149 m
24	71	Wetland of Peny Usadba	*Alisma*, *Sium*, *Typha, Lythrum salicaria*	2009	51.6046608	35.45381	151 m
25	71	Wetland of Peny Usadba	*Phragmites, Urtica dioica, Lycopus europaeus*, Apiaceae	2009	51.6046608	35.45381	151 m
26	72	Hollow with *Robinia*	*Robinia pseudoacacia, Acer tatarica, Salix*, Apiaceae, *Lamium, Atriplex/Chenopodium*, Poaceae, *Galium aparine, Centaurea cyanus*	2009	51.6032392	35.46033	151 m
27	73	*Triticum* field	*Convolvulus arvensis, Centaurea cyanus, Silene latifolia*, Brassicaceae, Cichorioideae, *Viola arvensis, Chenopodium, Cirsium*	2009	51.602574	35.45956	152 m
28	81	Ruderal vegetation in a village	*Polygonum aviculare, Plantago major, Arctium*, Apiaceae, *Achillea millefolium*, Brassicacea, *Convolvulus arvensis, Populus, Malus*, potato fields	2009	51.6000795	35.43324	157 m
29	82	Ruderal vegetation in a small garden	*Artemisia, Cirsium*, Apiaceae, *Achillea millefolium, Convolvulus arvensis*, Fabaceae, *Delphinium, Urtica dioica, Populus*	2009	51.5995002	35.43123	160 m
30	74	Grassland on a slope, oxbow wetland	*Centaurea scabiosa*, Apiaceae, *Agrimonia eupatoria, Echinops, Galium verum, Potentilla, Fragaria viridis,*	2009	51.5973437	35.45938	156 m

			Daucus carota, Cichorium, Salvia, Scabiosa, Artemisia, Euphorbia, Achillea millefolium				
31	75	Grassland on a slope, oxbow wetland	Poaceae, *Artemisia*, Apiaceae, *Cirsium arvense, Galium verum*, Apiaceae, *Daucus carota*, *Alopecurus pratensis, Agrimonia eupatoria, Centaurea scabiosa, Equisetum, Rumex, Euphorbia*	2009	51.5972739	35.45897	153 m
32	61	Oak forest, planted *	*Quercus robur, Acer platanoides, Prunus padus, Pyrus, Malus, Ulmus*	2009	51.5969735	36.16561	230 m
33	61.2	Oak forest, planted *	*Quercus robur, Sambucus nigra, Malus sylvatica, Urtica dioica, Salvia, Crataegus, Acer campestre, Acer tataricum, Acer platanoides*	2009	51.5969735	36.16561	230 m
34	59	Wetland of Peny (coring site)	*Phragmites, Lythrum salicaria, Filipendula, Lycopus europaeus, Salix*	2009	51.5968126	35.45876	151 m
35	58	Wetland of Peny (coring site)	*Phragmites, Lythrum salicaria, Filipendula, Lycopus europaeus, Salix*	2009	51.5966946	35.45877	152 m
36	76	*Triticum* field	*Triticum* (*Avena* and *Secale* from previous year), *Equisetum, Cirsium, Solanum dulcamara, Acer*	2009	51.5937334	35.45953	157 m
37	83	*Alnus* forest	*Alnus, Acer tatarica, Humulus, Urtica, Equisetum, Geum*	2009	51.5931004	35.4639	151 m
38	60	Mown steppe *	*Adonis vernalis, Knautia arvensis, Salvia pratense, Centaurea scabiosa, Festuca sulcata, Stipa pennata, Bromus riparius, Festuca pratensis, Convolvulus arvensis, Thymus, Filipendula vulgaris, Alchemilla millefolium, Ranunculus* sp., *Fragaria viridis, Pulsatilla* sp., *Campanula* sp., *Melampyrum cristatum, Potentilla argentea, Galium verum, Galium boreale, Trifolium* sp., *Carex humilis, Viola hirta, Viola rupestis*	2009	51.5818995	36.1443	250 m

39	60.2	Mown steppe *	*Adonis vernalis, Salvia pratense, Centaurea scabiosa, Stippa pennata, Festuca pratensis, Convolvulus arvensis, Thymus, Filipendula vulgaris, Alchemilla millefolium, Ranunculus* sp., *Fragaria viridis, Pulsatilla, Campanula, Melampyrum cristatum, Potentilla, Galium verum, Galium boreale, Trifolium, Carex humilis*	2009	51.5818995	36.1443	250 m
40	62	Steppe with annual mowing *	*Carex humilis, Thymus, Festuca, Plantago lanceolata, Adonis, Iris, Phlomis tuberosa, Pulsatilla patula, Centaurea jacea, Centaurea scabiosa, Cerastium, Polygonatum officinale*	2009	51.5807354	36.1347	249 m
41	62	Steppe with annual mowing *	*Carex humilis, Thymus, Festuca, Plantago lanceolata, Adonis, Iris, Phlomis tuberosa, Pulsatilla patula, Centaurea jacea, Centaurea scabiosa, Cerastium, Polygonatum officinale*	2009	51.5807354	36.1347	249 m
42	63	Steppe without mowing since 1934 *	*Prunus spinosa, Ulmus, Malus, Pyrus, Lavanthera, Cirsium arvense, Acer negundo, Acer platanoides, Lonicera tatarica, Inula hirta, Hypericum, Galium boreale, Polygonatum officinale, Bromus inermis, Agropyrum, Convolvulus arvensis, Veratrum nigrum, Serratula inermis, Delphinium, Vicia, Falcaria vulgaris, Euphorbia semivillosa, Stipa pennata, Agrimonia, Serratula heterophylla, Arrhenatherum, Sedum purpureum, Polygonatum, Peucedanum, Phleum pratense*	2009	51.5775758	36.13103	258 m
43	63.2	Steppe without mowing since 1934 *	*Prunus spinosa, Ulmus, Malus, Pyrus, Lavanthera, Cirsium arvense, Acer negundo, Acer platanoides, Lonicera tatarica, Inula hirta, Hypericum, Galium boreale, Polygonatum officinale, Bromus inermis, Agropyrum, Convolvulus arvensis, Veratrum nigrum, Serratula inermis, Delphinium, Vicia, Falcaria vulgaris,*	2009	51.5775758	36.13103	258 m

			Euphorbia semivillosa, Stipa pennata, Agrimonia, Serratula heterophylla, Arrhenatherum, Sedum purpureum, Polygonatum, Peucedanum, Phleum pratense				
44	63	Steppe without mowing since 1934 *	*Prunus spinosa, Ulmus, Malus, Pyrus, Lavanthera, Cirsium arvense, Acer negundo, Acer platanoides, Lonicera tatarica, Inula hirta, Hypericum, Galium boreale, Polygonatum officinale, Bromus inermis, Agropyrum, Convolvulus arvensis, Veratrum nigrum, Serratula inermis, Delphinium, Vicia, Falcaria vulgaris, Euphorbia semivillosa, Stipa pennata, Agrimonia, Serratula heterophylla, Arrhenatherum, Sedum purpureum, Polygonatum, Peucedanum, Phleum pratense*	2009	51.5775758	36.13103	258 m
45	64	Cow pasture *	*Adonis vernalis, Festuca pratensis, Festuca* sp., *Stipa*	2009	51.5750599	36.09117	250 m
46	64	Cow pasture *	*Adonis vernalis, Festuca pratensis, Festuca* sp., *Stipa*	2009	51.5750599	36.09117	250 m
47	64	Cow pasture *	*Adonis vernalis, Festuca pratensis, Festuca* sp., *Stipa*	2009	51.5750599	36.09117	250 m
48	109	Wetland of Zamostye (coring site)	*Phragmites, Salix, Acer, Alnus*, Poaceae; nearby pasture meadow: *Triglochin maritima, Taraxacum officinalis*, Poaceae; in water: *Lemna trisulca*	2013	51.184808	35.27988	135 m
49	110	Steppe on slope **	*Stipa*, Fabaceae, Euphorbiaceae, Solanaceae, *Centaurea*, *Anemone*, Poaceae, *Cirsium*, *Asparagus*, *Thalictrum*, *Potentilla*, Lamiaceae, *Artemisia*, *Adonis*, *Alchemilla*, *Trifolium*, *Silene*, *Polygala comosa*, *Prunus*, *Crataegus*, *Quercus*, *Malus*	2013	51.147772	35.24766	168 m
50	70	Wetland of Sudzha (coring site)	*Phragmites communis, Rumex, Solanum dulcamara, Salix, Urtica dioica, Cirsium, Rubus, Cuscuta*	2009	51.137479	35.28813	133 m
51	70.2	Wetland of Sudzha	*Phragmites communis, Rumex, Solanum dulcamara, Salix, Urtica dioica, Cirsium, Rubus, Cuscuta*	2009	51.137479	35.28813	133 m

52	68	Wetland of Kurilovka (coring site)	*Typha, Glyceria, Lythrum salicaria, Mentha aquatica*, Apiaceae, *Rumex*	2009	51.1364651	35.27698	135 m
53	69	*Acer platanoides-Fraxinus excelsior* forest	*Acer platanoides, Fraxinus excelsior, Quercus robur, Populus tremula, Asarum europaeum, Aegopodium podagraria, Polygonatum, Stellaria, Glechoma hederifolia, Mercurialis perennis,* Poaceae	2009	51.136331	35.22584	228 m
54	69.1	*Acer platanoides-Fraxinus excelsior* forest	*Acer platanoides, Fraxinus excelsior, Quercus robur, Populus tremula, Asarum europaeum, Aegopodium podagraria, Polygonatum, Stellaria, Glechoma hederifolia, Mercurialis perennis,* Poaceae	2009	51.136331	35.22584	228 m
55	69.2	*Acer platanoides-Fraxinus excelsior* forest	*Acer platanoides, Fraxinus excelsior, Quercus robur, Populus tremula, Asarum europaeum, Aegopodium podagraria, Polygonatum, Stellaria, Glechoma hederifolia, Mercurialis perennis,* Poaceae	2009	51.136331	35.22584	228 m
56	505	*Sphagnum* peatbog of Klukvennoe (coring site)	*Sphagnum, Pinus sylvestris, Betula alba, Eriophorum vaginatum, Vaccinium oxycoccos, Carex, Equisetum, Comarum palustre, Menyanthes trifoliata, Alnus, Frangula, Sambucus, Hypericum perforatum, Achillea, Poa, Matricaria*	2016	51.119183	35.461842	148 m
57	514	*Sphagnum* peatbog of Klukvennoe	*Sphagnum, Equisetum, Menyanthes trifoliata, Betula, Alnus, Salix*	2016	51.117963	35.464117	145 m
58	89	*Alnus* carr of Mzha 2 (coring site)	*Alnus, Lonicera, Prunus, Urtica,* Brassicaceae, *Galium rivale, Ficaria verna, Caltha palustris, Heracleum, Sambucus, Ulmus, Salix,* Apiaceae, Cyperaceae, *Filipendula, Humulus lupulis, Typha, Malus*	2013	49.822968	35.66144	120 m
59	104	*Pinus* forest	*Pinus sylvestris, Sorbus aucuparia, Acer tataricum, Quercus robur, Tilia, Fraxinus excelsior, Ulmus,* Poaceae, *Chelidonium, Geranium,* Euphorbiaceae,	2013	49.640024	36.36214	113 m

			Taraxacum officinalis, Fabaceae*, Polygonatum odoratum*				
60	101	Wetland of Omelchenki (coring site)	Poaceae, *Carex, Typha latifolia, Salix, Veronica, Equisetum*	2013	49.639693	36.41677	88 m

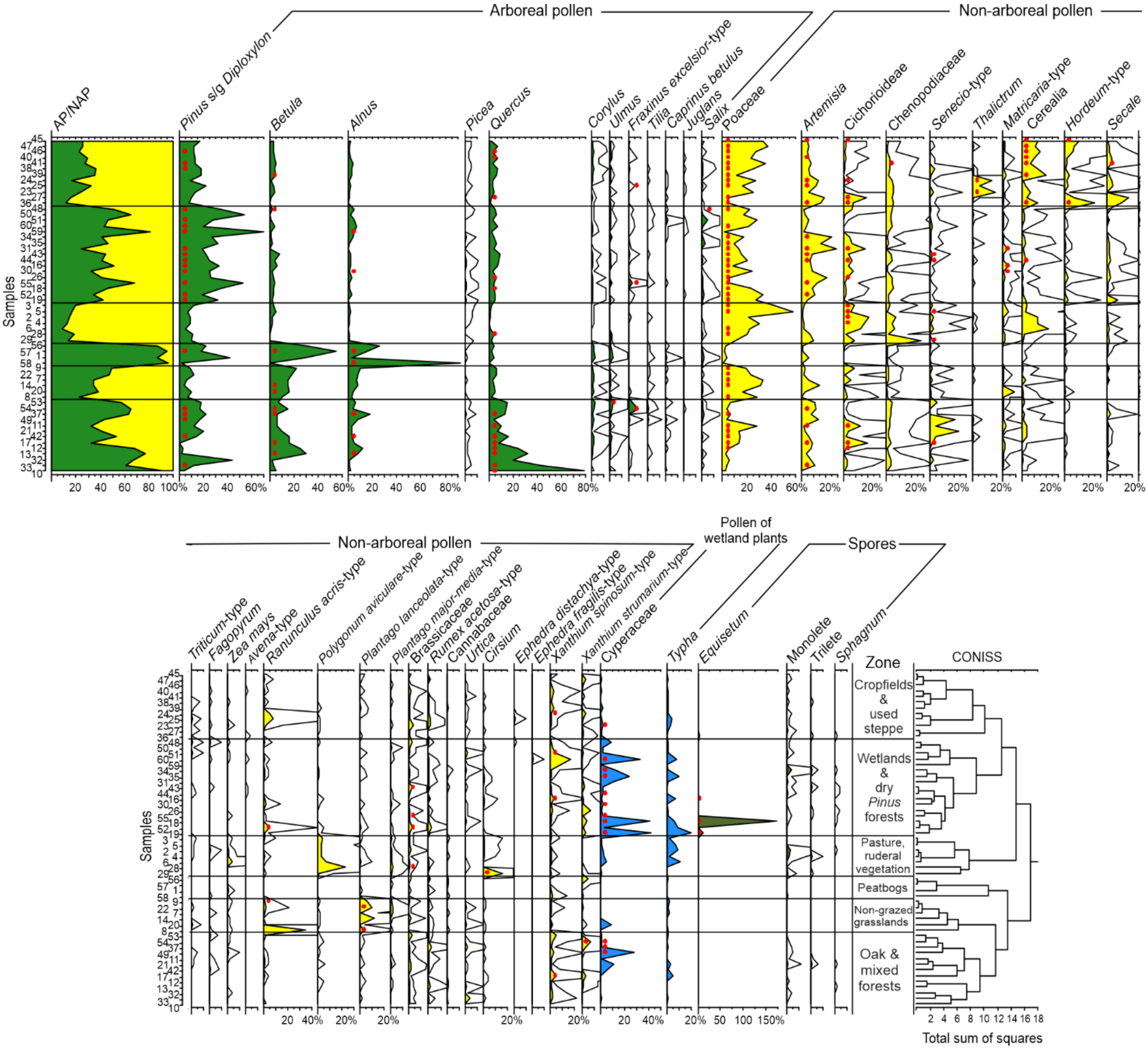

Fig. 5.5. Pollen diagram of the surface pollen samples of the East-European forest-steppe grouped by the unconstrained CONISS (Grimm 1987) into pollen zones named according to the vegetation on site. The presence of pollen clumps is marked with the red dots

We classify the samples in the following six groups based on the unconstrained cluster analysis results (Fig. 5.2): Cropfields & used steppe; Wetlands & dry *Pinus* forests; Pasture & ruderal vegetation; Peatbogs; Non-grazed grasslands; Oak & mixed forests.

Cropfields & used steppe group includes the samples from the Streletskaya steppe sites of the Central Black Soil Nature Reserve where openness is supported by mowing and grazing, *Triticum* fields, and wetlands surrounded by *Secale* and *Hordeum* fields. AP varies within 11-37%. Among NAP the dominant taxa include Poaceae (4-35%), *Artemisia* (5-19%), Cichorioideae (up to 19%), *Thalictrum* (up to 19%) and Chenopodiaceae (1-7%). Pollen of crops and ruderal taxa is in abundance indicating strong anthropogenic pressure on the territory. Pollen of the crops include Cerealia-type (1-20%), *Hordeum*-type (up to 25%), *Secale* (up to 18%), *Triticum*-type (up to 1%), *Fagopyrum* (0.2%), *Avena*-type (up to 0.4%) and *Zea mays* (up to 0.6%). Among the ruderal taxa *Ranunculus acris*-type (up to 7%), Brassicaceae (up to 4%), *Rumex acetosa*-type (up to 1%), *Xanthium spinosum* (up to 3%) and *X. strumarium*-types (up to 4%) dominate.

Wetlands & dry *Pinus* forests group includes the samples from wetlands incl. the coring sites of Zamostye, Sudzha, Omelchenki and Razdolye, surrounding grasslands, hollows, unmown since 1934 sites of the Streletskaya steppe of the Central Black Soil Nature Reserve, and two forest samples from pine and *Acer-Fraxinus* forests. AP of the zone varies within 24-81%. The dominant tree taxon is *Pinus* s/g *Diploxylon*-type (19-69%). Among NAP, Poaceae (2-34%), *Artemisia* (2-29%) and Cichorioideae (up to 18%) predominate. Crops’ and ruderal plants’ pollen also occur but in considerably lesser amount. However, in a few samples, the most abundant crop taxa of Cerealia, *Hordeum*-type and *Secale* reach 4%, 3% and 9% respectively, ruderal *Xanthium spinosum* and *X. strumarium*-types – 16% and 8%. This zone is characterized by high values of wetland taxa Cyperaceae (up to 42%), *Typha* (up to 20%) and *Equisetum* (up to 12%).

Pasture & ruderal vegetation group has the lowest AP values of 8-20% among the spectra. It contains the samples from the lakes’ surroundings and meadows used for grazing, and the samples from a village. Poaceae (10-59%), Cichorioideae (2-21%), Chenopodiaceae (1-28%), *Artemisia* (1-10%), Cerealia-type (1-22%), *Polygonum aviculare*-type (1-23%) and *Cirsium* (up to 16%) dominate. This zone has the highest values of ruderal taxa among the studied surface samples.

Peatbogs group includes the samples from forested *Sphagnum* peatbogs, an alder carr and the northernmost sample from a *Pinus-Acer-Ulmus* forest. AP values are within 87-96%. Dominant tree taxa are *Alnus* (3-92%), *Betula* (up to 55%) and *Pinus* (2-42%). This zone contains the least amount of ruderal and crop taxa.

The group of Non-grazed grasslands contains the samples from grasslands which have not been used for grazing in the recent time but are mostly surrounded by cropfields. AP values are within 23-49%. Poaceae (15-34%) dominate the taxa, followed by *Artemisia* (1-7%), Cichorioideae (1-9%) and Chenopodiaceae (up to 1%). Tree pollen is mostly represented by *Betula* (10-23%), *Alnus* (3-10%), *Pinus* (6-12%) and *Quercus* (2-6%). Ruderal *Ranunculus acris*-type and *Plantago lanceolata*-type reach 35% and 12%.

Oak & mixed forests group includes the pollen samples from oak stands and open areas around, *Alnus* and *Acer-Fraxinus* mixed forests, and unmown sites from the Streletskaya and Kurilovka steppes of the Central Black Soil Nature Reserve. AP varies within 32-91%. Among the tree pollen, *Betula* (2-31%), *Quercus* (4-79%), *Pinus* (up to 44%) and *Alnus* (1-18%) dominate. Among NAP, Poaceae (2-28%), *Artemisia* (1-12%), Cichorioideae (up to 20%), Chenopodiaceae (up to 5%) and *Senecio*-type (up to 22%) are abundant.

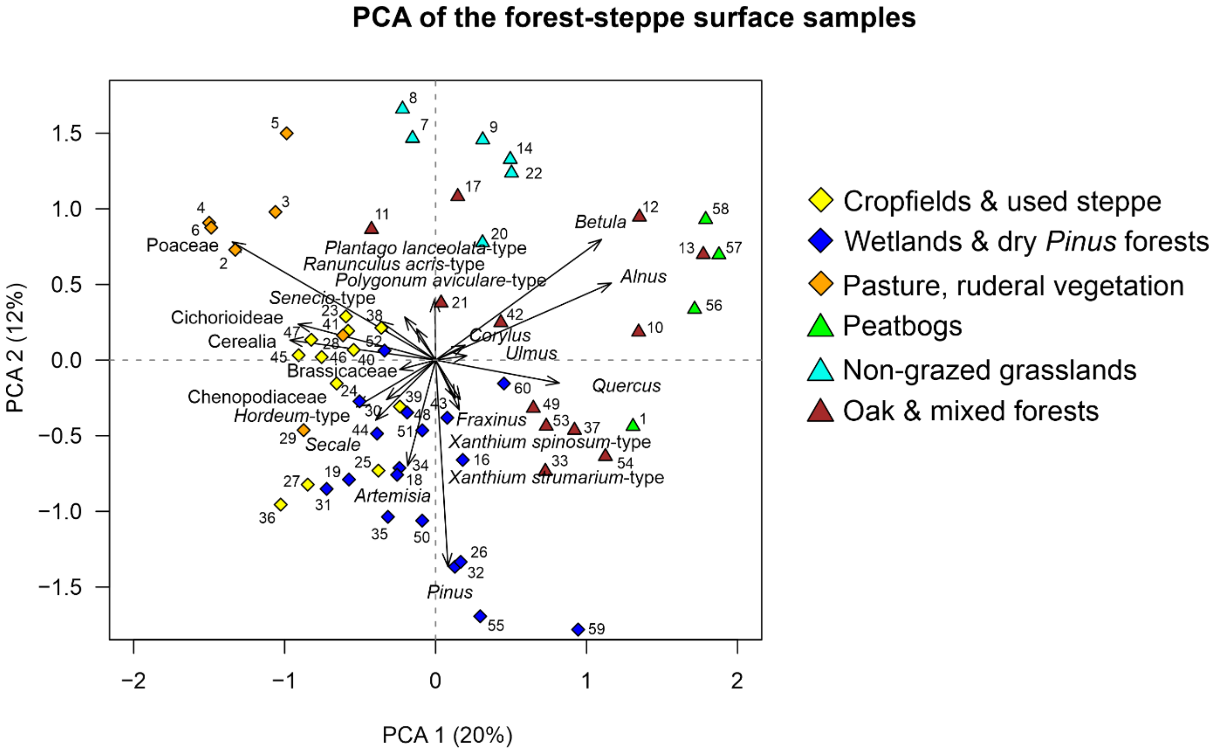

Fig. 5.3. PCA of the pollen spectra of surface samples from the East-European forest-steppe

The first axis of the PCA of the surface samples (Fig. 5.3) explains 20% of the variance and shows anthropogenically actively used sites from the Cropfields & used steppe and Pasture & ruderal vegetation pollen zones in the left-most part of the graph while forested Peatbogs and Oak & mixed forests sites are located to the right. Along the second axis, local moisture conditions seem to be reflected. Samples from dryer open areas, steppe and grasslands are in the upper part, while the samples from hollows, overgrown steppe sites from Central Black Soil Nature Reserve, wetlands and open forests are in the lower part of the graph.

Interpretation and discussion

Reflection of the vegetation in the spectra

The forests of the East-European forest-steppe vary in the dominant tree taxa. According to the description of potential natural vegetation of the East-European forest-steppe (Donita et al. 2004), the ecotone is characterized by a substantial proportion of deciduous broadleaf forests dominated mainly by oak *Quercus robur*. This is also reflected in the surface samples pollen diagram presented on the Fig. 5.2. Oak pollen is abundant in the "near-natural" pollen spectra, especially in oak and mixed forests. AP values in these samples range within 57-91% with the pollen of *Quercus* reaching 79% for oak stands and 5-15% for mixed forests. Pine dominates mainly among the samples of the Wetland & dry pine forests group. AP values in pine forests reach 81-87% with the pine pollen being within 42-69%. *Alnus* dominates alder forests and carrs (AP 63-96%), and is joined by *Betula* and *Pinus* in peatbogs (AP 86-95%).

The mosaic of vegetation of the forest-steppe is reflected in the pollen spectra well with the AP values ranging from 8% in pastures to 95-96% in peatbogs and carrs. The least amount of pollen of trees (≤20%) occurred in pastures, agricultural fields and in the settlements (samples # 28 and 29 taken in a village). The surrounding landscape at the sites was open represented by non-arboreal taxa (Table 5.2). The sites with the AP values between 20 and 37% are mostly occupied by grasslands and wetlands without intensive grazing surrounded by fields, and the sites of the Central Black Soil Nature Reserve areas where the openness is supported by annual mowing and grazing (Filatova 2012-2022).

Thus, the sites with the low amount of arboreal pollen belong to the pollen zones of Cropfields & used steppe; Pasture & ruderal vegetation and some sites of the Non-grazed grasslands (#7, 8, 9 and 14 surrounded by cropfields) representing anthropogenically changed landscapes. These samples display the highest amount of pollen of crops (30-49% on the fields, and up to 25-26% on the artificially maintained steppe sites of the reservation areas) and ruderal markers (up to 26-39% in the village and grasslands), and should not be considered reflecting natural vegetation of the East-European forest-steppe and used as modern analogues for quantitative climate reconstructions (Juggins 2013).

The rest of the samples including the open vegetation samples from non-grazed grasslands (# 20 and 22) and the steppe sites from the groups of Wetlands & dry *Pinus* forests and Oak & mixed forests could potentially be considered “near-natural” although some of them are in the vicinity of anthropogenic landscapes. These samples also display agricultural and ruderal disturbance but in considerably smaller amount. The minimum AP values for such sites do not go under 33-34% for the most open sites. We conclude that the use of surface samples from the East-European forest-steppe in the training set for pollen-climate reconstructions with the AP values smaller then 33-34% is undesirable.

The variation in “near-natural” spectra from the groups of Wetlands & dry *Pinus* forests, Peatbogs, Non-grazed grasslands and Oak & mixed forests is reflected along the y axis (Fig. 5.3) and can be explained by the local conditions on site (Erdős et al. 2019). Thus, the samples located in more humid areas with better hydrological conditions e.g. in river basins or at lower elevations (Table 5.2) reflect forested vegetation with higher AP values in the lower part of the graph, while its upper part reflects the samples from more arid locations at higher altitudes supporting more open vegetation with lower AP.

The problems of pollen records interpretation

Due to the semi-arid climate, there are few archives like lakes and mires in the forest-steppe, and the sediments cores of the East-European forest-steppe are often taken from wetlands (Borisova et al. 2006; Kasianova et al. 2023; Lukanina et al. 2022; 2023; Panin et al. 2017; Shumilovskikh et al. 2019). The majority of these pollen records reflect the dominance of pine forests throughout the Holocene, while open areas of the forest-steppe are underrepresented. Thus, the records of Zamostye, Omelchenki, Peny and Razdolye (Kasianova et al. 2023; Lukanina et al. 2022; 2023) show the dominance of *Pinus sylvestris* pollen among the AP giving the impression of prevalence of pine forests in the region. Pollen spectra of surface samples from wetlands are grouping together and characterized by a high amount of pine pollen (19-69%), originating from trees growing close to the sites. Therefore, the pollen records from mires are biased by their location and they do not reflect the full picture of the ecotone landscapes., This finding highlight the importance of a careful choice of the archives and interpretation of the vegetation. When reconstructing the dynamics of the treeline in East-European forest-steppe, pollen records from watersheds would potentially give a better insight into the dynamics of the forests.

Use of the surface samples for quantitative reconstructions

The main variability in the spectra from the East-European forest-steppe concerns forested and open areas connected to the land use. The pattern in the modern pollen spectra is poorly related to the latitudinal gradient (Fig. 5.2) and therefore does not reflect the ecological gradient despite a comparably large study area of over 200 km. Thus, the training set on its own cannot be used for transfer function pollen-climate reconstructions requiring a long ecological gradient (>3 SD units) such as WA and WAPLS (Braak and Juggins 1993; Braak and van Dame 1989; Juggins 2013).

Compare to the pollen training sets from the forest-steppes further east (Wang et al. 2022; Zhang et al. 2010; Zhao et al. 2012) and in North America (Minckley et al. 2008), where the transition from grasslands to wooded vegetation is explained mainly by climatic factors, the scale of the anthropogenic impact in East-European forest-steppe is too high for the spectra to reflect latitudinal patterns. Despite a comparably large study area of over 200 km and collection mainly from near-natural environments the pollen spectra reflect land-use rather than climate. Therefore, the “near-natural” samples of the current study could potentially be used for climate reconstructions only when combined with other surface samples from the neighboring vegetation zones.

Conclusions

The mosaic of vegetation of the forest-steppe is reflected in the pollen spectra well with the AP values ranging from 8% in pastures to 96% in peatbogs and carrs. The variability in the surface pollen spectra concerns forested and open areas, the distribution of which is connected firstly to the land use and secondly to the local conditions on site, rather than to the latitudinal gradient. Therefore, it does not reflect the climatic gradient despite a comparably large study area of over 200 km. The minimum AP values for the sites with “near-natural” vegetation of the ecotone should not be less than 33%.

The majority of the pollen records from the East-European forest-steppe reflect the dominance of pine forests throughout the Holocene. However, it does not reflect the full picture of the ecotone landscapes as the majority of the palynological archives are located in wetlands of the oxbow lakes and rivers where pine dominates. Therefore, it is important to be careful with the interpretation of the pollen records as they are biased by the local conditions. Pollen records from watersheds would potentially give a better insight into the dynamics of the forests.

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Statements and Declarations

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Chapter VI – Manuscript 5

Climate dynamics in the East-European forest-steppe since the Late Glacial

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In prep.

Abstract

Climate is a key element defining the existence of forest-steppes. In the present study, we provide the forest cover and climate reconstructions for the East-European forest-steppe ecotone over the last 14,800 years based on the modern analogue technique and weighted averaging partial least squares regression. For this, we use six pollen records obtained along the latitudinal gradient of the ecotone from the Kursk region in Russia and Kharkiv region in Ukraine. During the stadial periods of Late Glacial the ecotone was represented by steppe with semi-arid climate conditions (aridity index of ~0.4-0.5 and mean annual precipitation of ~300-350 mm/year). During the periods of warming forest-steppe was spreading along the rivers. The climate was semi-arid to dry sub-humid (aridity index of 0.4-0.6), possibly humid in river valleys with better hydrological conditions (aridity index up to 0.7). Throughout the Holocene the aridity index values and annual precipitation were rising from semi-arid (~0.35-0.4) with ~300mm/yr in the beginning to the humid values of up to 0.66-0.67 by 4.2 cal. kyr BP with the increase of precipitation from ~400 mm/yr to the modern values of ~600 mm/yr indicating the shift of the southern treeline southwards. The late Holocene forest-steppe dynamics is inextricably linked with the human activities in the region. During the periods of decreasing anthropogenic pressure the forest cover estimates reached the highest values in the late Holocene – up to 40-41% for the central part of the ecotone including the watersheds and the river valleys of the southern limits of the ecotone indicating that these areas could potentially be much more forested. The reconstructed aridity index for the late Holocene indicated humid climate conditions within the range of 0.65 to 0.8.

Introduction

East-European forest-steppe is one of the most complex extra-tropical ecosystems with an exceptionally high biodiversity (Donita et al. 2004; Erdős et al. 2018; Walter and Breckle 1994). Located at the junction of two contrasting vegetation zones – nemoral broadleaf forests and steppes, – it combines heterogenous communities creating an extraordinary variety of environmental conditions contributing to the qualitative saturation of the cenoses (Chernov 1975; Neronov 2015). Thus, the Central Black Soil Nature Reserve near Kursk noted 1287 species of vascular plants by the end of 2010 (Zolotukhin and Zolotukhina 2012-2023). Its meadow steppes rank amongst the most species-rich communities found anywhere (Donita et al. 2004) reaching 87 vascular plant species per m^2. Due to the presence of fertile chernozem soils, up to 80-85% of its territory was used as cropland by the year 2000 (Donita et al. 2004; Ramankutty et al. 2008). Considering the risks of the ecosystem loss due to the extensive use for agriculture and the ongoing climate warming, the knowledge of the history of the ecotone formation and the climate corresponding to the past vegetation changes may provide guidelines for future nature conservation attempts.

Climate is a key element defining the existence of forest-steppes (Erdős et al. 2018; Walter and Breckle 1994). In the temperate zone, humid environments support forests while grasslands occupy more arid areas (Dengler et al. 2014). Transitional nature of the East-European forest-steppe ecotone (from semi-humid to semi-arid climate conditions) allows the coexistence the forest and steppe components and their distribution is defined by relief, microclimate and soil composition (Donita et al. 2004). Forests occur in valleys, gorges, hollows, on the northern slopes, hills and mountain tops while steppes occupy warm and dry southern slopes, plateaus with clay and silt-rich soils.

Past climate can be traced from vegetation changes which in their turn can be reconstructed from fossil pollen data (Birks and Birks 2005). Recently, several studies on the past vegetation dynamics of the East-European forest-steppe ecotone have been conducted (Feurdean et al. 2015; 2021; Hájková et al. 2022; Kasianova et al. submitted; Kremenetski 1995; Lukanina et al. 2022; 2023; Novenko et al. 2009; 2014a; Shumilovskikh et al. 2018; 2019a; 2021a). Pine and pine-birch forest-steppe was spread here already during the interstadials of the Late Glacial (Borisova et al. 2006; Hájková et al. 2022; Lukanina et al. 2022). Sensitive to the north Atlantic climate change (Lukanina et al. 2022), the area was represented by dry steppe during the stadial periods. The region became ecotone in the beginning of the Holocene when the rise in temperatures and the retrieval of the glacier allowed forests to spread over the East-European Plain (Novenko 2016).

As an ecotone, the forest-steppe was a dynamic system also throughout the Holocene but due to the size of the region (over 2000 km), the climate and the corresponding vegetation changes varied in its western and eastern parts. Mixed pine-broadleaf forests developed in the west with the beginning of the Holocene (Hájková et al. 2022) turning to broadleaf forests by ~8 cal. kyr BP. More continental eastern part remained mostly treeless before ~10 cal. kyr BP developing a forest component significantly later (Lukanina et al. 2022; 2023). There are, however, similarities in the trends of the vegetation dynamics. Thus, the maximum of forest expansion occurred in the second half of the Holocene throughout the region (Hájková et al. 2022; Lukanina et al. 2022; 2023; Marinova and Atanassova 2006; Shumilovskikh et al. 2018) implying some underlying climate changes.

There have been several attempts to reconstruct the Late Glacial and Holocene climate dynamics on the European scale and more locally for individual regions based on the changes in vegetation (Bartlein et al. 2011; Davis et al. 2003; Mauri et al. 2015; Seppä et al. 2009; Velichko et al. 2002). Continental-scale reconstructions, however, focus on a broader scale and usually do not consider local differences especially if just few records per region are available (Mauri et al. 2015). Regional reconstructions in such cases can provide more reliable data. Due to the lack of well-dated pollen data covering the Late Glacial and Holocene previously, it was not possible to provide robust pollen-climate reconstructions for the continental part of the East-European forest-steppe.

It is also worth mentioning that the East-European forest-steppe ecotone experienced a heavy human impact since the Bronze Age (Lukanina et al. 2023). By today there is almost no natural vegetation remaining but a few semi-natural plots of Nature Reserves (Bartalev et al. 2011; Donita et al. 2004; Ramankutty et al. 2008). The absence of recent pollen spectra reflecting natural vegetation of the study region is an additional complication affecting the reconstructions. However, in the present study we attempt to provide reliable pollen-climate reconstructions for the continental part of the East-European forest-steppe since the Late Glacial.

Study area

Located in the southern part of the Mid-Russian Upland, the study area belongs to the Dnieper and Don river basins between the Kursk (Russia) and Kharkiv (Ukraine) regions. The landscapes represent undulating plateaus at an altitude of ~200-250 m above sea level dissected by river valleys. Parental rock for the soils are mainly loess sediments on which fertile chernozem soils have formed (Sycheva 2012; Velichko 2009).

The climate of the forest-steppe has a transitional position between the temperate and semi-arid climate of steppe (Donita et al. 2004). The annual precipitation is within 400-600 mm. Mean annual temperature is 5-6 °C with average January temperatures of -6 – -7 °C and average July temperatures of 19-20 °C (Fick and Hijmans 2017). A dry period of at least two months during late summer – early autumn does not permit the development of closed forests on a large scale (Donita et al. 2004). Thus, water supply, especially in the summer months is a limiting factor for the forest growth decisive for forest and steppe distribution together with a soil structure.

Potential natural vegetation represents a mosaic of forest patches and meadow steppes. In the mixed oak (*Quercus robur*) forests, some Central European species (*Acer plantanoides, Fraxinus excelsior, Corylus avellana, Tilia cordata*) occur (Bohn et al. 2004; Shahgedanova 2003). Pine and oak-pine forests (*Pinus sylvestris, Quercus robur*) are found on sandy soils together with *Prunus fruticosa, Genista tinctoria, Filipendula*. Hardwood alluvial forests (*Quercus robur, Ulmus laevis*) in combination with poplar and willow (*Populus nigra, Salix alba*) are typical for moist and wet sites (Bohn et al. 2004). The study area represents the eastern border of the *Carpinus betulus* areal and the southern border of *Picea abies* (Zerov 1950). The meadow steppes are dominated by *Stipa tirsa, S. pennata, Carex humilis, C. praecox, Filipendula vulgaris, Trifolium montanum, Onobrychis arenaria, Rhinanthus alectorolophus, Bunias orientalis, Bromus riparius, Festuca rupicola, Poa angustifolia* (Bohn et al. 2004).

Materials and Methods

Fossil pollen data

For the climate reconstructions, we used six sediment cores taken along the latitudinal gradient of the ecotone from three key sites – northern (N), central (C) and southern (S) (Fig. 6.1, Table 6.1) during the expeditions in 2009-2016. Peny peat core (Kasianova et al. submitted) of the northern key site was taken from a wetland covered by *Phragmitis australis*, *Salix* sp., *Artemisia vulgaris* and Cyperaceae located in the bed of the temporary Penka river, which is flooded during high melting water discharge in spring (Radyush 2010). Another northern coring site of Razdolye (Kasianova et al. submitted) represents a temporarily flooded depression ~40 km north of the Seim River overgrown by *Equisetum* sp., *Typha* sp., *Lythrum salicaria*, *Carex* sp. and Apiaceae. Three sediment cores (Zamostye, Klukvennoe and Sudzha) belong to the central key site. Zamostye and Sudzha cores originate from overgrown oxbow lakes near the Sudzha river (Lukanina et al. 2022; Shumilovskikh et al. 2019a). Klukvennoe core was obtained from a partially overgrown Klukvennoe lake located in a subrosion depression of a plateau. Omelchenki core from the southern key site was taken from a peatland near the Siverskyi Donets River (Lukanina et al. 2023).

The cores were radiocarbon-dated and studied for pollen. The radiocarbon ages were calibrated and the age-depth model was built using the R package 'bacon' based on Bayesian statistics (Blaauw and Christen 2011) and the package 'clam 2.3.8' (Blaauw 2010; Blaauw et al. 2021) with the IntCal20 calibration curve for Northern Hemisphere (Reimer et al. 2020). Zamostye and Klukvennoe cores cover the last 14,600-14,800 years. Omelchenki pollen record spans over the last 9,300 years. The cores of Sudzha, Peny and Razdolye have an age of 2,800, 1,100 and 200 cal. yrs BP respectively. Since the Razdolye core covers only the last 200 years when the area has already been anthropogenically changed (Kasianova et al. submitted), it has been excluded from the climate reconstructions. However, we use it to compare palaeo and modern vegetation of the region.

The percentages of pollen were calculated relative to the pollen sum of terrestrial plants excluding Cyperaceae and aquatics. Cyperaceae was excluded due to its local presence indicated by the pollen and macroremain records of the cores (Kasianova et al. submitted; Lukanina et al. 2022; 2023; Shumilovskikh et al. 2019a). The summary curve for broadleaf trees in Fig. 5.7 includes pollen of *Quercus, Tilia, Ulmus, Fraxinus, Corylus, Carpinus betulus* and *Acer*. Anthropogenic indicators' curve from the same diagram (Fig. 5.7) represents a group of land-use indicator pollen types following Behre (1981) and consists of taxa indicating arable land (Cerealia, *Triticum*-type, *Hordeum*-type, *Avena*-type, *Fagopyrum*, *Secale*), and ruderal communities (Brassicaceae, *Ranunculus acris*-type, Cannabaceae, *Urtica*, *Plantago major-media*-type, *P. lanceaolata*-type, *Polygonum aviculare*-type and *Rumex acetosa*-type). Principal component analysis (PCA) of the cores' pollen records was used to explore the variation in the pollen data to identify possible main climatic drivers in the fossil pollen spectra. We used R package 'vegan' version 2.6-2 (Oksanen et al. 2022) after performing square root transformation to reduce the effect of extreme values.

To provide forest cover reconstructions, modern analogue technique (MAT) based on matching analogues between modern and fossil pollen assemblages (Overpeck et al. 1985) was used. The data set of modern analogues consists of 726 modern pollen samples from a wide variety of landscapes in Eastern Europe and Siberia (Novenko et al. 2014a), combined with estimates of forest cover 20 km around the site from MODIS satellite images (Hansen et al. 2003). Calculations were carried out using the ‘analogue’ package (Simpson 2007). We used squared-chord distances (SCD) as the measure of similarity between pollen assemblages and weighted mean of the k-closest analogues. The number of the nearest analogues (k) was defined automatically using the lowest root mean square error of prediction (RMSEP) for the leave-one-out errors (Fig. S6.1, S6.2).

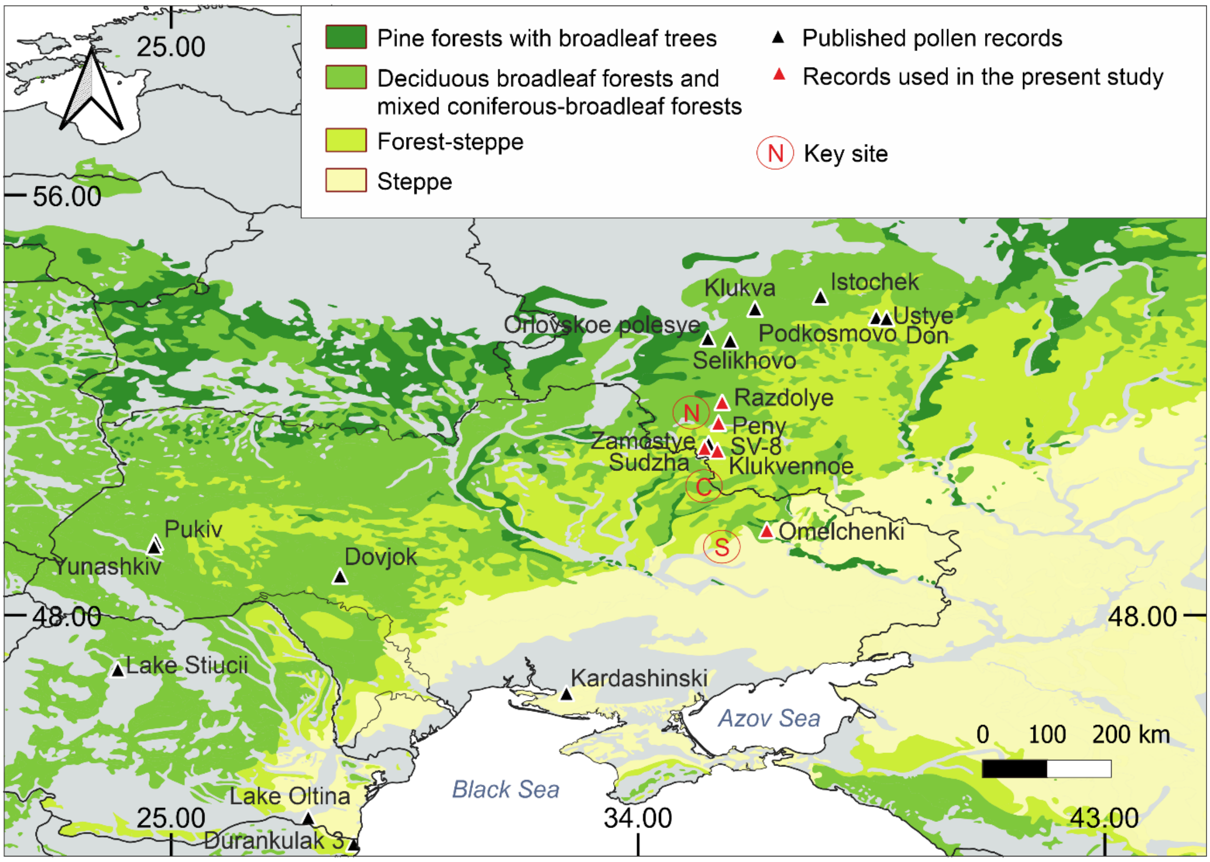

Fig. 6.1. Map of potential natural vegetation (Bohn et al. 2004) and pollen records from the East-European forest-steppe

Table 6.1 – Sediment cores from the East-European forest-steppe used for the climate reconstructions

Sediment core	Year of collection	Coordinates	Altitude, m a.s.l.	Key region	Length, cm	Age (cal. yrs BP)	Reference
Zamostye	2013	51.18481 N, 35.27988 E	135	center	250	~14,800	Lukanina et al. (2022)
Sudzha	2009	51.1375 N, 35.288056 E	134	center	267	~2,800	Shumilovskikh et al. (2019a)
Omelchenki	2013	49.63969 N, 36.41677 E	88	south	175	~9,800	Lukanina et al. (2023)
Peny	2009	51.596694 N, 35.458767 E	152	north	210	~1,100	Kasianova et al. (submitted)
Razdolye	2009	51.909586 N, 35.641356 E	194	north	80	~200	Kasianova et al. (submitted)
Klukvennoe	2016	51.119194 N, 35.461833 E	150	center	388	~14,600	Shumilovskikh et al. (in prep.)

Training pollen data set for climate reconstructions

The modern pollen dataset used for the climate reconstruction comprises personal data collected in the East-European forest-steppe within the study area, surface samples from the broadleaf forest vegetation zone in Eastern Europe and the forest-steppe area of Western Siberia from the Russian Pollen Database (Chepurnaya and Novenko 2015) and the Eurasian Modern Pollen Database (EMPD version 2) (Davis et al. 2020). In total it consists of 2287 samples. All the crop taxa including Cerealia, *Hordeum*-type, *Triticum*-type, *Secale*, *Avena*-type, *Fagopyrum* and *Zea*, invasive taxa of *Xanthium spinosum* and *X. strumarium*-types and the pollen of wetland and aquatic plants including Cyperaceae were excluded from the training set. Multivariate analyses were performed using R package 'vegan' (Oksanen et al. 2022). We used redundancy analysis (RDA) and variance partitioning to explore the effect of individual climatic factors on the data distribution.

To explore the effects of climate on the variation in the modern pollen data and for quantitative reconstructions, we chose the following climate variables: mean annual temperature (MAT), mean annual precipitation (MAP), potential evapotranspiration (ET) and the aridity index (AI) (Fig. 5.3). As a generalized function of precipitation, temperature and reference evapotranspiration, the aridity index (UNEP 1997) can be used to quantify precipitation availability over atmospheric water demand (Trabucco and Zomer 2018).

MAT and MAP were extracted from the WorldClim Version 2 database (Fick and Hijmans 2017) while the ET and AI values – from the Global Aridity Index and Potential Evapotranspiration Climate Database v2 (Trabucco and Zomer 2018). The databases provide the climate estimates for the time period 1970-2000 in high spatial resolution (each 30 seconds, ~1 km^2). Each climate variable was then tested with a variance inflation test to check its influence on the data distribution gradient.

Climate reconstructions

For modern analogue technique (MAT) (Magny et al. 2001; Overpeck et al. 1985), we used the entire training set of 2287 samples (Fig. 6.2A). To evaluate non-analogue situation for the fossil pollen spectra, we performed a PCA with both fossil and modern samples. We used squared-chord distances (SCD) as the measure of similarity between pollen assemblages and weighted mean of the k-closest analogues (Fig. S6.4). The number of the nearest analogues (k) was defined using the lowest root mean square error of prediction (RMSEP) for the leave-one-out errors.

For the weighted averaging partial least squares regression (WAPLS) (Braak and Juggins 1993), a shorted training set of 978 pollen samples from Eastern Europe was used. To check whether the response of the taxa to the climate variables is unimodal, we plotted pollen percentages of each taxon against the variable (Fig. S6.7). Based on the results, we removed the samples of the surface samples dataset and the taxa which could impact the climate reconstruction due to the differences in counting, strong local signal, errors in the public pollen databases, etc. The number of components used for the reconstruction was defined by the strongest model performance (R^2) and the lowest root mean square error of prediction for the leave-one-out errors. Climate reconstructions were carried out using the 'rioja' package (Juggins 2022).

Results and interpretation

MA climate reconstruction

Training set

12.24% of variance was explained by the constraining variables (MAT, MAP, AI and ET), with RDA axis 1 explaining 7.38% and RDA axis 2 explaining 3.91% of the variance (Fig. 6.2B). Aridity index, as a variable calculated through mean annual precipitation and reference evapotranspiration (Trabucco and Zomer 2018), which in turn is calculated through temperature is highly correlated with MAT and ET. However, all the variables passed the variance inflation test and are important for explaining the variance as all of them had inflation factors smaller than 10 (Braak 1988). Variance partitioning (Fig. 6.2C) shows the variance shared by the variables.

Since only MAP and AI are of interest for the climate reconstructions, the other variables (MAT and ET) were removed from the model. Together MAP and AI significantly explain 8.06% of the variance in the dataset ($p<0.001$). Variance partitioning indicated how much of the variance was explained by MAT (8.7%) and AI (6.6%) (Fig. 6.2D).

Two inference models were created for AI and MAP (Tables 6.2 and 6.3, Fig. 6.3). Bootstrapping was used as a cross-validation method. AI and MAP MAT models with 5 analogues performed best (R2=0.65, RMSEP=0.1754 for AI; R2=0.75, RMSEP=85.37 mm for MAP). The models have high errors at the ends of the gradient. Thus, the AI model performs best for the range of 0.4-1.0 predicting higher values in dryer conditions and lower values in wetter conditions (Fig. 6.3A). The MAP model underestimates the amount of precipitation in wet areas (Fig. 6.3B).

Table 6.2 – Performance of MAT calibration model for aridity index calculated with a bootstrap cross-validation exercise (nboot (number of repetitions) = 1000)

Number of analogues (k)	RMSEP	R^2	Avg. Bias	Max. Bias	Skill
1 (w. mean)	0.2018	0.63	-0.00754	0.5524	61.9
2 (w. mean)	0.1895	0.64	-0.00845	0.5837	63.9
3 (w. mean)	0.1824	0.65	-0.00921	0.6076	64.6
4 (w. mean)	0.1780	0.65	-0.00993	0.6288	64.9
5 (w. mean)	0.1754	0.65	-0.01056	0.6507	64.9

Table 6.3 – Performance of MAT calibration model for mean annual precipitation with a bootstrap cross-validation exercise (nboot = 1000)

Number of analogues (k)	RMSEP	R^2	Avg. Bias	Max. Bias	Skill
1 (w. mean)	99.578	0.72	-0.5128	263.61	71.7
2 (w. mean)	92.850	0.74	-0.8144	271.29	73.8
3 (w. mean)	89.046	0.75	-1.1422	276.31	74.7
4 (w. mean)	86.747	0.75	-1.4517	278.75	75.0
5 (w. mean)	85.370	0.75	-1.7600	280.42	75.1

Table 6.4 – Performance of WAPLS calibration model for aridity index with a bootstrap cross-validation exercise (nboot = 1000)

Number of components	RMSEP	R^2	Avg. Bias	Max. Bias	Skill	Delta RMSE	p
1	0.1118	0.65	-0.00012	0.2072	65.0	-40.70	0.001
2	0.1018	0.71	0.00001	0.2055	71.3	-8.96	0.001
3	0.0998	0.73	0.00009	0.1984	72.7	-1.98	0.001
4	0.1007	0.73	0.00006	0.1958	72.6	0.87	0.655
5	0.1014	0.73	0.00018	0.1947	72.4	0.75	0.921

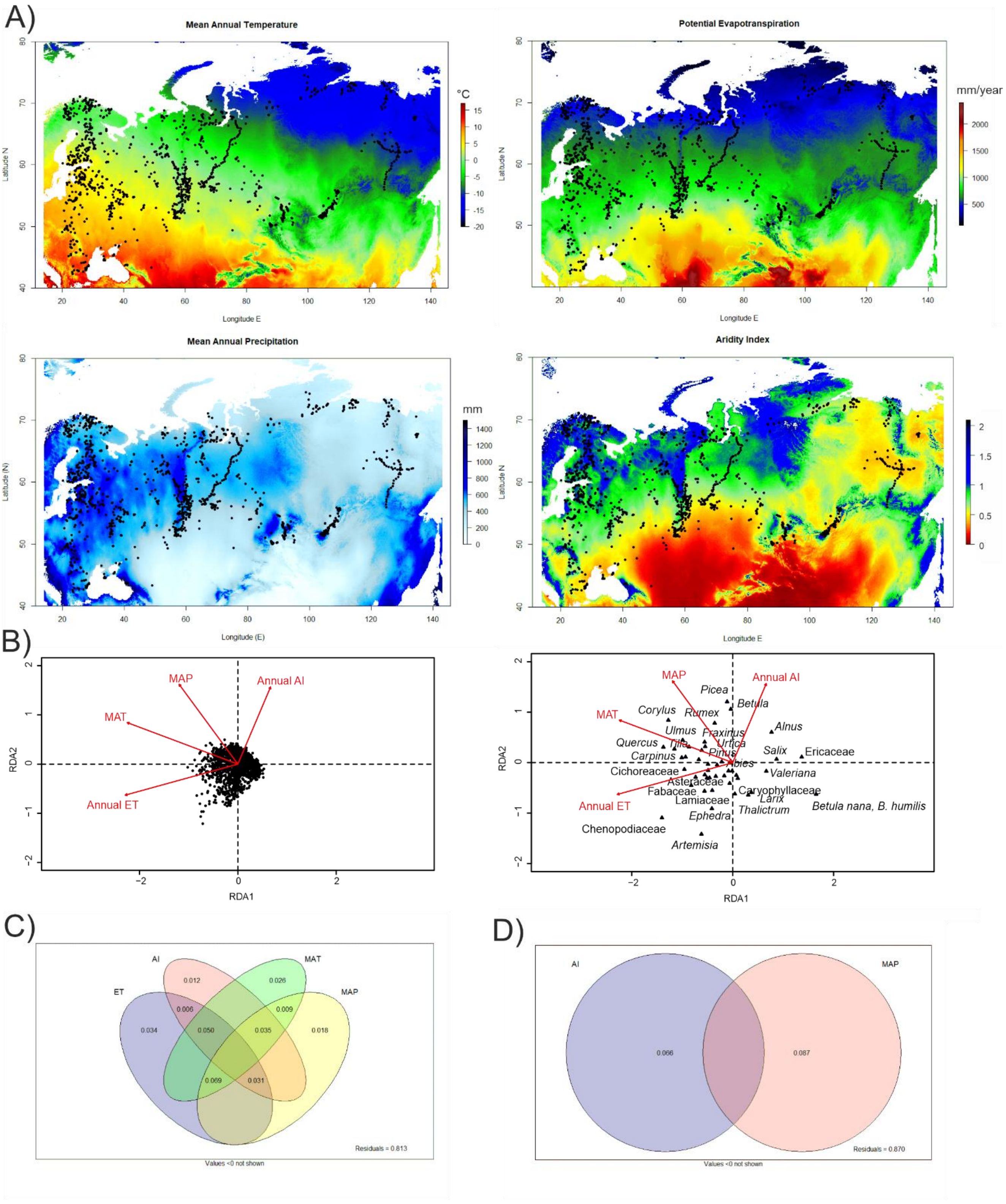

Fig. 6.2. A) Climate maps of the all modern pollen samples used for MAT reconstructions; B) RDA with sites and species of the training set; C) Variance partitioning of mean annual temperature (MAT), mean annual precipitation (MAP), annual evapotranspiration (ET) and aridity index (AI) for the full training set; D) Variance partitioning of the AI and MAP for the full training set

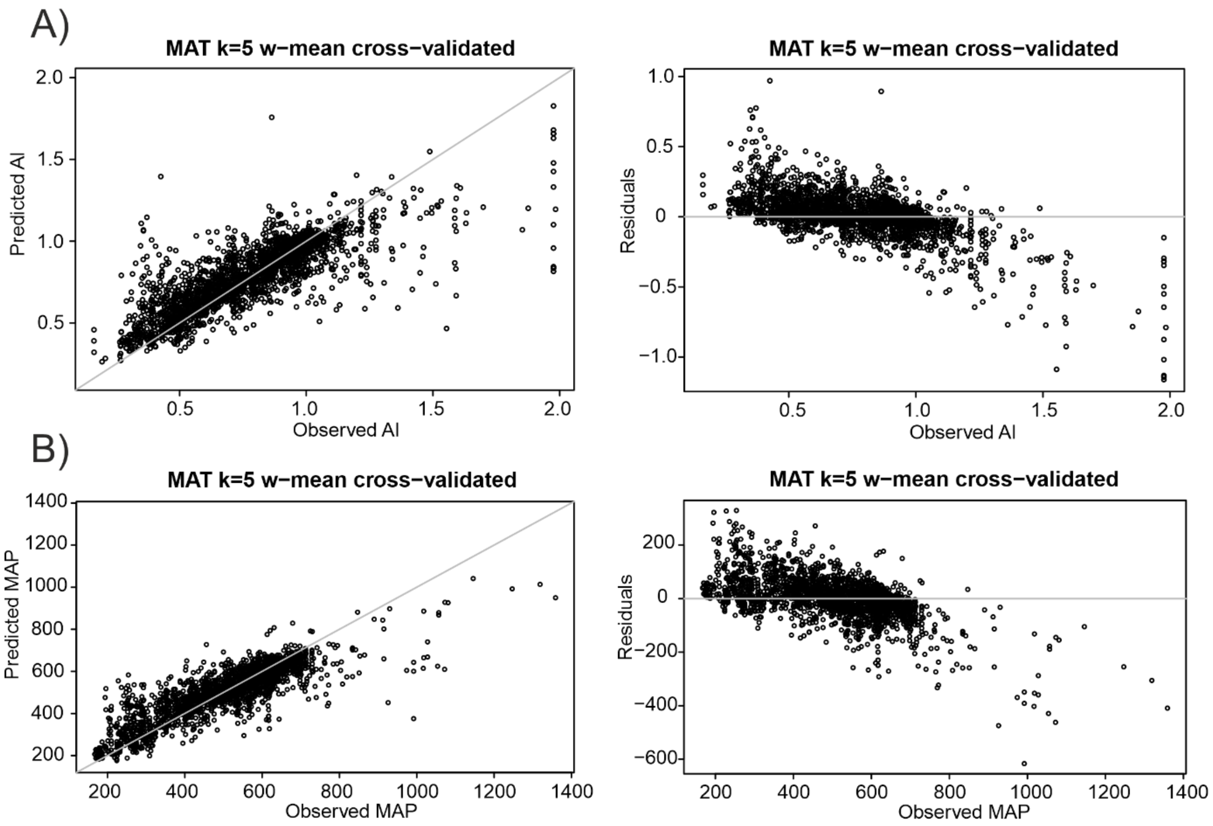

Fig. 6.3. Scatterplots of the aridity index (A) and mean annual precipitation (B) MAT inference models in bootstrapping cross-validation: predicted vs. observed and residuals (predicted vs. observed)

Analysis of the fossil spectra

The cores used in the present study originate from different areas with different dominant vegetation. As shown by the PCA (Fig. 6.4), the Sudzha core was located in a broadleaf forest dominated by oak while the dominant tree taxon for Zamostye, Omelchenki and Peny was pine. This local differences between the coring sites determine the major variation in the fossil pollen data. However, the second axis of the PCA shows a climatic signal which drove

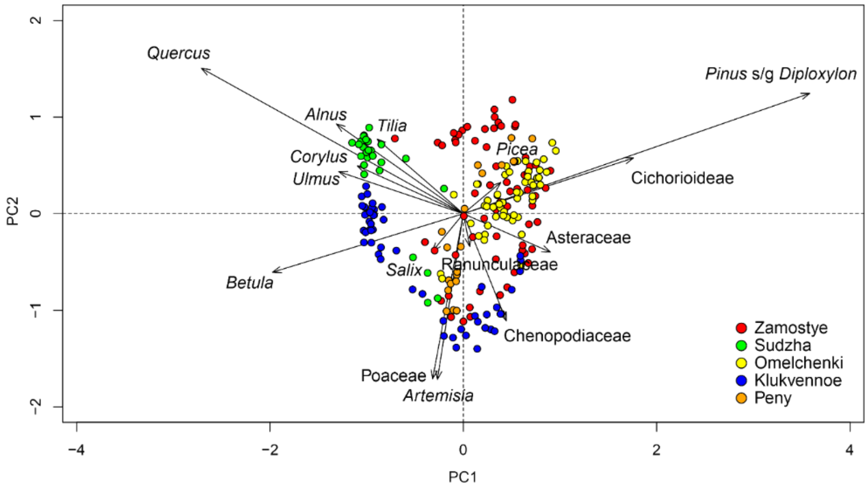

Fig. 6.4. PCA of the fossil pollen samples of the five cores: Zamostye, Sudzha, Omelchenki, Klukvennoe and Peny

the changes in vegetation through time – the interchange between forested and open areas. Hence, we consider climate variables reflecting moisture availability (MAP and AI) to be the drivers of the changes in the fossil spectra and the variables to be used in climate reconstructions.

As shown by the PCA of the surface samples and the cores' samples (Fig. 6.5), the cloud of the surface samples does not cover the fossil samples entirely implying non-analogue situations when using MAT.

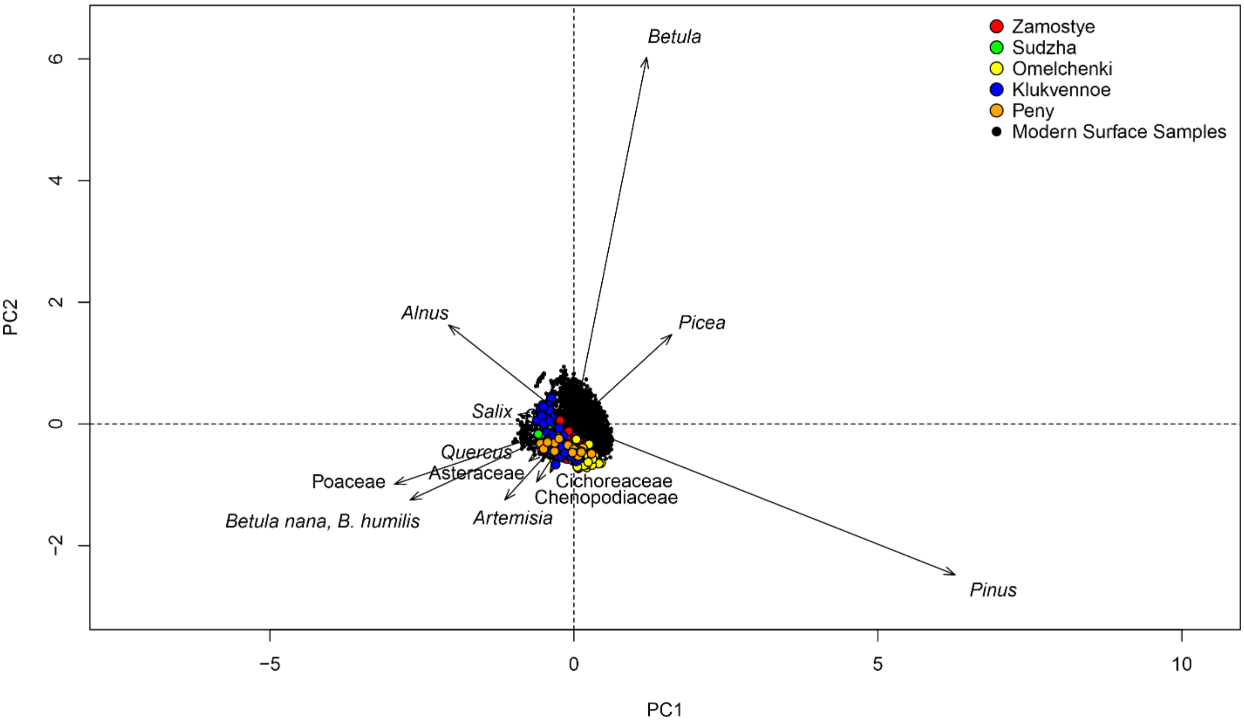

Fig. 6.5. PCA of surface and fossil samples

WAPLS training set and climate reconstructions

Due to non-analogue situations in the MA reconstructions (Fig. 6.5), we created and applied a WAPLS transfer function model to reconstruct climate conditions. Redundancy analysis for all four environmental variables showed that RDA axis 1 was connected with MAT, ET and AI and explained 11% of the variance. RDA axis 2 was connected with MAP and explained 4%. The training set reflected the changes in temperature impacting the evapotranspiration rather than the precipitation values. However, the interchange in open and forested areas remains the main gradient in the fossil samples, which in turn is strongly connected with the available moisture. Aridity index was chosen as a variable combining the effects of the temperature and the available moisture which could be reconstructed from the pollen records.

After running variance inflation test (Braak 1988), MAT and ET were excluded due to a strong correlation with AI (Fig. 6.6 A). RDA constrained for the two remaining variables (MAP and AI) explains 12% of the variance with RDA axis 1 explaining 10% and RDA axis 2 – 2% of the variance (Fig. 6.7). The value of λ_1/λ_2 (RDA1/RDA2) is greater than 1, indicating that the variables along RDA1 represent an important ecological gradient in the training set (Juggins 2013). According the variance partitioning (Fig. 6.6 B) AI alone explains 15% and 3% in correlation with MAP. Using AI as a sole constraining variable in RDA, the amount of variance significantly explained 9.2% (p<0.001) indicating the possibility of creating a transfer function for estimating AI from pollen percentages.

Bootstrapping indicate that three-component model performed best (R2=0.73, RMSEP=0.0998) (Table 6.4, Fig. 6.8).

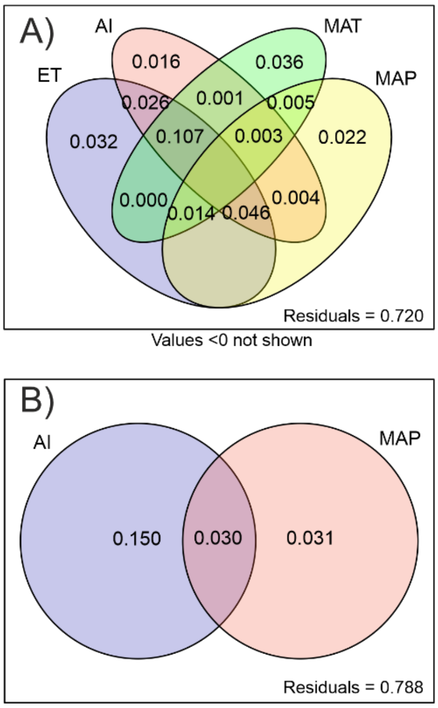

Fig. 6.6. Variance partitioning of all climate variables (A) and of AI and MAP (B) for the reduced training set

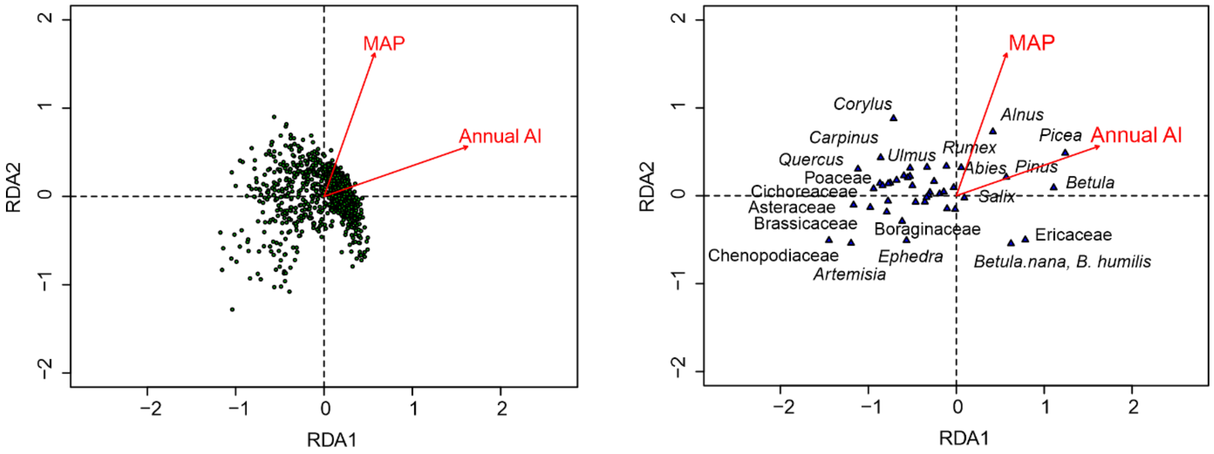

Fig. 6.7. RDA of the reduced training set with mean annual precipitation and aridity index

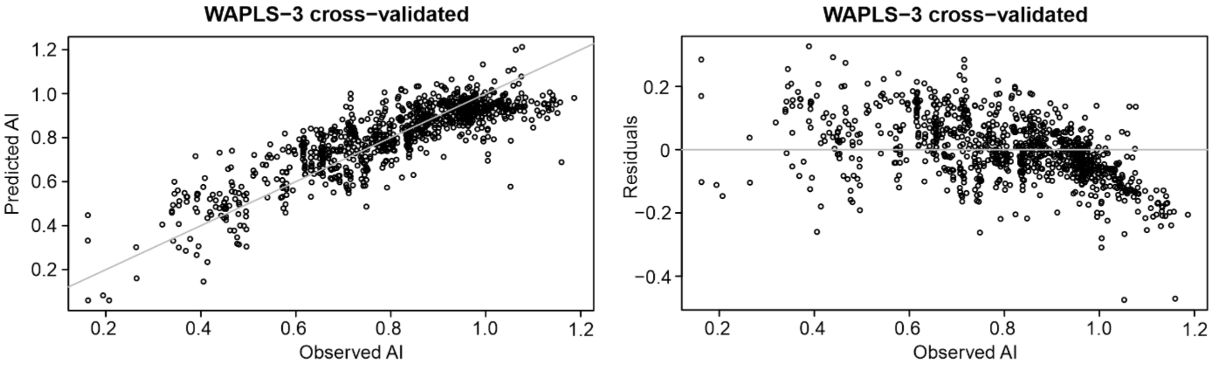

Fig. 6.8. Scatterplots of the three-component WAPLS AI model in bootstrapping cross-validation: observed vs. predicted values and residuals

Vegetation and climate reconstructions

The reconstructed forest cover estimates of the cores from the East-European forest-steppe ecotone allow the estimation of the southern treeline dynamics and its correlation with the reconstructed climate values. Due to the no-analogue situations and high SCD values for the cores of Omelchenki, Klukvennoe and Sudzha (Fig. S6.2), forest cover reconstructions should be interpreted with caution as well as non-analogue situations in the pollen-climate MAT reconstructions (Fig. S6.4). Furthermore, the forest cover is overestimated in the steppe areas due to the long-distance transport of some AP (Novenko et al. 2014a). Here, we consider 15 % of the reconstructed forest cover to be the steppe – forest-steppe boundary whereas ~30 % – a boundary between forest and forest-steppe (Ershov 2007). The aridity index climate estimations follow UNEP (1997) where AI<0.03 is considered hyper arid, 0.03-0.2 – arid, 0.2-0.5 – semi-arid, 0.5-0.65 – dry sub-humid and >0.65 – humid.

Center of the ecotone

Zamostye

Zamostye core was the oldest among the studied cores covering 14,800 years which shows the vegetation and climate dynamics since the Bølling interstadial (Lukanina et al. 2022). Originated from a meander of the Sudzha River down in the valley at an altitude of ~135 m a.s.l., Zamostye core had the best hydrological conditions for forests development. During the interstadial periods of the Late Glacial (Bølling and Allerød) ~14.8-14.3 cal. kyr BP and ~14.1-12.9 cal. kyr BP (Lukanina et al. 2022), pine forest-steppe was developing at the site while steppe prevailed during the stadial periods (Older and Younger Dryas) ~14.3-14.1 and ~12.9-11.7 cal. kyr BP.

Reconstructed aridity index values for the Late Glacial differ between the reconstruction methods. Modern analogue technique takes the analogues from the area around the Baikal Lake in Eastern Siberia and Western Siberia for the warming periods (Fig. S6.6) and from Yakutia, Baikal, Altai mountains and Western Siberia for the Younger and Older Dryas suggesting semi-arid climate throughout the Late Glacial (Fig. 6.9). However, the WAPLS reconstruction suggests dry sub-humid conditions for the Older Dryas and Bølling Interstadial, humid climate for Allerød when the forest-steppe developed at the site and semi-arid conditions for the Younger Dryas. Both reconstructions show the aridity index of 0.4 for the

Younger Dryas marking it as the driest period in the last 14,800 years. MAT-reconstructed annual precipitation varied within ~250-350 mm during the Late Glacial.

With the beginning of the Holocene, the reconstructed forest cover, aridity index values and precipitation increased. By ~9 cal. kyr BP the AI estimates reached ~0.65 for WAPLS and ~0.7 for MAT models when forests spread in the area (Fig. 6.9). ~6 cal. kyr BP aridity index increased further implying humid climate conditions for the second half of the Holocene within the Zamostye study area. Precipitation reached the modern values of ~600 mm/yr ~9 cal. kyr BP and were stable for the rest of the Holocene. Since around 3.3 cal. kyr BP the human impact on the environment became noticeable (Lukanina et al. 2022) and by ~600 cal. yrs BP the area was completely deforested. Thus, we consider the climate reconstructions for the last 1000 years invalid.

Klukvennoe

Klukvennoe record covers the time period of the last ~13,700 years and originates not in the river valley like Zamostye but from a plateau where the conditions are more arid. Together with Zamostye the records provide a full picture of the tree line dynamics in the region since the Late Glacial as the distribution of forests depends on the hydrological conditions within the ecotone. However, the Klukvennoe record still requires some age-depth model clarification for the Younger Dryas – beginning of the Holocene period (Fig. 6.9).

During the Bølling-Allerød warming the area was represented by a mosaic of forest and steppe patches with semi-arid to dry sub-humid climate with ~400 mm/year of precipitation. The analogues for the period were taken from the Mid-Russian Upland, the Altai-Sayan Mountains and the Baikal Lake area (Fig. S6.7). During the Younger Dryas sedimentation might have stopped or slowed down significantly and the period is likely not reflected in the record (Fig. 6.9). While forest-steppe was starting to spread in the river valleys with the beginning of the Holocene (at the Zamostye study site), steppe remained at more elevated areas like Klukvennoe until the middle of the Holocene. ~8 cal. kyr BP forest-steppe started to spread also on watersheds including the Klukvennoe site. However, the climate remained semi-arid until ~6-5.5 cal. kyr BP with 300-400 mm/year of precipitation. Early Holocene analogues were located in the Southern Urals, Altai and Yakutia while the mid-Holocene analogues were from Kazakhstan, Altai-Sayan Mountains and the Baikal Lake (Fig. S6.7).

During the late Holocene the forests reached dry elevated areas marking the shift of the forest-steppe border southwards. ~3.5 cal. kyr BP the reconstructed forest cover values reached 30-40%. The reconstructed aridity index values showed dry sub-humid to humid climate. However, WAPLS reconstruction might be biased by the spread of oak which drought-resistant species might have occurred in the Bulgarian modern samples (Fig. S6.5, S6.6). We consider MAT AI reconstruction to be more realistic.

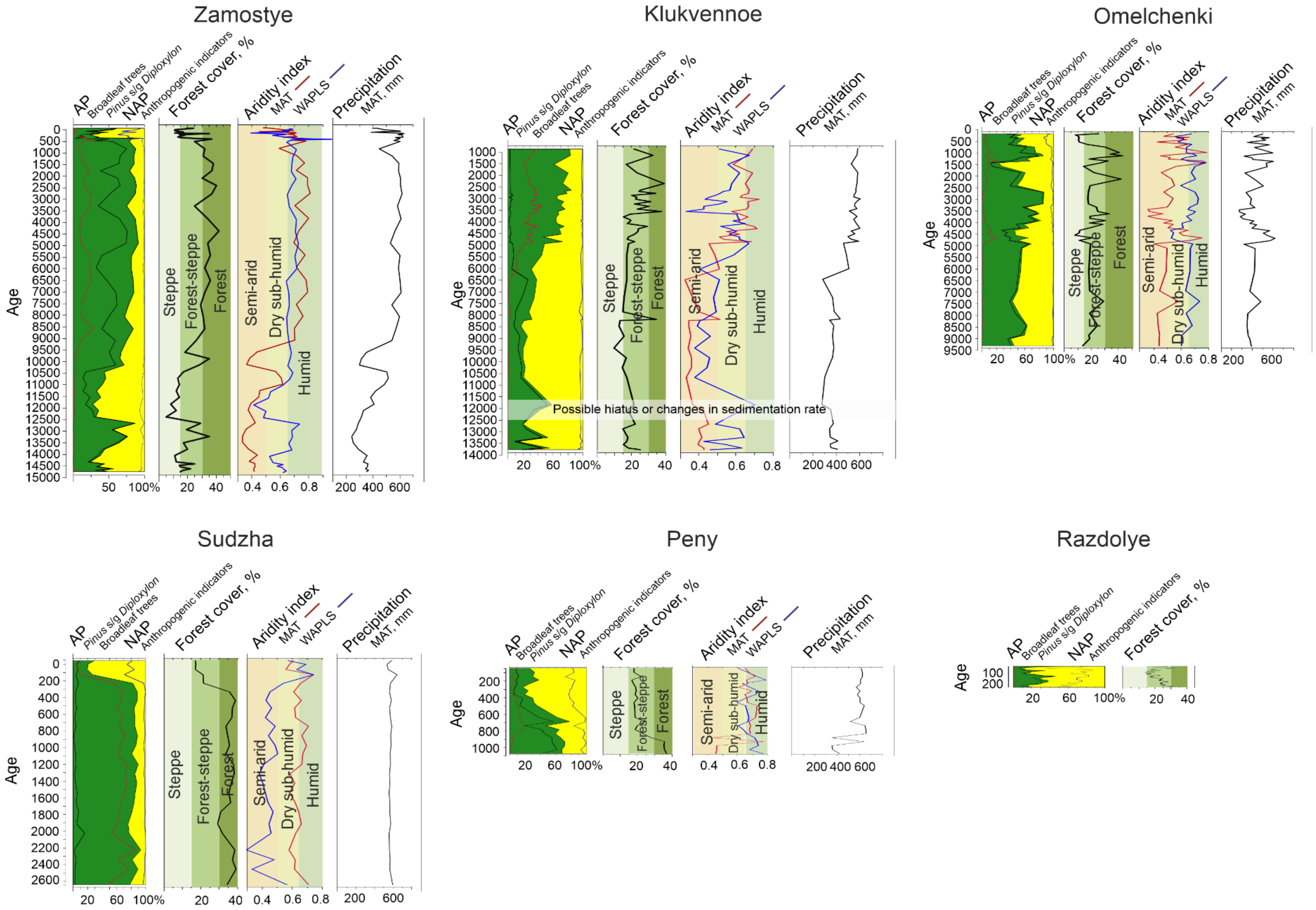

Fig. 6.9. Diagram of the AP/NAP values, reconstructed forest cover (the steppe/forest-steppe/forest border after Ershov (2007), Novenko et al. (2014a)), reconstructed aridity index (climate classes after UNEP (1997)) and mean annual precipitation for the cores from the East-European forest-steppe

Sudzha

The youngest core of the central key site Sudzha also originates in a river valley and covers ~2.6 cal. yrs BP. It reflects the late Holocene forest spread. Dominated by oak (Fig. 6.9), Sudzha also has a WAPLS oak bias similar to the Klukvennoe site. Therefore, we consider MAT AI reconstruction with dry sub-humid to humid climate more reliable for the Sudzha record with the mean annual precipitation values around 600 mm/year. Surface samples from Southern Urals, Central Russian Upland and Bulgaria became modern analogues for the reconstruction (Fig. S6.7). Around 200 cal. yr BP the study site was deforested.

South of the ecotone

Omelchenki

Located in a river valley, Omelchenki study site also has favourable hydrological conditions for forests. Omelchenki record covers ~9.3 cal. kyr BP. MAT and WAPLS aridity index reconstructions for the early Holocene differ. MAT reconstruction suggests semi-arid climate for the first half of the Holocene until ~4.8 cal. kyr BP with analogues from the Southern Urals, Western Siberia and Baikal Lake area (Fig. S6.7). WAPLS reconstruction shows dry sub-humid to humid values. Forest-steppe was spread in the area.

Omelchenki study area experienced a strong anthropogenic impact in the second half of the Holocene (Lukanina et al. 2023). In particular, the disappearance of broadleaf taxa due to possible livestock breeding affected the MAT reconstructions. Therefore, the WAPLS values showing humid climate conditions might be more reliable. Forests were spread during the periods of decreasing anthropogenic pressure (Lukanina et al. 2023). Precipitation amount increased from ~400 mm/year in the early Holocene to ~600 mm/year in the late Holocene.

North of the ecotone

Peny and Razdolye

The two northern sites of Peny and Razdolye have the shortest records of ~1100 and 200 cal. yr BP respectively – the time period of high anthropogenic pressure and deforestation. However, the Peny record shows that the area was covered with forests before it was completely deforested ~800 cal. yr BP. Aridity index reconstructions suggest humid climate for the area (Fig. 6.9).

Modern analogue technique took the climate analogues from Western Siberia and the Baikal Lake (Fig. S6.7) due to the absence of broadleaf taxa in the beginning of the Peny record which was likely anthropogenically caused (Kasianova et al. submitted). Therefore, we consider the WAPLS reconstruction the be more realistic for the beginning of the record.

Both northern records show very high amounts of anthropogenic markers. For the Razdolye record, they reached 66% indicating active land use and implying much higher potential forest cover values compare to the reconstructed 15-30% attributed to forest-steppe.

Discussion

When ~14.7 cal. kyr BP the Bølling-Allerød interstadial started (e.g. Svensson et al. (2008), Thiagarajan et al. (2014), Novenko (2016)) and the glacier was retreating, forest started to spread on the vast territories of the East-European Plain. Forest-steppe was slowly advancing into periglacial steppe (Velichko 2009) within the East-European forest-steppe ecotone. Possibly semi-arid or dry sub-humid climate conditions in river valleys (AI ≤ 0.55-0.6) allowed the development of forest-steppe by ~14.8-14.7 cal. kyr BP for the ecotone. Climate reconstructions of Borisova et al. (2006) based on the arealogram method (Grichuk 1969) suggest a region-analogue in headwaters of the Yenisey River with mean January temperature of -23 °C, July temperature of 17 °C and mean annual precipitation of 450 mm for the study region. Our precipitation reconstruction based on MAT show ~350 mm/year for the time period which in our opinion might be more probable considering generally dry climate conditions. An abrupt short cold event ~14.3 cal. kyr BP likely corresponding to GI 1d (Svensson et al. 2008) caused a reduction of forest cover to 11-12% returning wind-protected and moist areas of the ecotone to steppe vegetation (AI ≤ 0.5).

The following Allerød interstadial ~14.1 cal. kyr BP (Greenland interstadial GI 1a-c (Svensson et al. 2008)) likely had milder climate with aridity index reaching ~0.7 indicating humid environment and the development of forests in river valleys and semi-arid to possibly dry sub-humid climate (AI 0.4-0.6) for plateaus where the forest cover values were considerably lower (not more than ~22 % during the most favourable periods). However, a significant contribution to the increase in humidity might have been made by the thawing of permafrost, which increased the river runoff (Lukanina et al. 2022). Sycheva (2012) documented the presence of permafrost in the study region at that time.

~12.9 cal. kyr BP the coldest for the last 15,000 years period of Younger Dryas started (Svensson et al. 2008). Our reconstructions show steppe all over the central part of the ecotone and the driest climate conditions for the records with the aridity index of ~0.4 or lower for elevated areas indicating semi-arid climate and annual precipitation values of ~300 mm. These values are lower than the previous precipitation reconstructions by Muratova et al. (1993), Borisova et al. (2006) and Velichko et al. (2002) suggested. However, considering the lack of records available for climate reconstructions in the area until the recent period, broader scale of the reconstructions by Velichko et al. (2002) and Muratova et al. (1993), the limitations of the arealogram method used by Borisova et al. (2006) implying the necessity of the existence of modern analogues to the fossil spectra and the general agreement of the two types of reconstructions for the two records used – of Zamostye and Klukvennoe – we suggest that the values of the presented reconstructions might be more reliable.

With rise of the temperatures at the beginning of the Holocene (Svensson et al. 2008), the amount of available moisture was slowly increasing during the early Holocene. Forest cover reconstructions show a similar trend to the aridity index values. However, the process of forest spread was significantly faster in river valleys rather than on watersheds. By ~10.5-10 cal. kyr BP reconstructed forest cover values reached forest-steppe estimations in river valleys. At the southern limits of the modern ecotone the forest spread occurred later – ~9 cal. kyr BP. However, there was no forest on watersheds until at least 8 cal. kyr BP. Throughout the early Holocene the aridity index values were rising from semi-arid (~0.35-0.4) to dry sub-humid and possibly even humid ones in the river valleys of the central-northern parts of the ecotone (0.65-0.7 for river valleys in the center of the ecotone decreasing southwards and 0.45-0.5 on watersheds) by 8.2 cal. kyr BP. Precipitation increased from ~300mm/yr to ~400-450 mm/yr. ~600 mm/yr by 8.2 cal. kyr BP shown by the Zamostye MAP reconstruction might be exaggerated considering generally favourable microclimatic conditions at this study site.

European-scale Holocene climate reconstructions previously did not cover the study region (e.g. Davis et al. (2003), Mauri et al. (2015)). The westernmost part of the ecotone, however, was included due to the higher number of the available records. The trend the winter precipitation reconstruction by Mauri et al. (2015) of the lower-than-present slowly increasing precipitation values from the end of the Late Glacial – beginning of the Holocene to the end of the early Holocene period (Walker et al. 2018) is in line with our reconstructions. However, the opposite trend of decreasing summer precipitation since the similar-to-present values of the end of the Late Glacial to the lower-than-present values ~8.2 cal. yr BP seems doubtful for the study region considering slow but increasing presence of the forests in the ecotone. The annual precipitation reconstruction of the Klukva record (Fig. 6.1) located in the modern broadleaf forest vegetation zone shows 600-700 mm/yr for the time period of 9.7-8.2 cal. kyr BP (Novenko et al. 2019) indicating wetter conditions northwards and the establishment of similar in terms of amount of moisture conditions in the river valleys of the central-northern parts of the ecotone. The transformation of the study region and the establishment of the forest-steppe as an ecotone took place in the early Holocene by ~8.5-8 cal. kyr BP.

The middle of the Holocene was the period of further development and spread of forests in the ecotone. By the end of the mid-Holocene period ~4.2 cal. kyr BP forests covered most of the region. Thus, in the lowlands of river valleys the reconstructed forest cover reached 42% and on plateaus and at the southern limits – up to 30%. Climate changes of the middle Holocene allowed wider distribution of broadleaf trees – during the period they spread outside of the river valleys increasing their presence in the eastern parts of the East-European forest-steppe ecotone. The western part of the ecotone (e.g. the records of Pukiv, Yunashkiv, Dovjok, etc., Fig. 6.1) contained the broadleaf taxa already since the beginning of the Holocene indicating milder climate conditions westwards. Nonetheless, the increase in broadleaf component occurred in the west and the east during the middle Holocene implying the establishment of more favourable climate all over the region.

The aridity index changed from the semi-arid values of ~0.45 for the watersheds and the southern limit of the ecotone ~8.2 cal. kyr BP to the humid values of up to 0.66-0.67 by 4.2 cal. kyr BP with the increase of precipitation from ~400 mm/yr to the modern values of ~600 mm/yr indicating the shift of the southern treeline southwards during the middle of the Holocene. Shumilovskikh et al. (2018) showed a similar treeline dynamics for the northern border of the forest-steppe ecotone including the sites of Selikhovo, Podkosmovo, Istochek and Klukva (Fig. 6.1) (Novenko et al. 2014a; 2015; 2016b; 2017). This disproves the theory of Khotinsky (1984) about the exceptionally stable position of the southern forest-steppe border during the middle Holocene. The forest-steppe border was dynamic throughout the early and middle Holocene slowly shifting southwards.

The late Holocene forest-steppe dynamics is inextricably linked with the human activities in the region. Since the Bronze Age the region experienced deforestation due to the cattle breeding, agricultural activities and metallurgy (Lukanina et al. 2023). However, during the periods of decreasing anthropogenic pressure the forest cover estimates reached the highest values for the Holocene – up to 40-41% for the central part of the ecotone including the watersheds and the river valleys of the southern limits of the ecotone indicating that these areas could potentially much more forested. The reconstructed aridity index for all the cores indicate humid climate conditions within the range of 0.65 to 0.8 (Fig. 6.9).

Conclusions

The two methods of climate reconstructions presented in the paper allow the estimation of the climate conditions for the East-European forest-steppe ecotone. Both methods have limitations including the lack of modern analogues for the Late Glacial – early Holocene vegetation (Birks 2003) as well as the analogues of natural vegetation in the training set for modern anthropogenically changes ecosystems, the covariance (Juggins 2013) and the choice of the samples defining the climate gradient for WAPLS reconstructions, possible migrational lag (Mauri et al. 2015), etc. However, using several methods for climate reconstructions might provide more possibilities to overcome these difficulties and make the reconstructions more reliable.

The aridity index and precipitation reconstructions provided for the region allow the understanding of the climate and vegetation dynamics since the Late Glacial. Possibly semi-arid or dry sub-humid climate conditions in river valleys with AI ≤ 0.55-0.6 and MAP of ~350 mm/year allowed the development of forest-steppe by ~14.8-14.7 cal. kyr BP. An abrupt short cold event ~14.3 cal. kyr BP caused a reduction of forest cover to 11-12% returning wind-protected and moist areas of the ecotone to steppe vegetation (AI ≤ 0.5). The following Allerød interstadial ~14.1 cal. kyr BP likely had milder climate with aridity index reaching ~0.7 indicating humid environment and the development of forests in river valleys and semi-arid to possibly dry sub-humid climate (AI 0.4-0.6) for plateaus where the forest cover values were considerably lower (not more than ~22 % during the most favourable periods). ~12.9 cal. kyr BP Younger Dryas brought the driest climate conditions for the records with the aridity index of ~0.4 or lower for elevated areas indicating semi-arid climate and annual precipitation values of ~300 mm.

Throughout the early Holocene the aridity index values were rising from semi-arid (~0.35-0.4) to dry sub-humid and possibly even humid ones in the river valleys of the central-northern parts of the ecotone (0.65-0.7 for river valleys in the center of the ecotone decreasing southwards and 0.45-0.5 on watersheds) by 8.2 cal. kyr BP. Precipitation was increasing from ~300 mm/yr to ~400-450 mm/yr. The establishment of the forest-steppe as an ecotone took place in the early Holocene by ~8.5-8 cal. kyr BP. During the middle of the Holocene, the aridity index changed from the semi-arid values of ~0.45 for the watersheds and the southern limit of the ecotone ~8.2 cal. kyr BP to the humid values of up to 0.66-0.67 by 4.2 cal. kyr BP with the increase of precipitation from ~400 mm/yr to the modern values of ~600 mm/yr indicating the shift of the southern treeline southwards. The late Holocene forest-steppe dynamics is inextricably linked with the human activities in the region. During the periods of decreasing anthropogenic pressure the forest cover estimates reached the highest values for the Holocene – up to 40-41% for the central part of the ecotone including the watersheds and the river valleys of the southern limits of the ecotone indicating that these areas could potentially be much more forested. The reconstructed aridity index for all the cores indicate humid climate conditions within the range of 0.65 to 0.8.

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Supplementary material

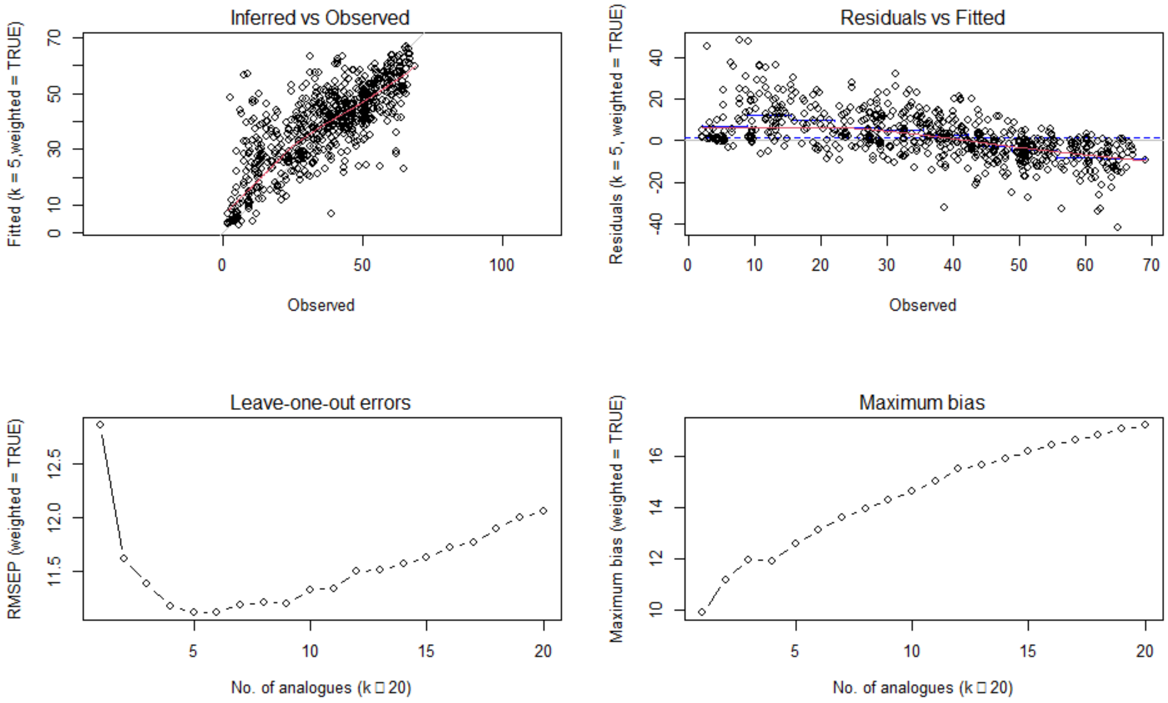


Fig. S6.1. Modern analogue technique for the forest cover reconstructions of the sediment cores of Zamostye, Klukvennoe, Omelchenki, Sudzha, Peny and Razdolye

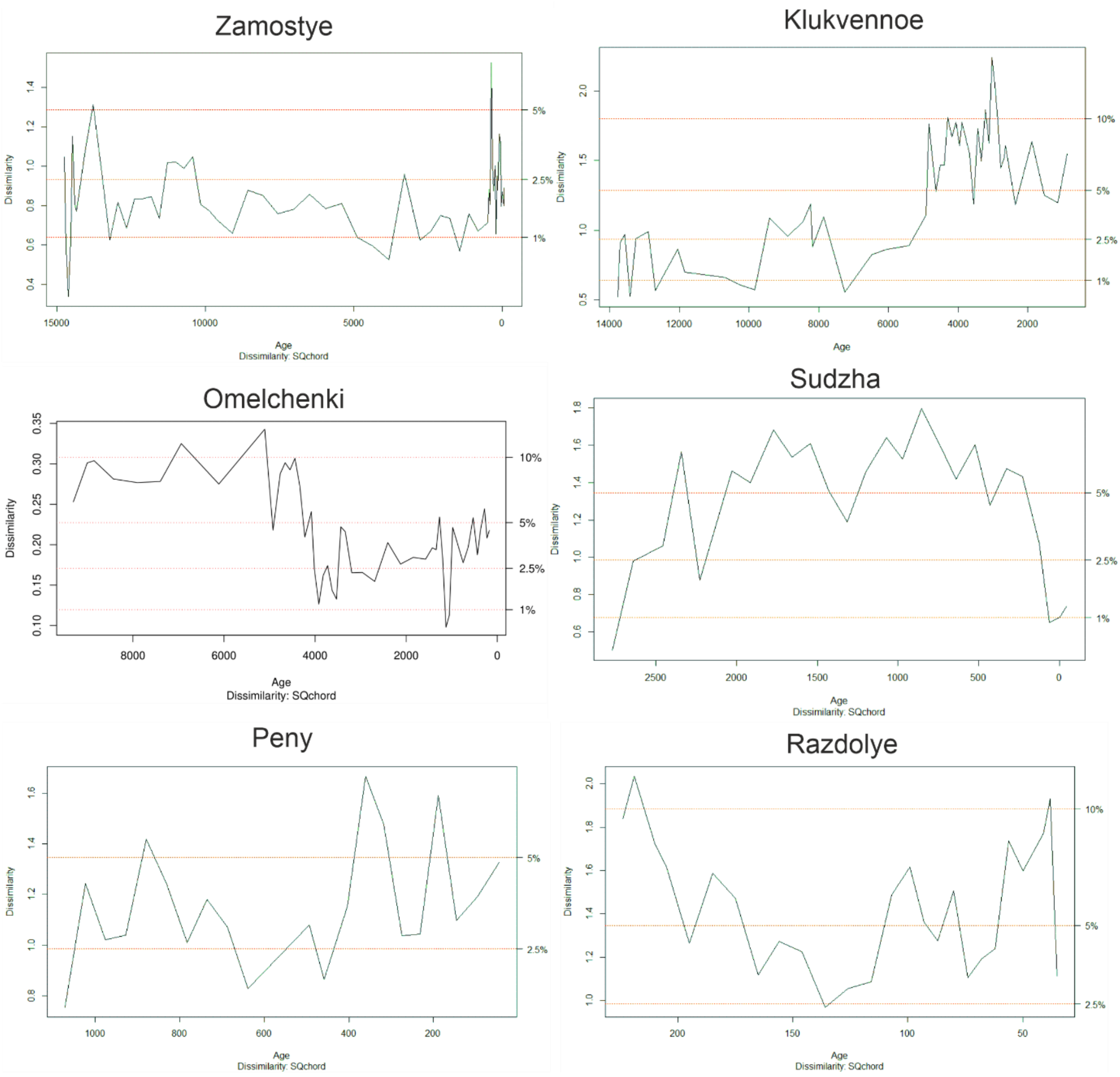


Fig. S6.2. SCD values for the forest over MAT reconstructions of the cores of Zamostye, Klukvennoe, Omelchenki, Sudzha, Peny and Razdolye

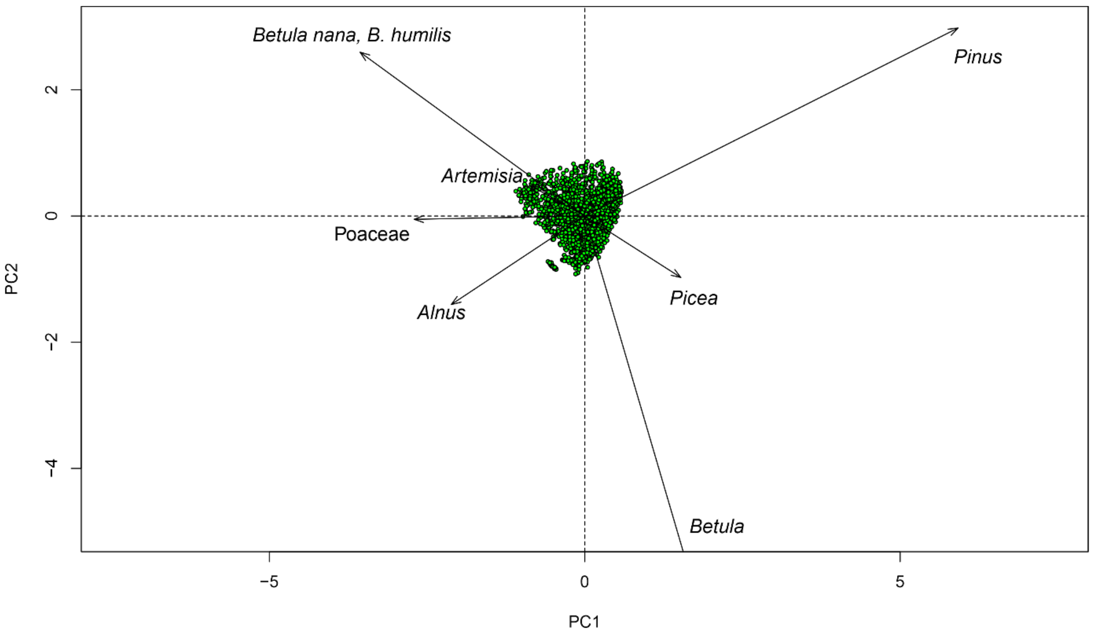


Fig. S6.3. PCA of surface pollen samples used for MAT pollen-climate reconstructions

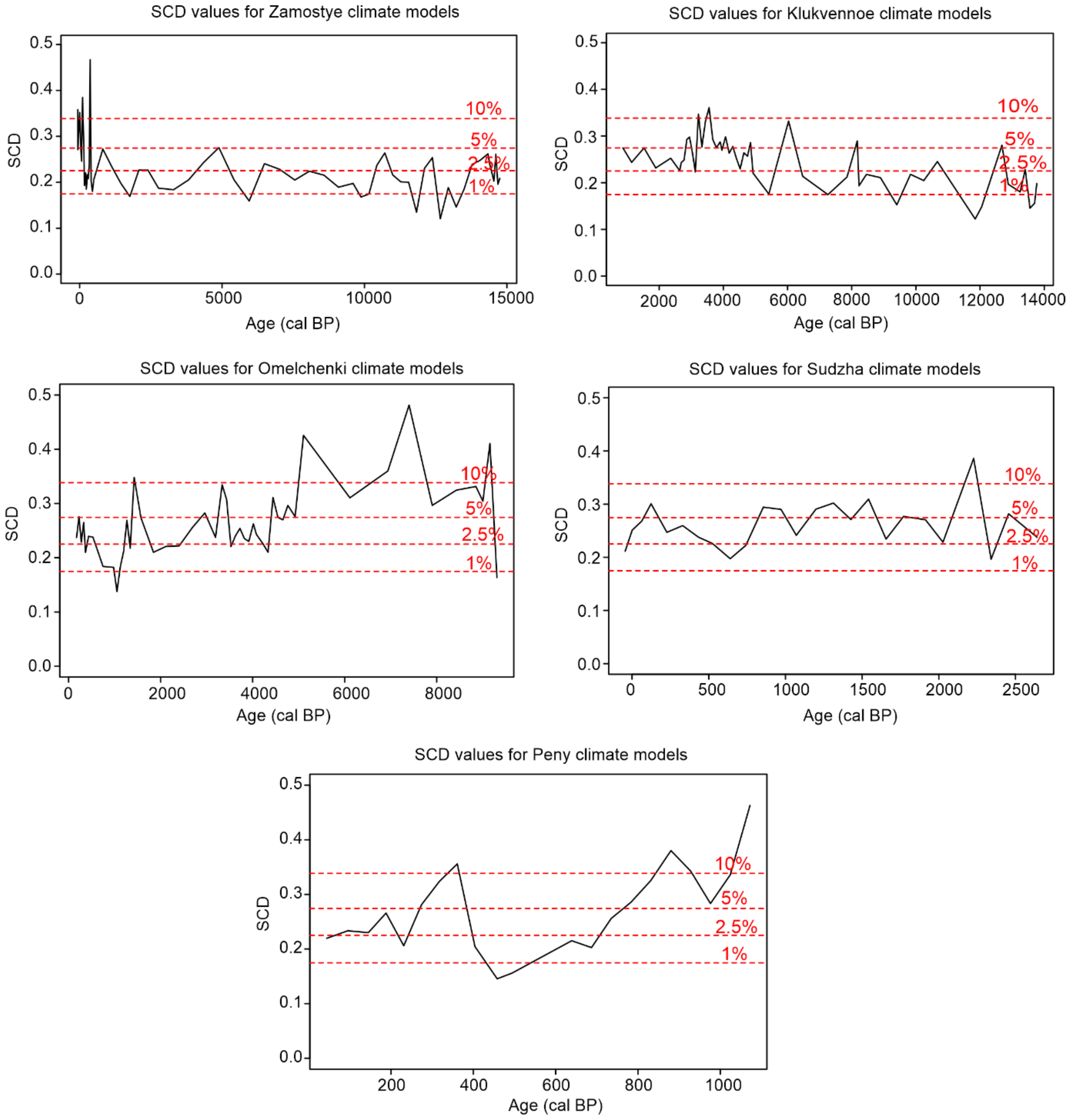
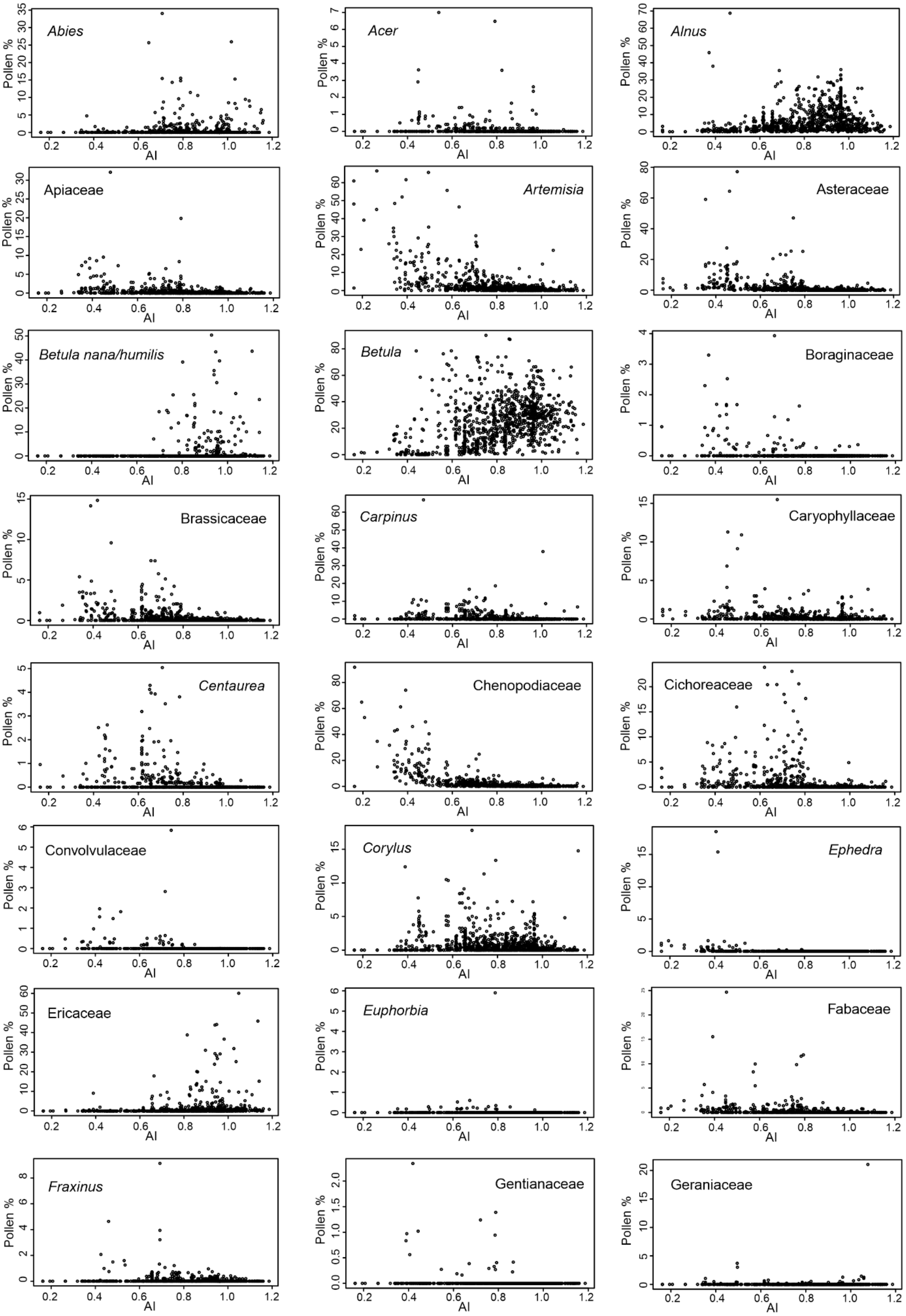


Fig. S6.4. Squared-chord distances (SCD) of the MAT pollen-climate reconstructions. The values above 5% mark non-analogue situation

Fig. S6.5. Map of the WAPLS training set pollen samples


Abies
Acer
Alnus
Apiaceae
Artemisia
Asteraceae
Betula nana/humilis
Betula
Boraginaceae
Brassicaceae
Carpinus
Caryophyllaceae
Centaurea
Chenopodiaceae
Cichoreaceae
Convolvulaceae
Corylus
Ephedra
Ericaceae
Euphorbia
Fabaceae
Fraxinus
Gentianaceae
Geraniaceae
Pollen %
AI
0.2
0.4
0.6
0.8
1.0
1.2

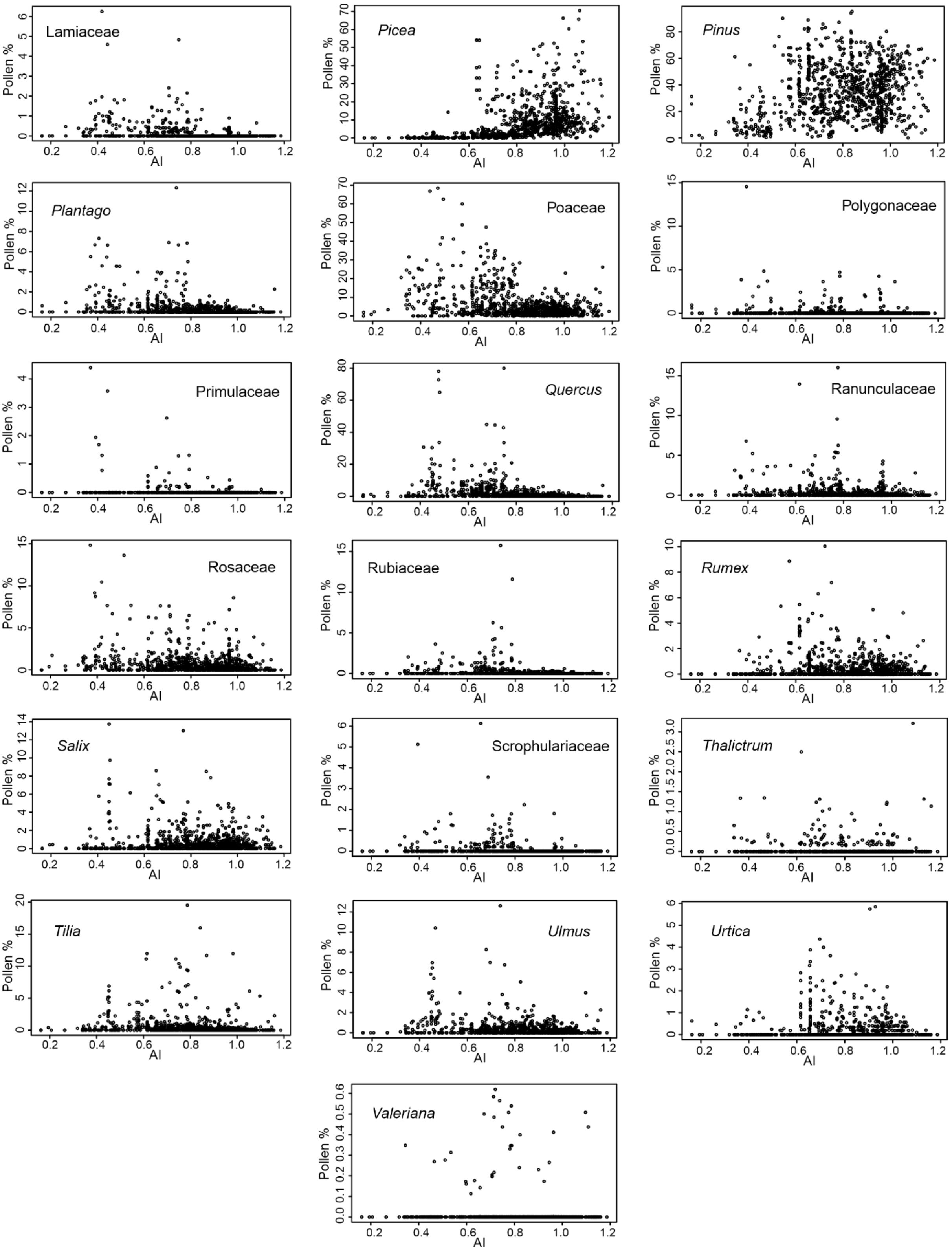
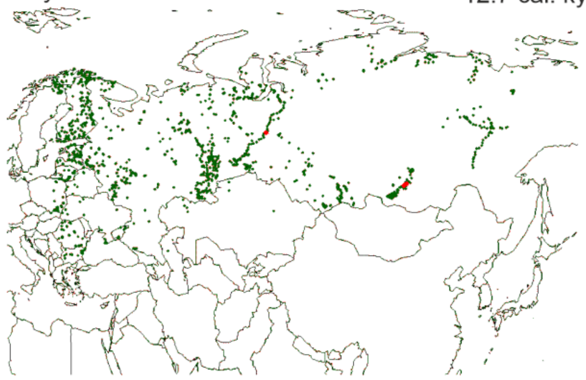
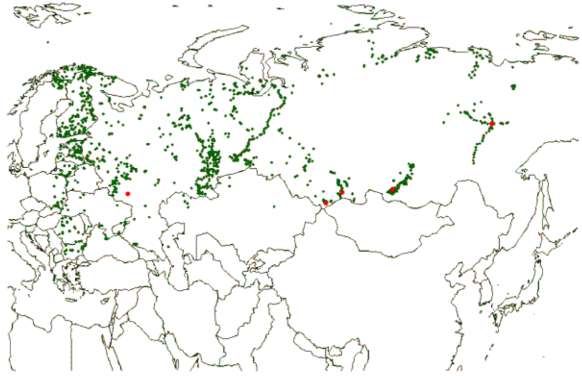


Fig. S6.6. Scatterplots of the WAPLS training set taxa percentages plotted against the aridity index values of the sampling site

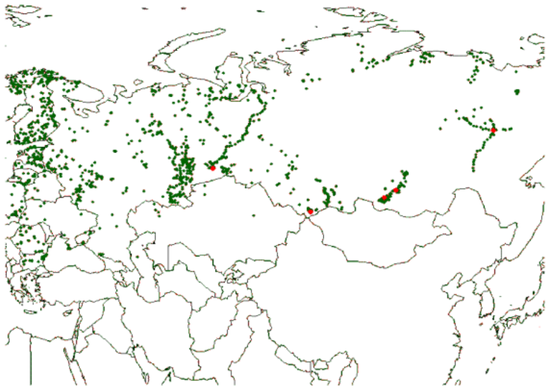
Zamostye 12.7 cal. kyr BP



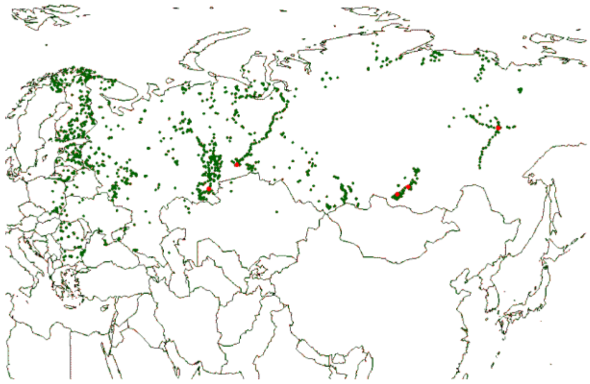
Klukvennoe 12.7 cal. kyr BP



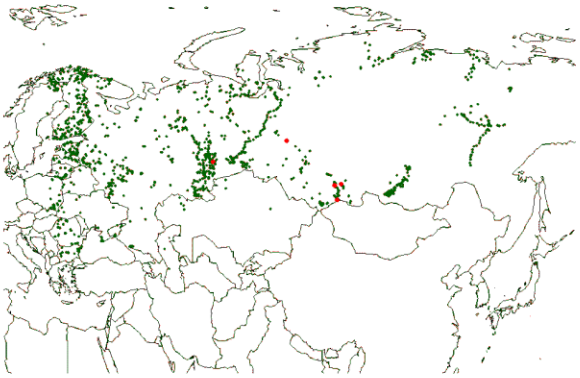
Zamostye 12.4 cal. kyr BP



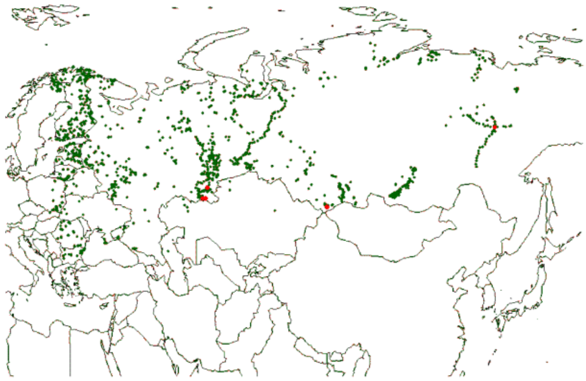
Klukvennoe 12 cal. kyr BP



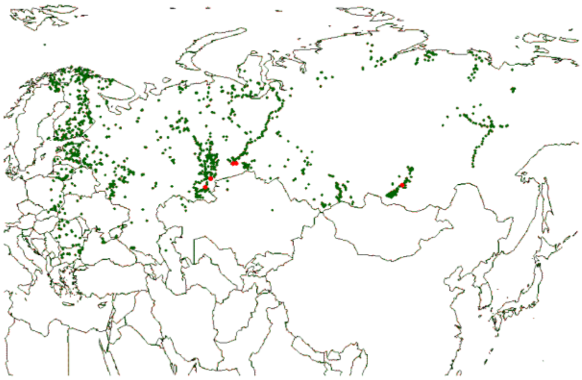
Zamostye 11 cal. kyr BP



Klukvennoe 9.8 cal. kyr BP



Omelchenki 9 cal. kyr BP



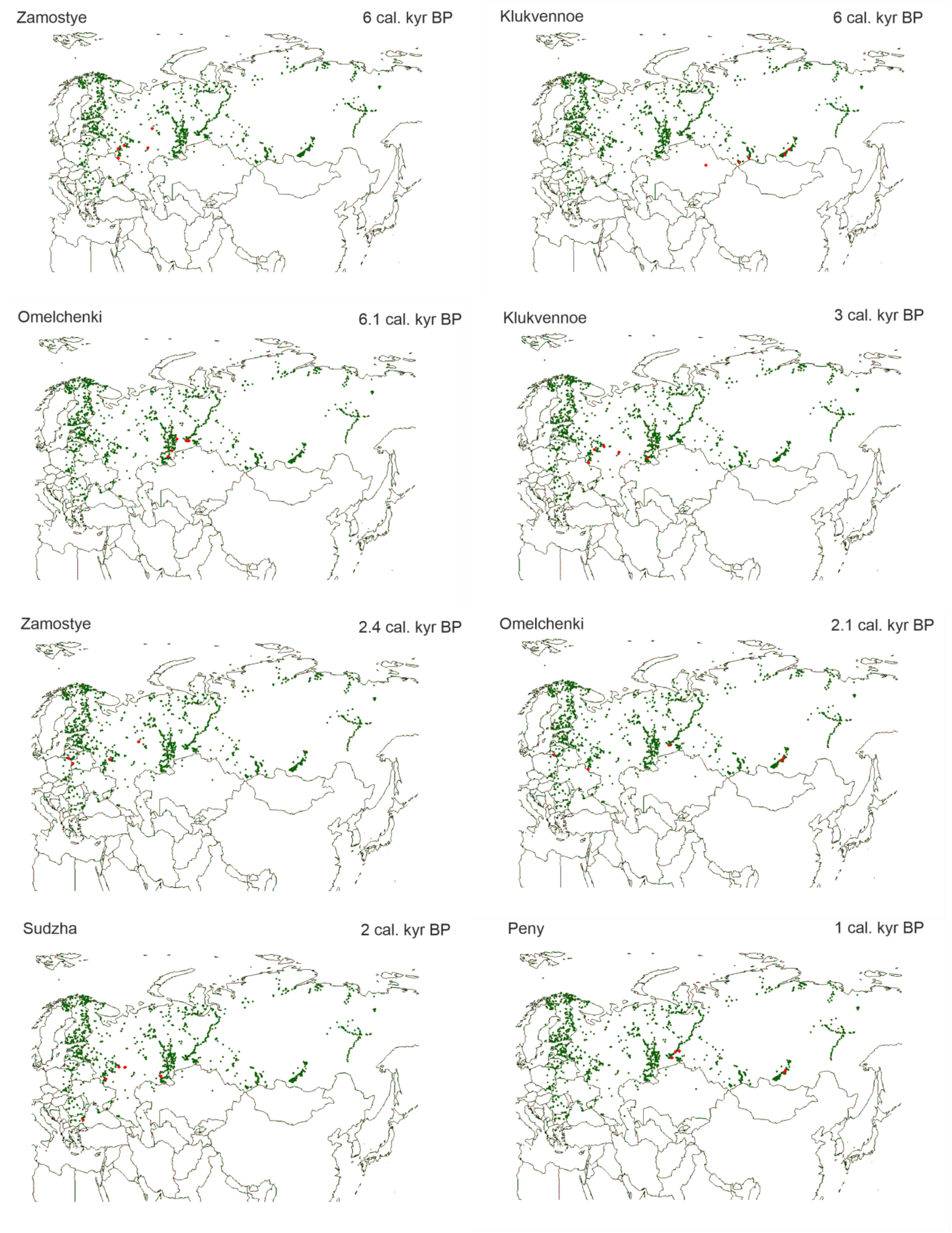


Fig. S6.7. Maps of modern analogues for the MAT climate reconstructions of the sediment cores of Zamostye, Klukvennoe, Sudzha, Omelchenki and Peny for different time periods (used analogues are marked by red colour)

Chapter VII – Synthesis

The present-day vegetation of the East-European forest-steppe was shaped by climate, human activities and fires over thousands of years. In the current chapter I would like to summarize the results gained by the multi-proxy analyses, forest cover and climate reconstructions of the previously discussed sediment cores, and describe past vegetation dynamics of the ecotone.

Vegetation and climate dynamics

~14,700 years ago, the changes in the north Atlantic triggered the Bølling-Allerød interstadial followed by deglaciation processes in Europe (Novenko 2016; Thiagarajan et al. 2014). Prior to the warming, the area of modern East-European forest-steppe was represented by periglacial steppe landscapes in the zone where continuous permafrost becomes sporadic (Velichko 2009). Some sparsely distributed forest patches in areas with sufficient moisture occurred and were replaced by periglacial tundra further north. The Late Glacial was a transition period from the ice age to the interglacial and consisted of several alternations of climate warming and cooling events (Svensson et al. 2008) which triggered changes in the vegetation of the East-European forest-steppe region.

Following the interstadials, a forest-steppe dominated by pine – *Pinus sylvestris* – together with *Betula, Picea, Alnus fruticosa, Salix* and possibly *Pinus sibirica* was spreading in the river valleys. The first such interstadial corresponding to GI 1e (Rasmussen et al. 2014) reflected in the studied records started ~14.8-14.7 cal. kyr BP when forest-steppes with up to ~25% of forest cover developed at sites with favourable hydrological conditions. The next Greenland interstadials GI 1a-c started ~13.9-13.8 cal. kyr BP and had a longer duration (Svensson et al. 2008). The forest cover reached 35% for river valleys and 22% for watersheds. The aridity index reconstructions by the WAPLS transfer function method indicated dry sub-humid climate for the first warming (AI ~0.6-0.64) and possible humid climate conditions (up to 0.7 on watersheds and 0.75 for the river valleys) for the second one. MAT-reconstructed precipitation values did not exceed 400 mm/yr. Such an increase in available moisture can be also explained by melting permafrost increasing surface runoff (Wang et al. 2021). Incisions in the LGM terraces and the formation of large river palaeochannels indicate a higher-than-present water runoff during 18-13 cal. kyr BP (Panin et al. 2017). The floods rose above the present-day levels as indicated by large levees and overbank loams on LGM terraces.

Similar processes were happening in the western part of the East-European forest-steppe around the same time period (Hájková et al. 2022). The arboreal pollen reached 90% indicating the development of forests dominated by *Pinus sylvestris* and milder and wetter conditions in the area of the Carpathian Mountains compare to the study region.

Sensitive to the North Atlantic changes (Lukanina et al. 2022), the region was represented by dry or meadow steppes (Borisova et al. 2006; Muratova et al. 1993; Spiridonova 1991) during the stadial periods of the Late Glacial corresponding to GI 1d ~14.3 cal. kyr BP and GS 1 ~12.9 cal. kyr BP commonly known as the Younger Dryas (Rasmussen et al. 2014; Svensson et al. 2008). During the stadials, semi-arid conditions prevailed (AI ~0.35-0.4 reconstructed by MAT and ~0.4-0.55 by WAPLS) with ~300 mm/yr of precipitation.

The spread of forest into steppe followed the Holocene warming ~11.7 cal. kyr BP when milder climate conditions and the retrieval of the glacier allowed the development of forests all over the East-European Plain (Novenko et al. 2015; Novenko 2016; Zanon et al. 2018). The western part of Volyno-Podolian meadow steppes of the ecotone was covered by pine *Pinus sylvesrtis* open forests with *Betula*, *Picea* and some admixture of broadleaf trees including *Ulmus, Corylus, Tilia* and *Quercus* already since the beginning of the Holocene by ~11.5 cal. kyr BP (Hájková et al. 2022). By ~10 cal. kyr BP the amount of arboreal pollen reached the modern values in south of the broadleaf forest vegetation zone (Novenko et al. 2015) implying the development of pine-birch forests to the north of the ecotone. Within the ecotone in its central parts, pine-birch forest-steppe developed ~10.5-10 cal. kyr BP in the river valleys spreading southwards by ~9 cal. kyr BP. However, the forests reached the watershed areas only by ~8 cal. kyr BP. Throughout the early Holocene the aridity index values were rising from semi-arid (~0.35-0.4) to dry sub-humid and possibly even humid ones in the river valleys of the central-northern parts of the ecotone (0.65-0.7 for river valleys in the center of the ecotone) decreasing southwards and on watersheds (0.45-0.5) by 8.2 cal. kyr BP. Precipitation increased from ~300mm/yr to ~400-450 mm/yr. Therefore, we reject the first hypothesis as the dynamics of the forest-steppe in the study region was much more complex. The delay between the establishment of warmer conditions of the beginning of the Holocene and the rise in moisture availability sufficient for the development of the forest-steppe ecotone took more than 3000 years.

Milder conditions of the river valleys allowed the spread of broadleaf trees such as *Quercus robur*, *Tilia, Corylus* and *Ulmus* already in the early Holocene and by ~8.5 cal. kyr BP broadleaf forest dominated at the Zamostye study area within the river valley. The situation was different on arid watersheds and at the southern limits. On the watersheds of the center of the ecotone, broadleaf forests were not spreading until ~6.5-6 cal. kyr BP while in the south – until ~5 cal. kyr BP. As an ecotone, East-European forest-steppe reacts to climate changes better than the areas within biomes. Dynamic throughout the Holocene, it reflected climate patterns of the Northern Hemisphere evidenced by the Greenland cores (Svensson et al. 2008) and insolation (Berger and Loutre 1991).

The summer insolation of the Northern Hemisphere was at its peak in the early Holocene decreasing during the middle Holocene to the late Holocene (Berger and Loutre 1991). The temperatures in Greenland, highest in the early mid-Holocene, were also decreasing towards the late Holocene (Svensson et al. 2008). The spread of the broadleaf trees outside of the river valleys coincided with decreasing summer insolation and temperatures in the late mid-Holocene and late Holocene lowering evapotranspiration values and increasing the amount of available moisture (Berger and Loutre 1991; Svensson et al. 2008).

Similar trend was true for the forest development in general. By ~6.5 cal. kyr BP forests developed within the river valleys of the center of the ecotone where the reconstructed forest cover values reached ~37%. Simultaneously the forest cover increased to 19% at Klukvennoe indicating forest-steppe on the watershed. ~4.5-4 cal. kyr BP the forest cover estimates have risen to ~42% in the valleys and up to ~30% on the watersheds and in the south suggesting the spread of forests until the southern limits of the ecotone. Around the same time the broadleaf component reached the highest values in the records. The climate reconstructions show a slow constant increase in available moisture throughout the Holocene which promoted consistent increase in forest cover and the broadleaf component of the forests.

The aridity index was changing from ~0.45-0.5 of semi-arid climate ~8.2 cal. kyr BP to 0.66-0.7 of the humid climate by ~4.5-4 cal. kyr BP.

In the western Volyno-Podolian part of the ecotone with milder climate conditions and higher moisture availability, broadleaf forest became dominant earlier than in the study region by ~9 cal. kyr BP (Hájková et al. 2022; Kremenetski 1995). The forest cover, however, likely did not change as significantly as the arboreal pollen has almost not changed the values since reaching ~80-90% in the early Holocene. The share of the broadleaf taxa, however, kept growing throughout the middle Holocene similarly to the study region.

The northern limits of the ecotone within the upper Don River area to the north-east from the study region, as shown by Shumilovskikh et al. (2018) have a very similar trend with the studied records (working hypothesis 2). A strong increase in the forests' development as well as their broadleaf component happened around 5 cal. kyr BP reaching its maximum in the late Holocene by 4-2.5 cal. kyr BP (Novenko et al. 2014a; 2016b; 2017).

The late Holocene was the most forested time period for the East-European forest-steppe ecotone. ~2.5-2 cal. kyr BP the central part of the ecotone was entirely covered with forests both in the river valleys and on watersheds reaching the southern limits of the modern ecotone with ≥ 40% of the reconstructed forest cover. The forest maxima is reflected in all the available records from the subcontinental forest-steppe (Borisova et al. 2006; Hájková et al. 2022; Kremenetski 1995; Marinova and Atanassova 2006; Novenko et al. 2014a; 2014b; 2016b; 2017; Shumilovskikh et al. 2018; 2019a; Spiridonova 1991). The reconstructed aridity index values indicate humid climate (0.65-0.8) with mean annual precipitation of 600 mm/yr.

The region of the modern forest-steppe ecotone was dynamic throughout the Holocene evolving from the steppe landscapes of the early Holocene to the forests of the late Holocene. Exceptionally stable steppe boundary (Khotinsky 1984) doesn't seem to be possible considering the width of the ecotone of around 200 km. However, it is hard to judge on the natural extent of the forest-steppe due to a very strong human impact particularly at its the southern limits in the late Holocene and the sensitivity of the southern treeline to human activities (Lukanina et al. 2023).

Human impact

Favourable for people throughout Palaeolithic (Spiridonova 1991; Velichko 2009), the area of the modern East-European forest-steppe region was quite populated already since the Upper Palaeolithic times. However, the spread of agricultural societies and the following deforestation started to change the landscape of the ecotone drastically already by ~3.5 cal. kyr BP (Lukanina et al. 2023).

Many researches link the Holocene thermal maximum to the Neolithic revolution as one of its driving forces (Ashraf and Michalopoulos 2010; Bar-Yosef 1998). Holocene climate reconstructions for Central Europe show the beginning of the warm period around 8 cal. kyr BP, with the highest annual temperature close to 6 cal. kyr BP (Davis et al. 2003). Rising winter and summer temperatures are observed for the records from the western part of the East-European forest-steppe and forest zones through a substantial increase in broadleaf taxa and a decline in pine (Hájková et al. 2022; Kremenetski 1995; Schwörer et al. 2021). Milder climate conditions could have favoured the adoption of agriculture in the west of the ecotone by ~7.3 kyr BP (Motuzaitė Matuzevičiūtė and Telizhenko 2016).

In more continental eastern part of the forest-steppe, a significant broadleaf forest expansion occurred not earlier than ~6.5 cal. kyr BP (Lukanina et al. 2022; Novenko et al. 2014a; 2016b; 2017). Sufficient moisture of forest-steppe and favourable summer and winter temperatures might have provided proper conditions for the start of agriculture in more continental areas of the ecotone. ~1000-1200 years of difference between the establishment of a milder climate in the west and the east might explain the gap in the adoption of agriculture by the Dnieper-Donets culture foragers living within the study region at that time compare to the agricultural societies of western Ukraine (Anthony 1995).

However, meadow steppes of the forest-steppe ecotone were attractive for the development of stock breeding as a basis of subsistence economy for the Copper Age cultures ~5 cal. kyr BP at the southern limits of the ecotone. The decrease in forest cover ~4.8 cal. kyr BP and the increase in charcoal might be explained by the development of metallurgy in the region following the arrival of the Yamnaya culture (Shramko et al. 1977), and the existence of the nearby Donetsk copper mines (Chernykh 1976).

The change in moisture balance by the beginning of the late Holocene was beneficial for agriculture and supported the switch of the main activities of the Bronze Age cultures from nomadism to farming even at the southern limits of the ecotone. From the time of the Srubnaya culture ~3.5 cal. kyr BP, the area experienced significant deforestation reflected as a decrease of arboreal pollen and the forest cover associated with the increase of agricultural and ruderal markers. Corresponding with the decline in the forest cover local fire events might indicate land clearance for farming or the use of slash-and-burn agriculture. Remarkable deforestation events were attributed to the Chernyakhiv archaeological culture from the 3-5th centuries CE (Lyubichev 2019; Shramko et al. 1977) when the forest cover estimates dropped to 14%, and since the 10th century CE after the defeat of the Khazar Khaganate by Kievan Rus (Lukanina et al. 2023).

By the 13th century CE a total deforestation reached the northern limits of the ecotone due to the use of the land for agriculture. Disrupted during the Tatar-Mongol invasions, it continued in the 15th century under the control of the Grand Duchy of Lithuania, while the minimum of the reconstructed forest cover was registered in the 17th century CE (Kasianova et al. submitted) when the Belgorod defence line protected the fertile chernozem soils of the forest-steppe against invaders. The conversion of the forest-steppe into an agrarian steppe left over only very small patches of semi-natural vegetation today. Therefore, the third hypothesis was rejected as the process of deforestation was complex. Significant deforestation started ~3.5 cal. kyr BP while the total deforestation was gradual since the last ~800 yrs ago.

Fire impact

During the Late Glacial (14.8-12.5 cal. kyr BP), charcoal concentration and influx were low, suggesting low fire activity. Low fire in open pine-dominated forests is surprising but can be explained by melting permafrost with the onset of warming likely increasing surface runoff (Wang et al. 2021). Fire activity in flammable vegetation was hampered by the presence of water or water saturated soil, decreasing flammability through fuel moisture.

Fire activity strongly increased during the Younger Dryas. Severe and/or frequent burnings occurred in dry steppe environments documented by pollen. The dominance of grass-type charcoal particles during the Younger Dryas also indicated steppe landscapes.

Adapted to frequent fires, grassland vegetation provided enough fuel for short and frequent fires (Leys et al. 2018; Neary and Leonard 2020).

The Holocene fire regime at Zamostye is in line with the long-term fire dynamics in Central and Eastern Europe with the early Holocene maximum, mid-Holocene minimum and anthropogenically caused fires in the late Holocene (Feurdean et al. 2020). Dry climate conditions together with sufficient fuel provided by the forest-steppe vegetation induced its high flammability in the early Holocene (Feurdean et al. 2020; Pausas and Ribeiro 2013). Furthermore, pine trees dominated the vegetation and were more prone to ignition than temperate broadleaf deciduous trees due to lower leaf moisture, volatile compounds and resins, retention of dead biomass in the crown, ladder fuels and slower litter decomposition (Feurdean et al. 2020). Early Holocene fires are known for the records from Central and Eastern Europe (Feurdean et al. 2012; Feurdean et al. 2013; Florescu et al. 2018; Lukanina et al. 2022). Feurdean et al. (2020) provided the time period of ~10.5-8 cal. kyr BP as the time with the highest biomass burning in the early Holocene. Drier conditions at the southern limits of the forest-steppe ecotone promoted more severe wildfires compare to the its central and northern parts. The fires' intensity decreased after ~7 cal. kyr BP simultaneously with the reduction of forest cover and, consequently, the amount of fuel and some expansion of the broadleaf trees with positive effects on fuel moisture and a dampening effect on biomass burning compare to the pine forest-steppe (Feurdean et al. 2020). The fire events after that might have had anthropogenic nature.

With the spread of broadleaf forests and rising aridity index in my study region, the amount of background charcoal decreased further ~5-4 cal. kyr BP and was low in the second half of the Holocene. Micro-charcoal, on the other hand, somewhat increased due to the human-induced deforestation likely following the development of metallurgy (Chernykh 1976) and a better particles transport indicating regional fires. The late Holocene fire dynamics was strongly connected with the human activities as the further development of forests and increased humidity would likely keep the fire activity at a low level. Detected fire events strongly correlated with the periods of low arboreal pollen content and forest cover together with a higher content of crops' pollen implying burning of wood after land clearance or the use of slash-and-burn agriculture. Such fire events occurred during the periods of Catacomb and Srubnaya cultures ~3.8-3.6 and ~3.3 kyr BP, Scythoid ~2.5 kyr BP, Chernyakhiv ~1.7-1.8 kyr BP, and Penkivka ~1.4 kyr BP. Later fire events belonged to the Kievan Rus period (10th and 13th centuries CE) and to the early 19th century. Due to the vast majority of the land used for agriculture in the late Holocene, the role of wildfires on the vegetation has become less important compare to the human impact (Pavleichik and Chibilev 2018).

Conclusions

The vegetation of the East-European forest-steppe is highly sensitive to moisture availability caused by the northern hemispheric climate changes. Thus, the stadial periods of the Late Glacial caused the steppe spread while forest-steppe was developing during the interstadials. The spread of forest into steppe followed the Holocene warming ~11.7 cal. kyr BP when milder climate conditions and the retrieval of the glacier allowed the development of forests all over the East-European Plain. The region became an ecotone between forest and steppe by ~8 cal. kyr BP with the development of forest-steppe outside of river valleys. During the Younger Dryas and early Holocene, the ecosystem was affected by forest fires, but in later periods of time their role has decreased. The spread of the broadleaf trees coincided with decreasing summer insolation and temperatures in the late mid-Holocene and late Holocene lowering evapotranspiration values and increasing the amount of available moisture. During the late Holocene the region became entirely forested including its southern limits.

The southern treeline is extremely sensitive to human activities and was largely defined by those over the past ~3500 yrs. With the development and spread of agriculture, local societies induced deforestation and fires to clear the land. Since the last 800 yrs the area of the ecotone became deforested reaching the minimum forest cover in the 17th century. The conversion of the forest-steppe into an agrarian steppe left over only very small patches of semi-natural vegetation today.

Considering the current global warming the southern tree line is likely to shift northwards bringing the area to the mid-Holocene conditions with the dominance of steppe. Lower aridity index and therefore moisture availability will increase the risks of droughts affecting agriculture in the region.

Perspectives

East-European forest-steppe is vast territory which remains largely understudied. The eastern part of the ecotone lacks palynological records over a thousand kilometres including the Central-Russian-Volgian and Trans-Kamian-Volgian areas and with just few available records from the Kungur-Krasnoufimsk forest-steppe (Shumilovskikh et al. 2021b) making it impossible to fully understand the forest-steppe dynamics at its full extent over the Holocene. The absence of such knowledge provides the risks for nature conservation and agriculture due to the current climate warming.

The region of Moldavian-Ukrainian steppes also lacks modern well-dated palynological studies. As a region in between comparably well-studied Volyno-Podolian meadow steppes and my study region, the records from there can fill the gap between the two areas allowing more details on the west-eastern gradient of the ecotone revealing the history of the spread of the broadleaf taxa during the Holocene and also the interstadials of the Late Glacial providing new insights on the broadleaf taxa dynamics and refugia. A comparison of the data from the subcontinental and sub-Mediterranean subcontinental forest-steppe would help understanding of the forest-steppe vegetation development due to the climate differences.

The pollen records allow the reconstructions of moisture availability as a major climate factor impacting the vegetation of the region. The records of other proxy (e.g. chironomids or GDGTs) can provide quantitative reconstructions of the temperature. Such full-scale climate reconstructions would allow global climate models evaluation.

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Appendix A

Identified pollen, spores and non-pollen palynomorphs (NPP) of the records – complete list and photos of selected taxa

Abbreviations of palynological records:

- Z: Zamostye pollen and NPP record from the central key site (Chapter 2)
- O: Omelchenki pollen and NPP record from the southern key site (Chapter 3)
- SS: pollen record of the surface pollen samples from the East-European forest-steppe

Table of identified pollen, spores and NPP taxa

Family	**Pollen taxon**	**Record**
Adoxaceae	*Sambucus nigra*-type	Z, O, SS
Alismataceae	*Alisma*-type	Z, O, SS
	Sagittaria sagittifolia	Z, O, SS
Apiaceae	Apiaceae	Z, O, SS
Asteraceae	*Artemisia*	Z, O, SS
	Centaurea cyanus	Z, O, SS
	Centaurea jacea-type	Z, O, SS
	Centaurea montana-type	Z, O, SS
	Centaurea scabiosa-type	Z, O, SS
	Cichorioideae	Z, O, SS
	Cirsium	Z, O, SS
	Matricaria-type	Z, O, SS
	Saussurea-type	Z, O, SS
	Senecio-type	Z, O, SS
	Xanthium spinosum-type	Z, O, SS
	Xanthium strumarium-type	Z, O, SS
Betulaceae	*Alnaster (Alnus fruticosa)*	Z
	Alnus	Z, O, SS
	Betula	Z, O, SS
	Carpinus betulus	Z, O, SS
	Corylus	Z, O, SS
Boraginaceae	Boraginaceae	SS
	Echium	Z
	Onosma	O
Brassicaceae	Brassicaceae	Z, O, SS
Campanulaceae	*Jasione montana*-type	Z, O, SS
	Legousia-type	SS

	Phyteuma-type	Z, O, SS
Cannabaceae	Cannabaceae	Z, O, SS
	Humulus lupulus	SS
Caprifoliaceae	*Centranthus*	O, SS
	Lonicera	Z, O, SS
	Valeriana	Z, SS
	Valeriana elongata-group	O
	Valeriana officinalis-group	O
	Valeriana dioica-type	O
Caryophyllaceae	Caryophyllaceae	Z, O, SS
Chenopodiaceae	Chenopodiaceae	Z, O, SS
Cistaceae	*Helianthemum*	O
Convolvulaceae	*Calystegia*	O, SS
	Convolvulus arvensis-type	Z, O, SS
Cornaceae	*Cornus*	SS
Cyperaceae	Cyperaceae	Z, O, SS
Droseraceae	*Drosera*	O
Elatinaceae	*Elatine*	SS
Ephedraceae	*Ephedra distachya*-type	Z, O, SS
	Ephedra fragilis-type	Z, O, SS
Ericaceae	Ericaceae-*Empetrum*-group	O
	Calluna vulgaris	O, SS
Euphorbiaceae	*Euphorbia*	SS
Fabaceae	Fabaceae	SS
	Lathyrus-*Vicia*-type	Z, O, SS
	Lathyrus-type	SS
	Medicago sativa	cf. SS
	Onobrychis	Z, O, SS
	Pisum sativum	O
	Trifolium	Z, SS

	Trifolium pratense-type	O
	Trifolium repens-type	O
	Vicia-type	Z
Fagaceae	*Castanea*	O
	Quercus	Z, O, SS
Gentianaceae	*Gentianella germanica*-type	Z
Geraniaceae	*Geranium*	Z, O, SS
Grossulariaceae	*Ribes*	Z, O, SS
Haloragaceae	*Myriophyllum*	Z
Hydrocharitaceae	*Hydrocharis morsus-ranae*	SS
Hypericaceae	*Hypericum perforatum*-type	Z, SS
Iridaceae	*Iris*	Z, cf. SS
Juglandaceae	*Juglans*	SS
Juncaginaceae	*Triglochin*	Z, SS
Lamiaceae	*Ballota*-type	SS
	Galeopsis-Ballota-group	Z, SS
	Lamiaceae	SS
	Mentha-type	Z, O, SS
Lemnaceae	Lemnaceae	Z, O, SS
Lentibulariaceae	*Utricularia*	O
Linaceae	*Linum alpinum*-type	SS
Lythraceae	*Lythrum*	Z, O, SS
Malvaceae	*Tilia*	Z, O, SS
Montiaceae	*Montia fontana*	Z
Nymphaeaceae	*Nymphaea*	O
Oleaceae	*Fraxinus excelsior*-type	Z, O, SS
Onagraceae	*Epilobium*	Z
Orobanchaceae	*Rhinanthus*-type	Z, O, SS
Papaveraceae	*Papaver rhoeas*-group	cf. Z
	Corydalis-group	Z

	Hypecoum pendulum	SS
Pinaceae	*Abies*	Z, O
	Picea	Z, O, SS
	Pinus s/g *Diploxylon*	Z, O, SS
	Pinus s/g *Haploxylon*	Z
Plantaginaceae	*Plantago albicans*	Z
	Plantago lanceolata-type	Z, O, SS
	Plantago major-media-type	Z, O, SS
	Veronica-type	Z, O, SS
	Callitriche stagnalis	Z, SS
	Callitriche obtusangula	SS
Plumbaginaceae	Plumbaginaceae	Z
Poaceae	*Avena*-type	Z, O, SS
	Cerealia-type	Z, O, SS
	Zea mays	O, SS, cf. Z
	Hordeum-type	Z, O, SS
	Poaceae	Z, O, SS
	Poaceae (>37 mcm)	Z, SS
	Secale	Z, O, SS
	Triticum-type	Z, SS
Polemoniaceae	*Polemonium*	Z
	Polemonium caeruleum	Z
Polygalaceae	*Polygala comosa*-type	Z
Polygonaceae	*Bistorta*-type	Z
	Fagopyrum	Z, O, SS
	Polygonum aviculare-type	Z, O, SS
	Polygonum raii	Z, O, SS
	Rumex acetosa-type	Z, O, SS
	Rumex aquaticus-type	Z, O, SS
	Persicaria amphibia	Z, O

	Persicaria maculosa-type	Z, O
Potamogetonaceae	*Potamogeton natans*-type	Z, O, SS
	Potamogeton pectinatus-type	Z, O, SS
Primulaceae	*Anagallis*-type	SS
	Androsace alpina-type	Z, O, SS
Ranunculaceae	*Ranunculus acris*-type	Z, O, SS
	Ranunculus arvensis-group	Z
	Ranunculus repens	SS
	Thalictrum	Z, O, SS
Rhamnaceae	*Frangula alnus*	O
	Rhamnus-type	Z
Rosaceae	*Agrimonia*-type	Z
	Alchemilla-group	O, SS
	Aruncus-type	Z, O, SS
	Geum-type	Z, SS
	Potentilla-type	O, SS
	Rosa	O, SS
	Rosaceae	Z, O, SS
	Rubus	SS
	Prunus	SS
	Sanguisorba officinalis	Z, O, SS
	Sorbus-group	Z, SS
Rubiaceae	Rubiaceae	Z, O, SS
Rutaceae	*Dictamnus albus*	cf. O
Salicaceae	*Populus*	SS
	Salix	Z, O, SS
Sapindaceae	*Acer*	Z, O, SS
Saxifragaceae	*Saxifraga aizoides*-group	SS
Scorpulariaceae	Scorpulariaceae	Z, O, SS
Solanaceae	*Nicandra physalodes*	SS

	Solanum dulcamara	O, SS
	Solanum nigrum-type	Z, cf. SS
Typhaceae	*Sparganium*-type	Z, O, SS
	Typha latifolia-type	Z, O, SS
Ulmaceae	*Ulmus*	Z, O, SS
Urticaceae	*Urtica*	Z, O, SS
Violaceae	*Viola odorata*-type	Z, O, SS

Family	**Spore taxon**	**Record**
	Monolete	Z, O, SS
	Trilete	Z, O, SS
Sphagnaceae	*Sphagnum*	Z, O, SS
Equisetaceae	*Equisetum*	Z, O, SS
Ricciaceae	*Riccia* cf. *sorocarpa* HdV-165	Z, O

Family	**Algae taxon**	**Record**
	HdV-128	Z, O
	HdV-225	Z
	HdV-229	Z, O
Zygnemataceae	*Mougeotia* sp. HdV-133	Z, O
	Mougeotia sp. HdV-134	Z, O
	Pseudoschizaea NN-61	Z, O
	Spirogyra sp. HdV-132	Z, O
	Spirogyra sp. HdV-130	Z, O
	Zygnema-type HdV-314	Z, O
	Zygnemataceae HdV-58	Z, O
Desmidiaceae	Desmidiaceae /*Closterium idiosporum*-type HdV-60	O

Family	**Animalia taxon**	**Record**
	Copepode or Protozoa HdV-179	Z, O

	HdV-307a	Z, O	
	HdV-307b	Z, O	
	Invertebrata HdV-187a	O	
	Invertebrata HdV-187b	Z, O	
	Invertebrata HdV-187c	Z, O	
	Invertebrata HdV-187d	Z, O	
	Invertebrata mandible	Z	
	Invertebrata remains	Z, O	
	HdV-219	O	
Arcellidae	*Arcella* sp. HdV-352	Z, O	
Conochilidae	*Conochilus natans*-type (Rotifera) HdV-69	Z, O	
Eurycercidae	*Eurycercus* cf. *lamellatus* (Cladocera) HdV-72d	Z	
Notommatidae	*Cephalodella exigua* (Rotifera) HdV-70		O
Trichuridae	*Trichuris* sp. HdV-531		Z, O

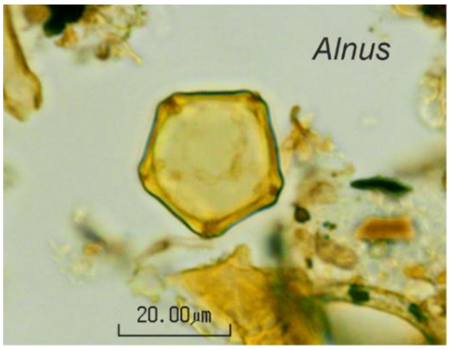
Family	**Fungi taxon**	**Records**
	cf. UG-1129	Z
	HdV-145	Z
	HdV-3a	Z
	UAB-40	Z
	Uredospores	Z, O
	Valsaria-type HdV-263	O
	UG-1081	O
	cf. *Excipularia fusispora* EMA-38	O
Davidiellaceae	Aff. *Cladosporium* BAA-2	O
Diporothecaceae	*Diporotheca* sp. / *D. rhizophila* HdV-143	Z
Geoglossaceae	*Geoglossum sphagnophilum* HdV-77A	Z
Glomeraceae	*Glomus* cf. *fasciculatum* HdV-207	Z, O
Helotiaceae	*Bryophytomyces sphagni* HdV-27	Z, O
Lasiosphaeriaceae	*Arnium*-type HdV-261	Z, O
	Cercophora sp. HdV-112	Z
	Apiosordaria verruculosa HdV-169	O

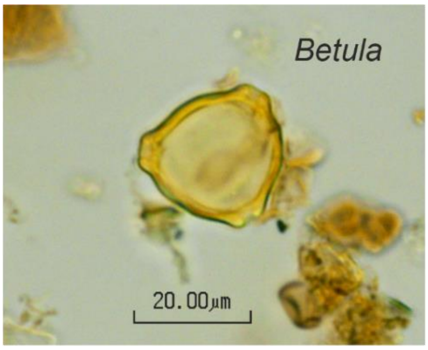
Microthyriaceae	cf. *Microthyrium* spec. HdV-8	Z
Podosporaceae	*Podospora*-type HdV-368	O
Podosporaceae/ Lasiosphaeriaceae	*Podospora*/*Cercophora* BRN-9	O
Sordariaceae	*Sordaria*-type HdV-55a	Z, O
	Apiosordaria verruculosa HdV-169	
	Gelasinospora cf. *reticulispora* HdV-2	O
	Neurospora crassa/*Neurospora* sp. HdV-55c	O
	Ascospores of *Sordaria* HdV-55b-2	O
Trematosphaeriaceae	*Caryospora callicarpa* NN-13	Z
Trichosphaeriaceae	*Brachysporium* HdV-1024	Z
	Brachysporium sp. UG-1099	Z
Tubeufiaceae	*Helicoon pluriseptatum* HdV-30	Z, O

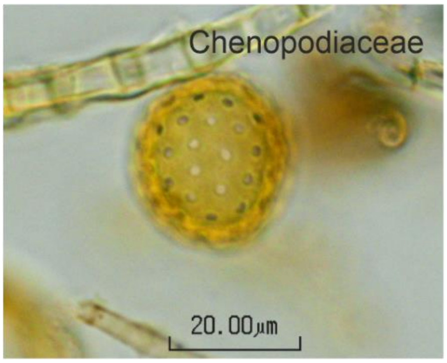
Family	**Plants**	**Records**
Ceratophyllaceae	*Ceratophyllum* sp. HdV-137	Z, O
	Spiralic tracheid (Cormophyta) EMA-68	Z, O

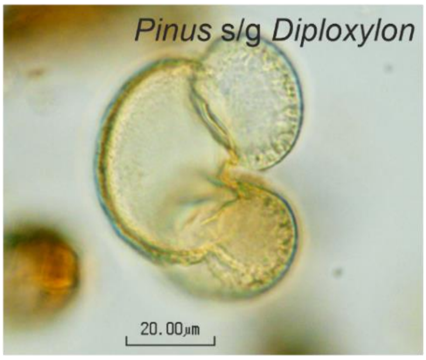
Other NPP	**Records**
HdV-224	O
BM-1	Z
EMA-14	Z
EMA-21	Z, O
HdV-234	Z
HdV-257	Z
HdV-41	Z, O
HdV-986	Z
HdV-989	Z, O

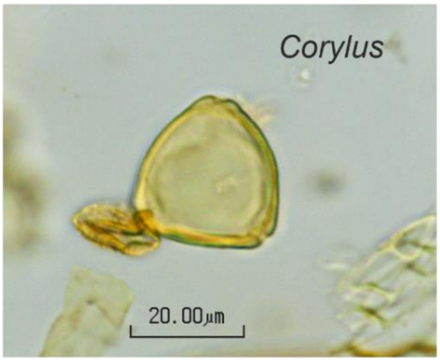
Plates of selected pollen, spores and NPP taxa

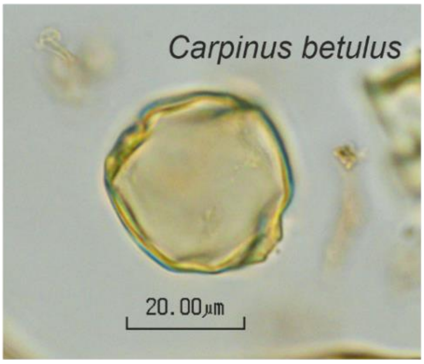


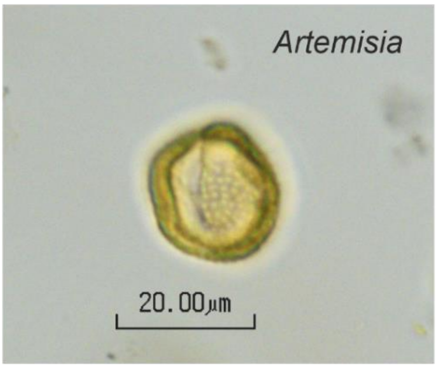


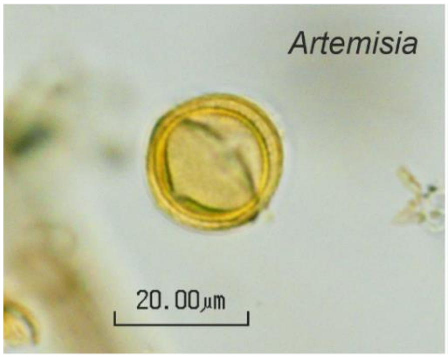


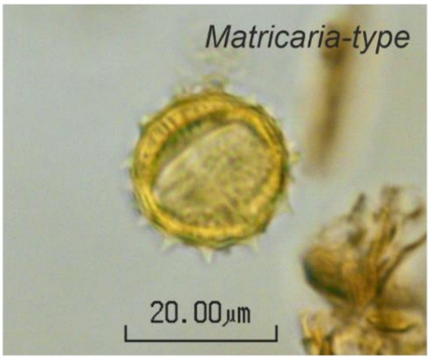


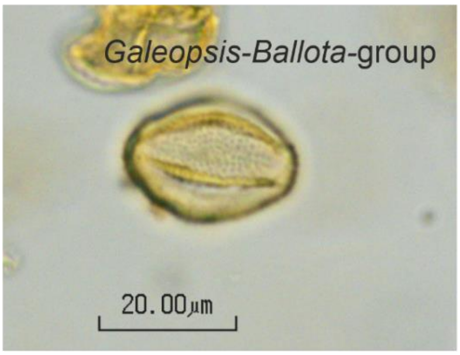


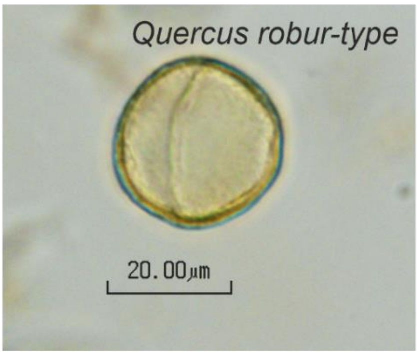


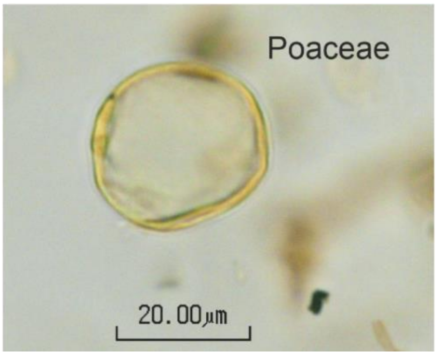


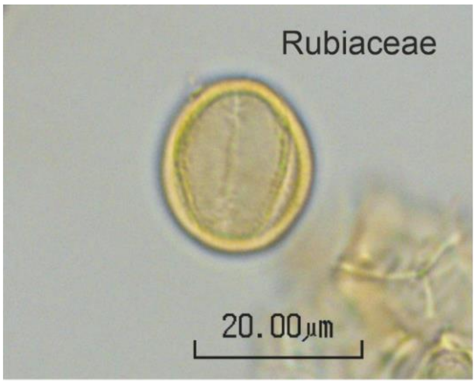


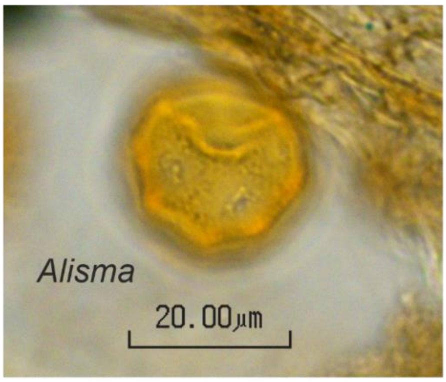


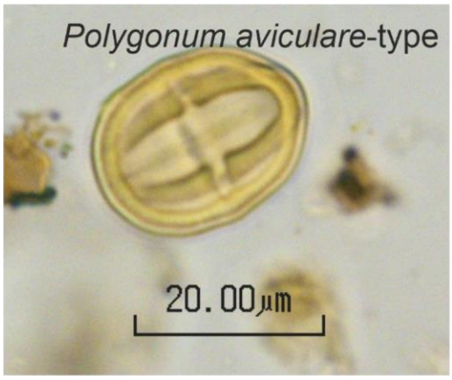


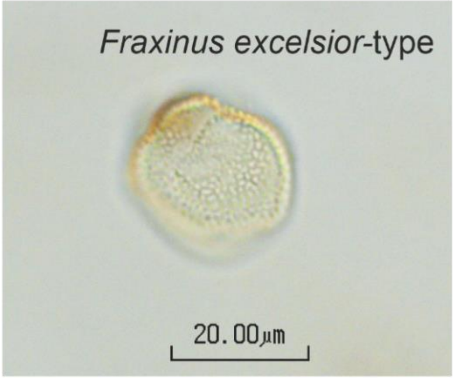


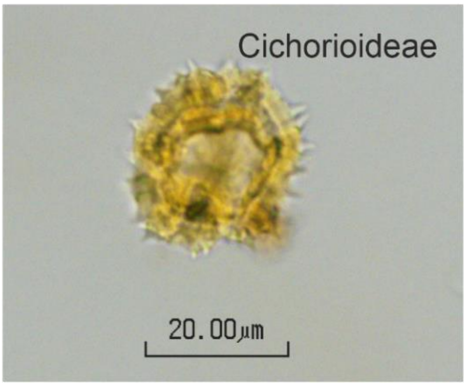


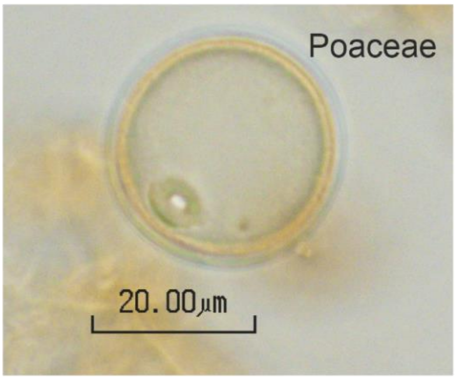

Rubiaceae
20.00µm

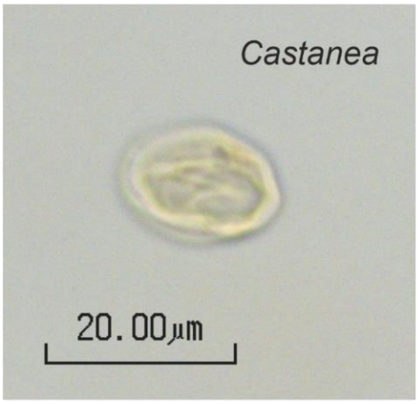

Alisma
20.00µm


Polygonum aviculare-type
20.00µm

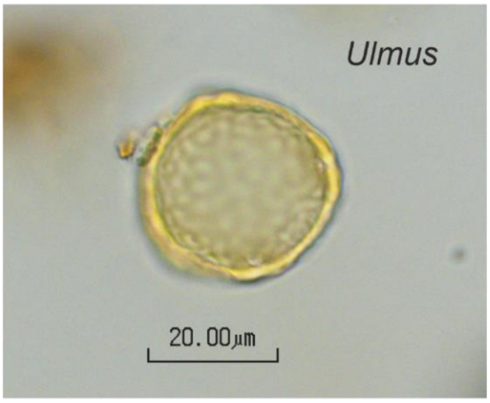

Fraxinus excelsior-type
20.00µm

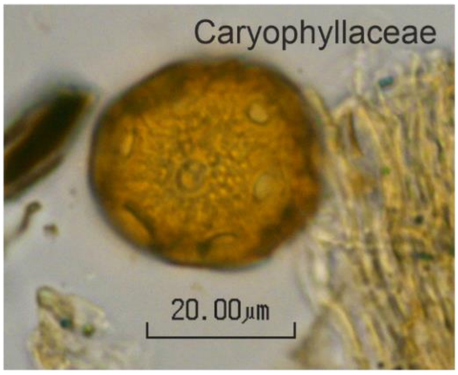

Cichorioideae
20.00µm

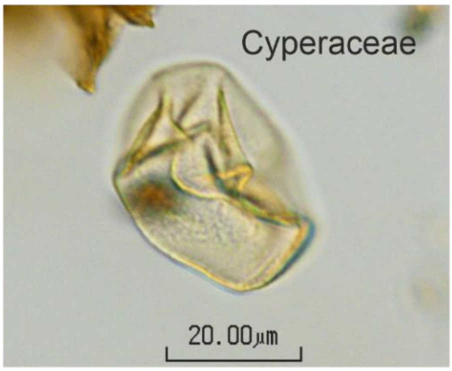

Poaceae
20.00µm

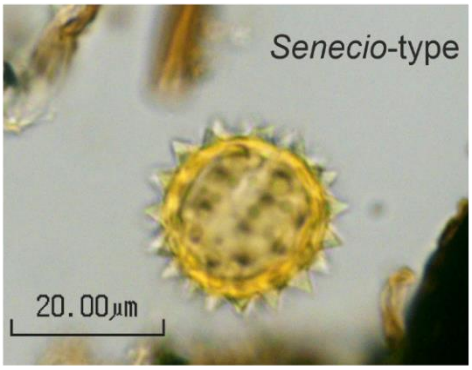

Castanea
20.00µm

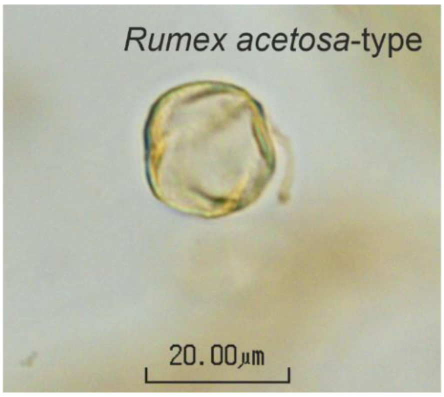

Salix
20.00µm

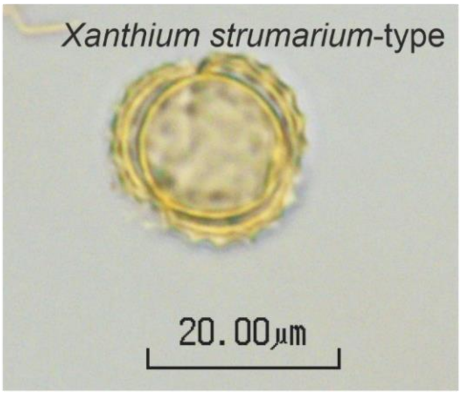

Ulmus
20.00µm

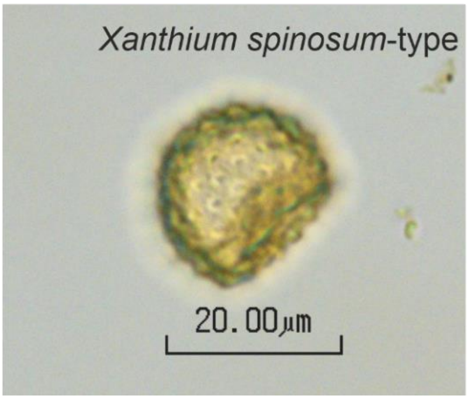

Caryophyllaceae
20.00µm

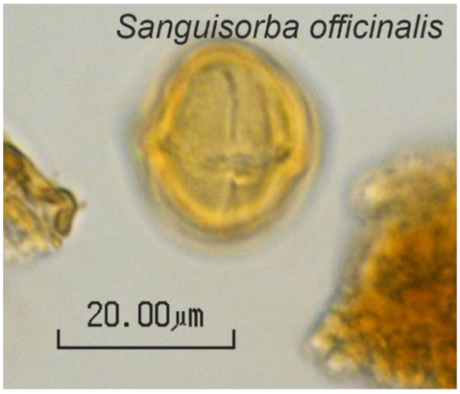

Cyperaceae
20.00µm

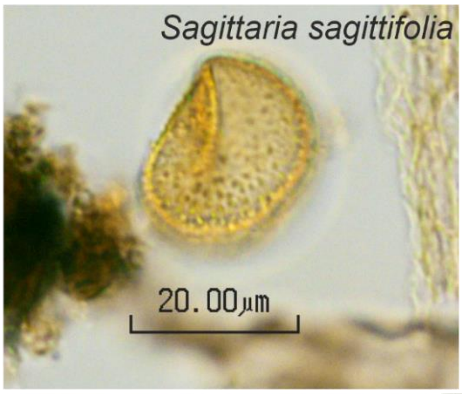

Senecio-type
20.00µm

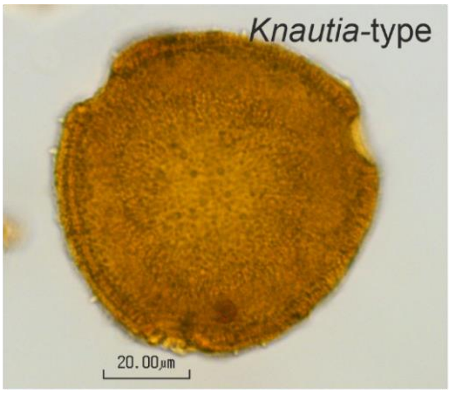

Rumex acetosa-type
20.00µm

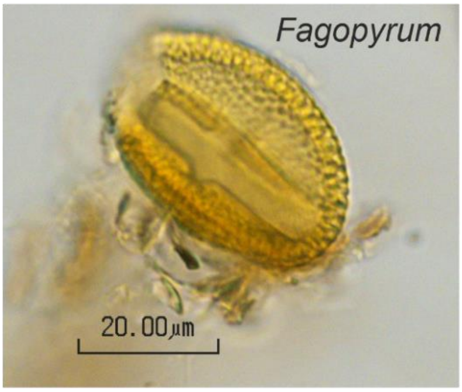

Xanthium strumarium-type
20.00µm

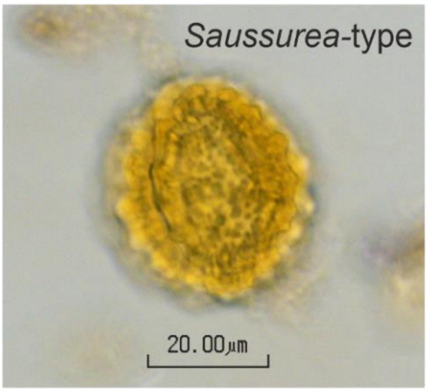

Xanthium spinosum-type
20.00µm


Sanguisorba officinalis

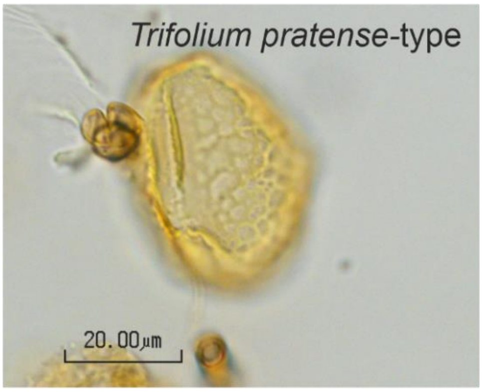

Sagittaria sagittifolia

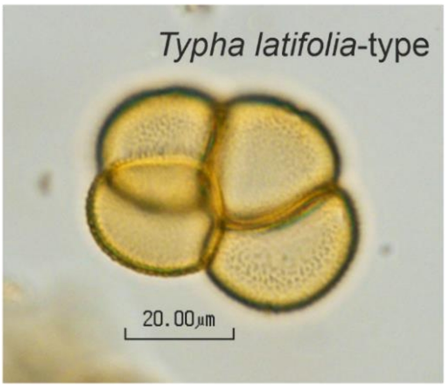

Knautia-type

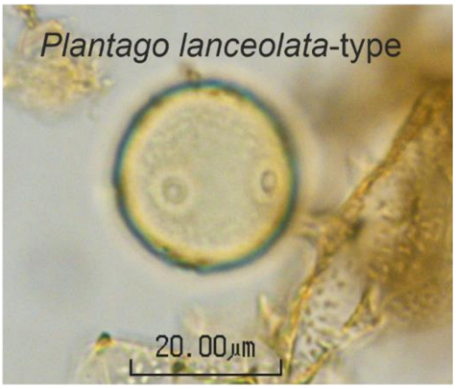

Fagopyrum

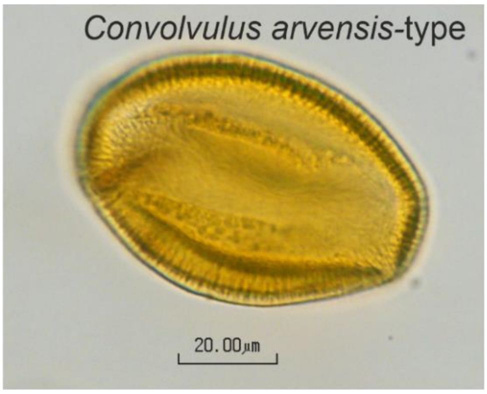

Saussurea-type


Thalictrum

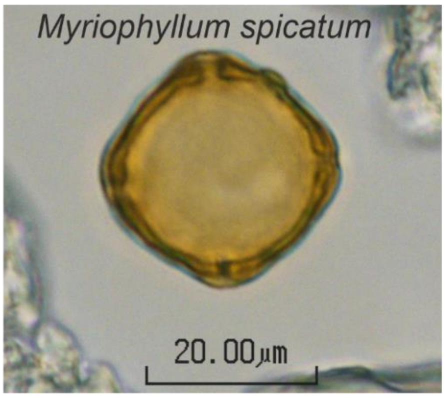

Trifolium pratense-type

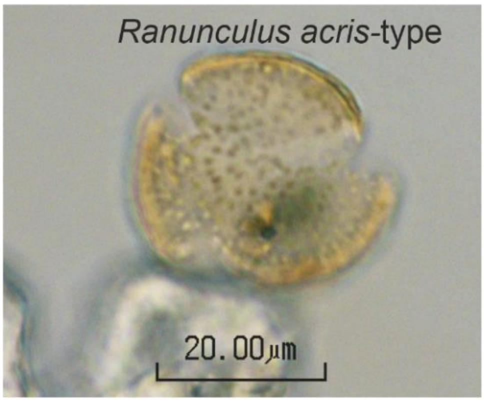

Typha latifolia-type

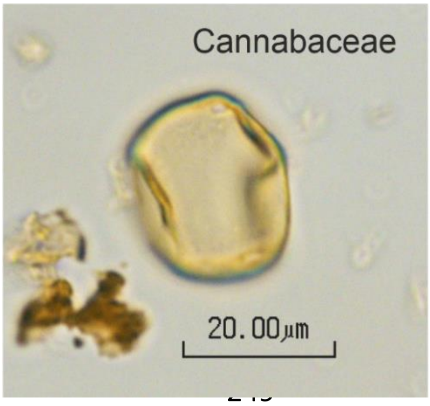

Plantago lanceolata-type

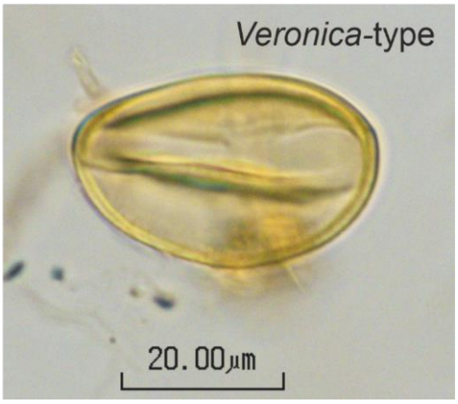

Convolvulus arvensis-type

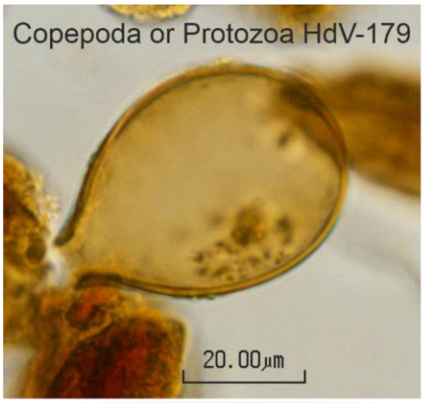

Vicia-type


Myriophyllum spicatum

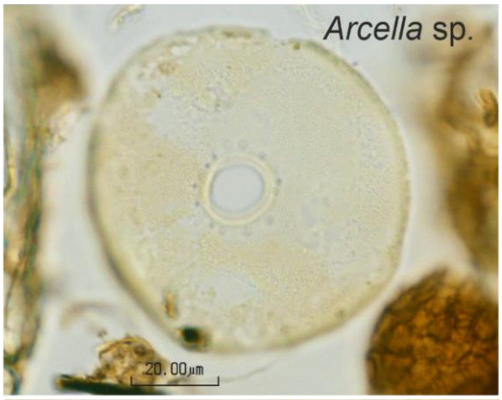

Ranunculus acris-type

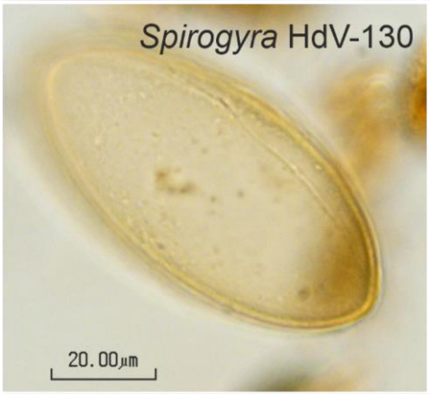

Cannabaceae

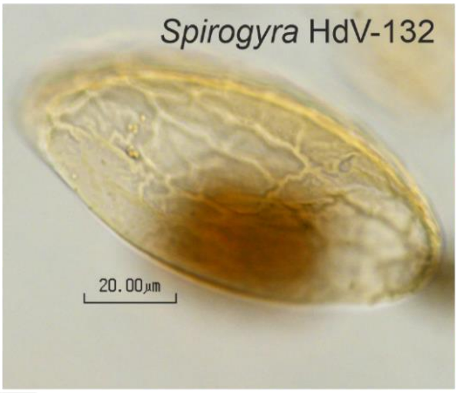

Veronica-type

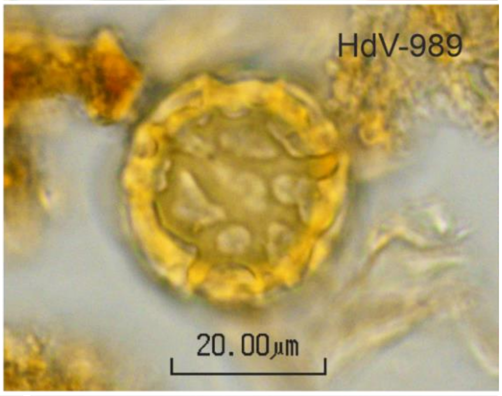

Copepoda or Protozoa HdV-179

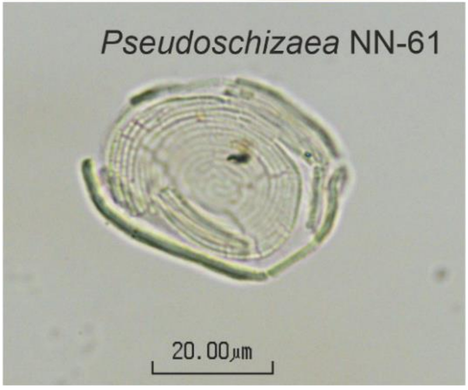

Glomus-type

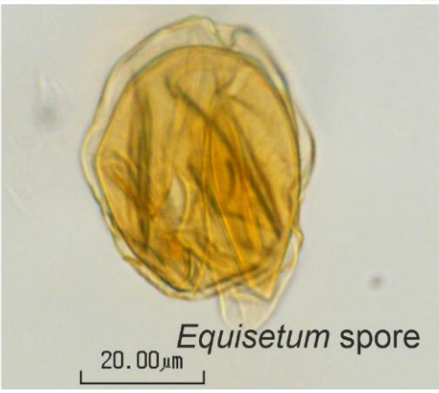

Arcella sp.


Spirogyra HdV-130


Spirogyra HdV-132

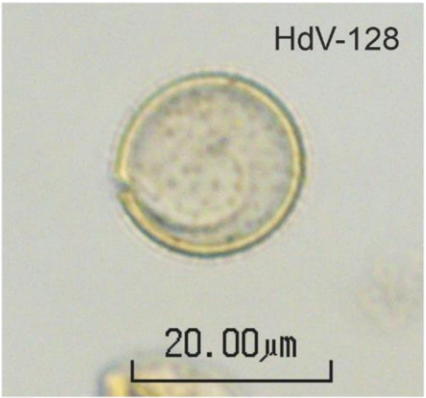

HdV-989

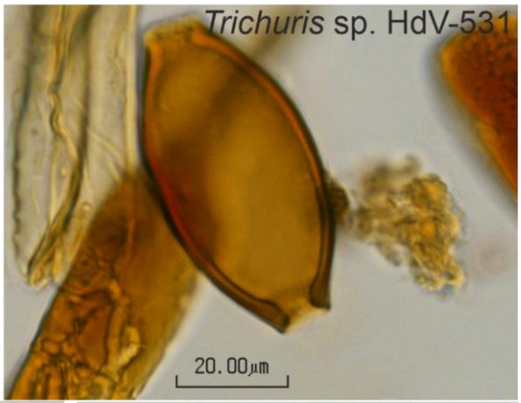

Pseudoschizaea NN-61

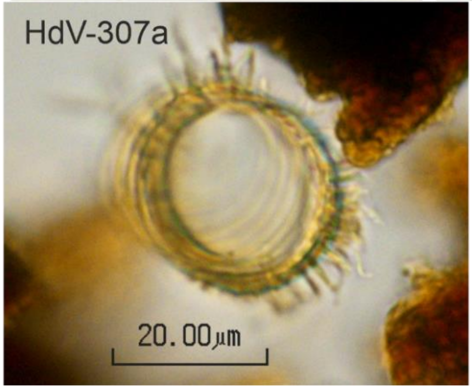

Equisetum spore

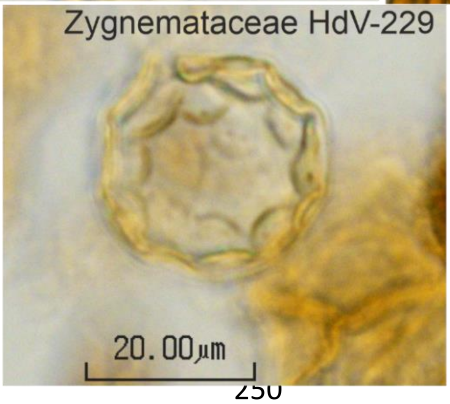

Uredospore

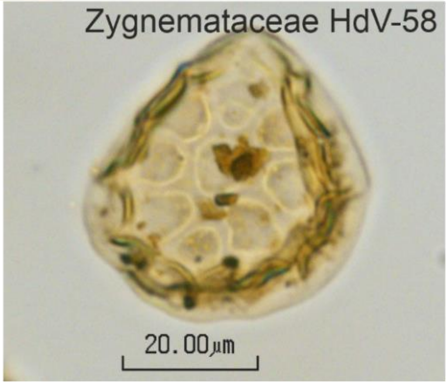

Trilete spore

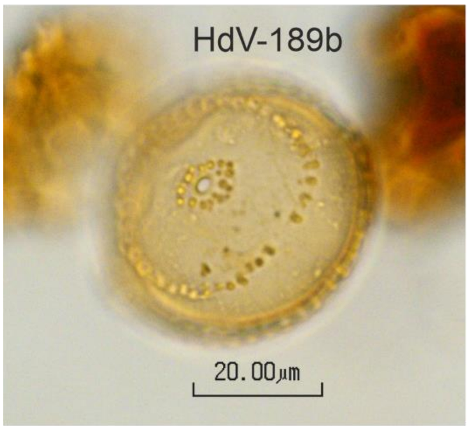

HdV-128

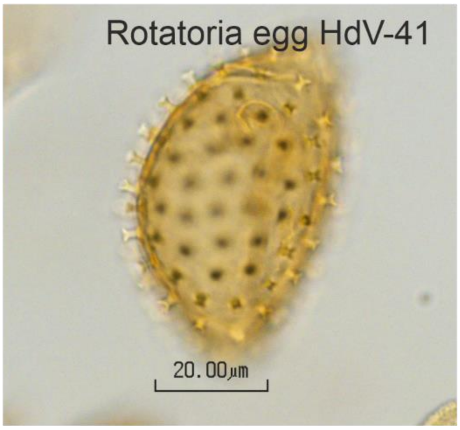

Trichuris sp. HdV-531

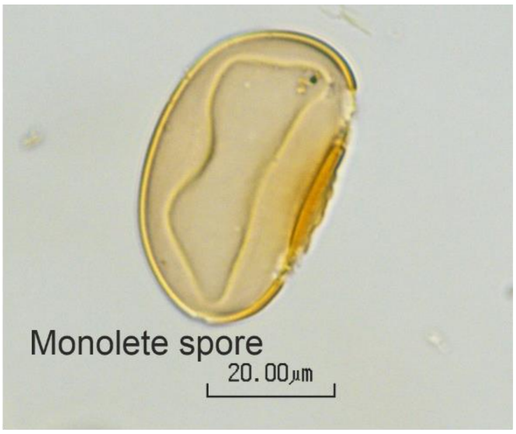

HdV-307a

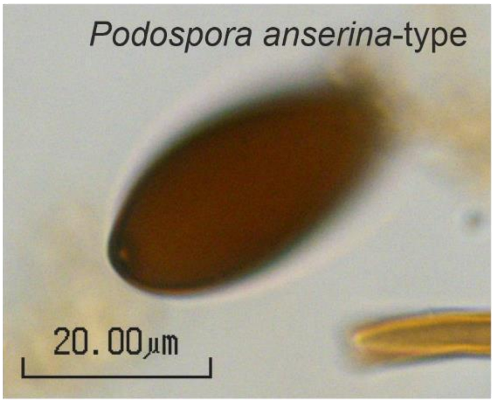

Zygnemataceae HdV-229

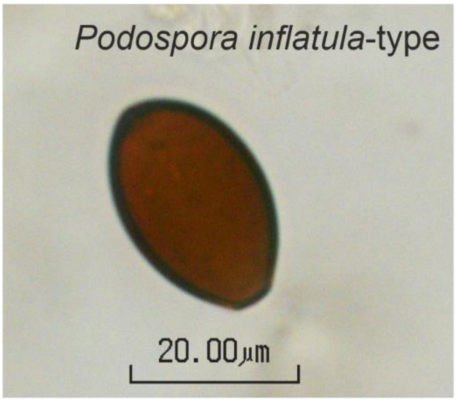

Zygnemataceae HdV-58

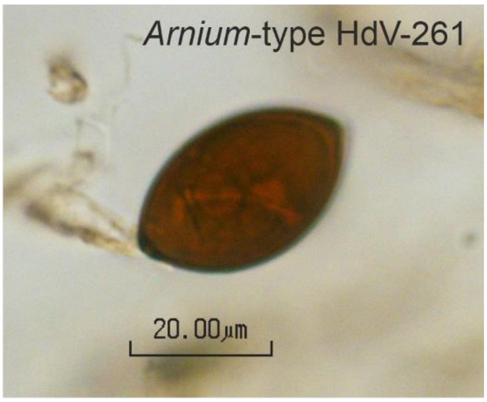

HdV-189b

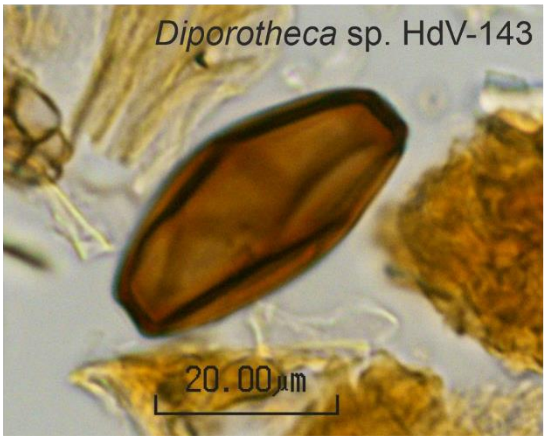

Rotatoria egg HdV-41

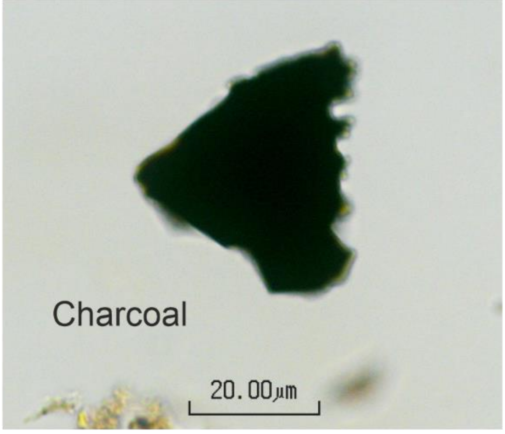

Monolete spore


Podospora anserina-type


Podospora inflatula-type


Arnium-type HdV-261

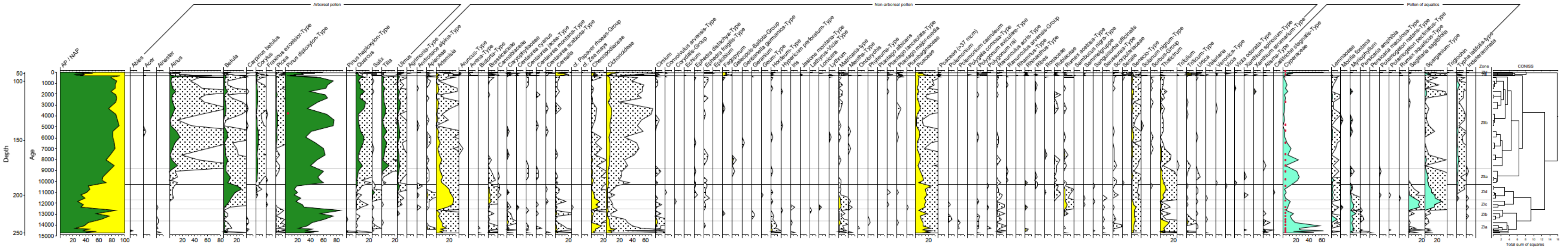

Diporotheca sp. HdV-143

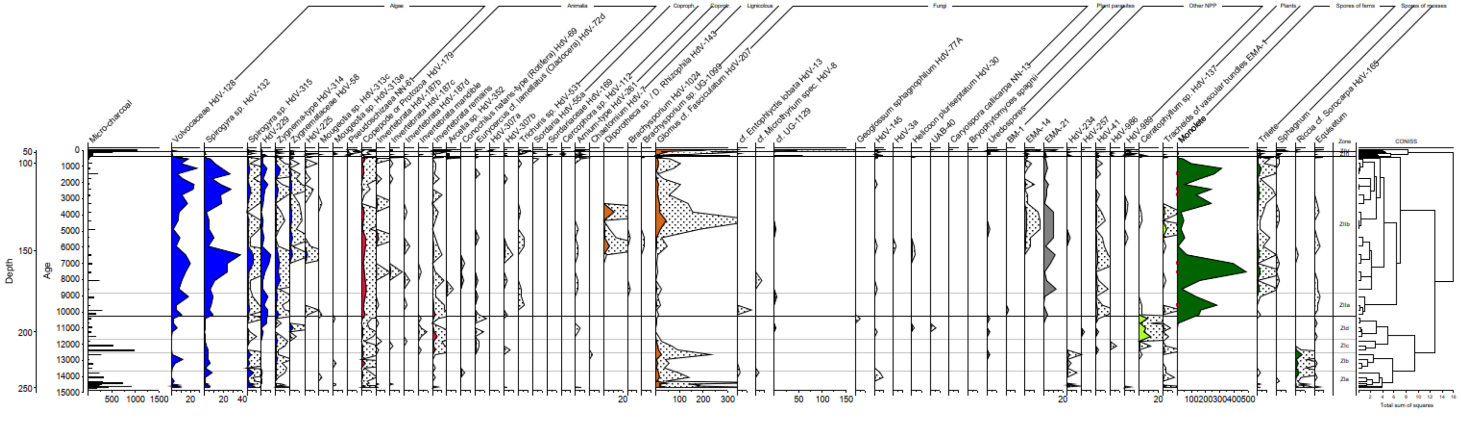

Charcoal

Appendix B

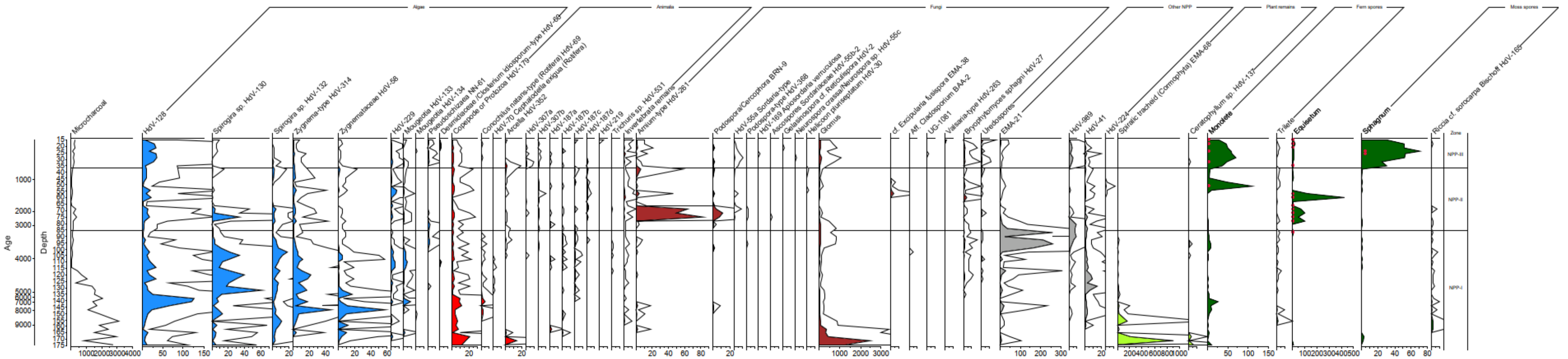
Complete pollen, spores, NPP and charcoal records

Zamostye pollen and NPP records





Omelchenki pollen and NPP records



Surface samples pollen record