The transformation of the forest steppe in the lower Danube Plain of south-eastern Europe: 6000 years of vegetation and land use dynamic

Angelica Feurdean[1,2,3]*#, Roxana Grindean[3] #, Gabriela Florescu[3,4,5], Ioan Tanţău[3,] Eva Niedermeyer[2],

Andrei-Cosmin Diaconu[3], Simon M Hutchinson[6], Anne Brigitte Nielsen[7] Tiberiu Sava[8], Andrei Panait[2],

Mihaly Braun[9] Thomas Hickler[1,2]

[1]Department of Physical Geography, Goethe University, Altenhöferallee 1, 60438 Frankfurt am Main, Germany

[2]Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage, 25, 60325, Frankfurt am Main, Germany

[3]Department of Geology, Babeș-Bolyai University, Kogălniceanu 1, 400084, Cluj-Napoca, Romania

[4]Department of Geography, Stefan cel Mare University, 13 Universităţii Street, 720229, Suceava, Romania

[5]Department of Botany, Faculty of Science, Charles University, CZ-128 01 Prague, Czech Republic

[6]School of Science, Engineering and Environment, University of Salford, Salford, M5 4WT, UK

[7]Department of Geology, Lund University, Sölvegatan 12, 22362 Lund, Sweden

[8]Horia Hulubei National Institute for Physics and Nuclear Engineering (IFIN-HH), Reactorului 30, 077125, Măgurele, Romania

[9]Institute for Nuclear Research of the Hungarian Academy of Sciences, H-4026 Debrecen, Bem tér 18/C, Debrecen, Hungary

Correspondence to: Angelica Feurdean (Feurdean@em.uni-frankfurt.de)

# These authors contributed equally to this work

Abstract

Forest steppes are dynamic ecosystems, highly susceptible to changes in climate and land use. Here we examine the Holocene history of the European forest steppe ecotone in the Lower Danube Plain to better understand its sensitivity to climate fluctuations and human impact, and the timing of its transition into a cultural forest steppe. We used multi-proxy analyses (pollen, *n*-alkane, coprophilous fungi, charcoal, and geochemistry) of a 6000-year sequence from Lake Oltina (SE Romania), combined with a REVEALS model of quantitative vegetation cover. We found the greatest tree cover, composed of

xerothermic (*Carpinus orientalis* and *Quercus*) and temperate (*Carpinus betulus*, *Tilia, Ulmus* and *Fraxinus*) tree taxa between 6000 and 2500 cal yr BP. Maximum tree cover (~50%) occurred between 4200 and 2500 cal yr BP at a time of wetter climatic conditions. Compared to other European forest steppe areas, the dominance of *Carpinus orientalis* represents the most distinct feature of the woodland's composition during that time. Forest loss was under way by 2500 yr BP (Iron Age) with REVEALS

35 estimates indicating a fall to ~20% tree cover from the mid-Holocene forest maximum linked to clearance for agriculture, while climate conditions remained wet. Biomass burning increased markedly at 2500 cal yr BP suggesting that fire was regularly used as a management tool until 1000 cal yr BP when woody vegetation became scarce. A sparse tree cover, with only weak signs of forest recovery, then became a permanent characteristic of the Lower Danube Plain, highlighting recurring anthropogenic pressure. The timing of anthropogenic ecosystem transformation here (2500 cal yr BP) was in between that in

40 central eastern (between 3700 and 3000 cal yr BP) and eastern (after 2000 cal yr BP) Europe. Our study is the first quantitative land cover estimate at the forest steppe ecotone in south eastern Europe spanning 6000 years and provides critical empirical evidence that the present-day forest steppe /woodlands reflects the potential natural vegetation in this region under current climate conditions. This study also highlights the potential of *n*-alkane indices for vegetation reconstruction, particularly in dry regions where pollen is poorly preserved.

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1. Introduction

The projected changes in climate and increasing human environmental impacts are generating global concern about the functioning of ecosystems as well as the provision of ecosystem services (IPCC, 2014; IPBES, 2019). In comparison to the more forested mesic areas of Europe, the drier lowland ecosystems (woodlands, grasslands) and the provisioning (e.g. wood,

50 crops) and regulating services (e.g. soil protection) they provide, have been more strongly impacted by climate change and human activities (Magyari et al., 2010; Tonkov et al., 2014; Feurdean et al., 2015; Kuneš et al., 2015; Novenko et al., 2016; Shumilovkiksh et al., 2018, 2019; Jamrichová et al., 2019; Vinze et al., 2019; Clearly et al., 2019; Gumnior et al., 2020). This partly reflects the lowlands' deeper and more fertile soils and the greater accessibility of the terrain which have promoted extensive agro-pastoral activities and therefore human settlement. Lowlands also include more frequent ecotones i.e.,

55 woodland/grassland borders, which are naturally more sensitive to climate change (Bohn et al., 2003).

According to Bohn et al. (2003), the potential natural vegetation in the study area, the easternmost part of the Lower Danube Plain, also known as the Southern Dobrogea Plateau, is forest steppe, i.e., woodland patches within a matrix of graminoid and forb dominated communities, bordering steppe grasslands i.e., treeless vegetation dominated by graminoids and forbs. This forest steppe and steppe vegetation extends over 6000 km along an east-west gradient across Eurasia (Fig. 1) under

60 climate conditions delimited by a ca. 2 month long late-summer drought for the forest steppe zone and 4–6 months for the steppe (Walter, 1974). However, according to the management plan for the region (Planul de Management, 2016), there are currently few patches of natural steppe vegetation preserved in the Southern Dobrogea Plateau as most have become ruderal

steppe. This, and the fact that the region is one of the most important agricultural areas in south-eastern Europe, suggest that the current vegetation is very different from its natural state, though exactly how different is not known. This is highly relevant
65   as grasslands can be one of the most species-rich vegetation communities in the world (in terms of alpha-diversity) and provide unique farmland biodiversity services (Dengler et al., 2014). Although many grassland species can persist in, or even critically depend on human-dominated landscapes, the increasing intensity of land use is considered the greatest cause of grassland biodiversity decline (Dengler et al., 2014; Feurdean et al., 2018). The Lower Danube Plain represents one of the oldest areas of human occupation in Europe and thus may offer a rich source of information on cultural and societal evolution from a
70   hunter-gatherer to sedentary society (Bălășescu and Radu, 2004; Weininger et al., 2009; Wunderlich et al., 2012; Nowacki et al., 2019c). Determining the variations in cultural rise and transformation with changes in surrounding vegetation and food resources can add an important dimension to our understanding of the evolution of societies within their environment.

Palaeoecological records provide a way to assess the past natural vegetation of a region and the legacy of anthropogenic impacts on the landscapes (Willis and Birks, 2006). However, due to the dry climate of the Lower Danube
75   Plain, very few palaeoecological archives are available to document past natural vegetation types. This leaves many open questions, such as: When and why did the forest cover decline, and how does this landscape composition compare to other forest steppe areas in central-eastern Europe (Magyari et al., 2010; Feurdean et al., 2015; Kuneš et al., 2015), south-eastern Europe (Tonkov et al., 2014; Marinova 2006) and the Eastern European Plain (Novenko et al., 2016; Shumilovkiksh et al., 2018). Most of the archaeological and loess deposits in the region are devoid of an absolute chronology, have poor lithological
80   context and lack favourable pollen preservation (Tomescu 2000). Nevertheless, based on these fragmentary records, it appears that steppe may have covered the landscapes of this region in the early Holocene, while forest-steppe vegetation may have expanded during a moist phase of the mid Holocene (Feurdean et al., 2014; Tomescu et al., 2004; Wunderlich et al., 2012; Hansen et al., 2015). In addition, models of deforestation rates, using a scenario that accounts for population history and technological advances, suggest that the extent of deforestation in the lower Danube basin has increased continuously since
85   4000 cal yr BP (Kaplan et al., 2009; Giosan et al., 2012). However, comparative results from pollen-based and modelling outcomes have shown that some model-based land cover reconstructions strongly underestimated anthropogenic land cover change in most regions in Europe (Gaillard et al., 2010), although, recent studies show a closer match between the two reconstruction techniques (Kaplan et al., 2018). Indirect evidence for the Holocene persistence of steppe grasslands in this region comes from the genetic investigation of steppe species including *Adonis vernalis*, *Astragalus exscapu*s, *Stipa capillata*,
90   and *S. pulcherrim*, which mostly show a unique genetic diversity reflecting the continuous occurrence and limited past migration of these steppe elements within Europe (Kropf et al., 2020; Plenk et al., 2020).

Here we present a pollen-based quantitative vegetation reconstruction, along with records of long-chain higher plant-wax *n*-alkanes, charcoal, coprophilous fungi and geochemistry to determine lake catchment and in-lake ecosystem changes from Lake Oltina, south-eastern Romania. We aim to explore the role of the climate, natural and anthropogenic disturbances
95   on the dynamics of the Lower Danube Plain landscapes, and, more specifically, address the following research questions:

i)   Is forest steppe the natural vegetation type of the Lower Danubian Plain under climatic conditions similar to those at present?

ii)   Has the tree cover been more extensive in the past and was it composed of more moisture demanding taxa?

100 iii)   When did this area undergo the most marked land cover and land use and was this transformation continuous?

This is the first pollen based quantitative land cover estimate in the forest steppe of south eastern Europe and allows the hypothesis of the naturalness of steppe/forest steppe ecosystems in this region to be critically tested. It further determines its sensitivity to climate and anthropogenic impact, which will inform environmental decision making to mitigate the

105 desertification phenomena currently threatening the study area. Our results can also be used to better test land cover change scenarios in anthropogenic land use and land cover models (Harrison et al., 2020).

2 Study area

2.1 Geography, climate and vegetation

110 Lake Oltina (44°09'16"N 27°38'13"E, 7 m a.sl.) is located on the floodplain of the Danube river, the Lower Danubian Plain, in south-eastern Romania (Fig. 1). It is the largest fluvial lake on the Danube floodplain with a surface area of 33 km^2 and is part of a Natural Reserve and a NATURA 2000 site (ROSPA0056; Management Plan 2016). The lake has a major tributary, Caranaua Fetii, and is connected to two smaller lakes, Ceamurlia and Iortmac, located upstream as well as to the Danube river via an artificial dam built to prevent flooding (Telteu, 2014). The climate in the study region is termed excessively temperate

115 continental with a mean annual temperature of ca. 11°C, a mean January temperature of ca. -1 °C and a mean summer temperature of 25°C. Annual precipitation is about 400 mm (Adamclisi Weather Station). The geology of the catchment comprises limestone and loess deposits, whereas the soils are represented mainly by haplic and luvic chernoziums and phaenozems, (IUSS WRB 2006). Friable steep loess deposits are frequently eroded delivering a clastic sedimentary influx into the lake (Romanescu et al., 2013).

120 The main potential vegetation types of the region include forest, forest steppe and calciphile steppe (Bohn at al., 2003). The main forest types are: thermophilous mixed deciduous broadleaf forests (subtypes G21, G22 and G34 according to Bohn et al. 2003); mesophytic deciduous broadleaf forests (subtypes F49, F67); forest steppe (subtype L13) and steppe (subtype M5). Additionally, alluvial forests (subtypes U19, U20), halophytic vegetation (P33) and tall reed vegetation and sedge swamps (R1) prevail (Bohn et al., 2003). Corine Land Cover data (2012) indicates that the present land cover within a 20 km

125 radius of the lake comprises ca. 65% arable land and orchards, 19% steppe and semi-natural grassland and 16% deciduous forest (Grindean et al., 2019; S1). Important tree species in forests within this radius, and thus the most relevant for the pollen source area, are *Quercus pubescens, Q. pedunculiflora, Q. robur, Q. cerris, Q. virgiliana, Carpinus orientalis, Acer tataricum, Tilia tomentosa*, *Fraxinus excelsior*, *Ulmus minor,* whereas hygrophilous tree taxa, growing along the Danube River, are

represented by *Populus nigra*, *P. alba*, *Salix alba* and *S. fragilis*. Shrubs occur abundantly either as understory vegetation or

130   as thickets and are composed of *Fraxinus ornus, Cotinus coggygria, Prunus mahaleb*, *P. spinosa*, *P. cerasifera*, *Rosa canina*, *Pyrus communis*, *Crataegus monogyna*, *Amorpha fruticosa*, *Gleditsia triacanthos*, *Elaeagnus angustifolia* and *Ailanthus altissima*. Natural grassland steppic species are common on calcareous slopes and include *Stipa stenophylla*, *S. ucrainica*, *S. capillata*, *Poa angustifolia*, *Festuca valesiaca*, *Botriochloa ischaemum*, *Artemisia austriaca*, *Agrostis tenuis*, *Carex humilis*, *Centaurea orientalis*, *Astragalus ponticus* and *Thymus marschallianus* (Sârbu et al., 2009; Grindean et al., 2019).

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3 Material and Methods

3.1 Core collection, lithology and chronology

Sediment cores were extracted with a Livingstone piston corer (1m long, 5cm diameter) from the central part of the lake (1.8m water depth) in spring 2016. The less consolidated sediment at the surface (36cm) had previously been retrieved with a gravity

140   corer in 2014. A lithostratigraphic description was made according to changes in texture, colour, magnetic susceptibility and the organic carbon content (LOI).

Volume magnetic susceptibility (κ_{vol}) was measured with a Bartington Instruments Ltd MS2 meter and E point sensor (Bartington Instruments, 2008). For LOI, samples were dried overnight at 105 °C, combusted for 5 hours at 550°C and then for 2 hours at 900°C, and LOI is expressed as percentage loss of the dry weight (Heiri et al., 2001). A composite sedimentary

145   core record totalling 964 cm was constructed using the uppermost 10 cm from the gravity core and ten overlapping Livingstone core sections. To determine the erosion and anoxic conditions in the lake, elemental geochemical concentration was measured on 190 sediment samples (extracted at ~5 cm intervals along the core) and subsequently dried and homogenised using a non-destructive Niton XL3t 900 X-Ray Fluorescence analyser (fpXRF). NCS DC73308 was employed as a Certified Reference Material (CRM). Measurement follows the procedure described by Hutchinson et al. (2015).

150   The chronology was established based on eighteen AMS ^{14}C measurements (Table 1). Attempts to constrain the chronology of the top core via ^{210}Pb and ^{137}Cs gamma assay measurements failed to produce any meaningful results probably due to surface sediment mixing. An attempt to establish a tephra-based chronology also failed due to a poor match to any known volcanic eruptions. The radiocarbon age estimates were converted into calendar years BP via BACON software (Blaauw and Christen, 2011) using the INTCAL13 data set of Reimer et al. (2013). An age–depth curve was derived based on a smoothing spline

155   model (Fig 2; for details on age depth construction see S2).

3.2 Vegetation reconstruction

3.2.1 Pollen based quantitative reconstruction of land cover using the REVEALS model

To determine the past vegetation cover we used pollen analysis on samples of 1 cm^3 at intervals ranging between 5 and 10 cm

160   (a total of 105 samples) along the composite core. Sediment preparation followed the protocol of Goeury and de Beaulieu (1979). We identified the pollen grains using the atlases of Reille (1995, 1999) and calculated the pollen percentages on the basis of the total sum of terrestrial pollen grains. We corrected for biases in taxon-specific pollen productivities and dispersal,

and thereby produced a quantitative reconstruction of the vegetation cover in the region surrounding Lake Oltina using the Regional Estimates of Vegetation Abundance from Large Sites, i.e., REVEALS model (Sugita, 2007). In this model, we used

165 pollen productivity estimates (PPE) for the most characteristic plant taxa from the studied region. For 13 plant taxa that include five woody and eight herbaceous and shrubs taxa we have used PPEs measured in this particular region (Grindean et al., 2019). We have complemented these with literature-based PPEs for 14 additional taxa that significantly contribute to the regional vegetation composition (Table 2). We used the Sugita (2007) dispersal model with default settings for neutral atmospheric conditions and wind speed (3 m/s). The literature-based fall speed of each pollen type (Table 2) is used to model dispersal.

170 The spatial extent of the regional vegetation is set at a 100 km radius. The vegetation cover reconstructed using REVEALS always adds up to 100%, which means that taxa not included in the model, as well as non-pollen producing areas, are ignored. The 27 taxa selected for our REVEALS model represent between 77 and 95 of the percentages in the terrestrial pollen sum. Significant changes in the vegetation assemblages were defined using stratigraphically constrained cluster analyses (incremental sum of squares method) of REVEALS based vegetation cover percentages in Tilia (Grimm, 2004).

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3.2.2 Leaf wax *n*-alkanes based climate and vegetation reconstruction

To determine the climate conditions and the predominant vegetation type, 60 sediment samples were selected along the composite core to determine the concentration of higher-plant derived *n*-alkane homologues. *n*-Alkanes are an integral part of higher-plant leaf epicuticular waxes, highly resistant to degradation and among the most stable lipid components of the

180 protective waxes coating terrestrial plant leaves (Eglinton and Eglinton, 2008; Sachse et al., 2012). *n*-Alkanes were extracted from freeze-dried and finely ground sediment samples (ca. 1 g dry weight) with a Büchi Speed Extractor at 75 °C and 100 bar using 20 ml of a mixture of dichloromethane/methanol (9:1) for 10 min, which was repeated three times. Total lipid extracts (TLE) were dried under a stream of N2 at 36 °C. The a-polar fraction containing *n*-alkanes was eluted from the TLE by silica-gel column chromatography using hexane. *n*-Alkanes were subsequently isolated from the a-polar fraction using urea-

185 adduction (Vasiliev et al.,2013). *n*-Alkanes homologues were separated and quantified by gas chromatography/mass spectrometry (GC/MS) using a Thermo Finnigan Trace GC equipped with a HP-5MS column (30 m x 0.25 mm x 0.25 μm) connected to a Thermo Finnigan DSQ II mass spectrometer. The GC oven was held at 70 °C for 1 min, ramped at 10 °C/min to a final temperature of 280 °C, which was held for 15 min. *n*-Alkanes were identified by comparison of their mass spectra and retention time to an external standard (n-C7 to n-C40; Supelco) at a concentration of 25 ng μl. They were quantified using

190 total ion chromatogram peak areas calibrated against the external standard. Precision of the quantification is 96% as inferred from the standard deviation of repeated standard runs (n = 5). Concentrations of individual *n*-alkanes were expressed as ng μl dry weight of sediment.

In this study, we calculated the ratio of straight-chain *n*-alkanes of different chain (homologues) lengths as these have been previously used as proxies for the relative contribution of various types of plants in lacustrine sediments (e.g. Ficken et al.,

195 2000; Zhou et al., 2005). Average chain length (ACL) is an indicator of the relative abundance of short (C_{16}-C_{20}) vs long chain *n*-alkanes and may be linked to the predominance of higher taxonomic plants over lower taxonomic plants including algae

(Ficken et al., 2000; Eglinton and Calvin, 1967). Within the long chain *n*-alkanes, the abundance of *n*-alkanes with *n*-C_{31} and *n*-C_{33} may be indicative of grass predominance, whereas *n*-C_{27} and *n*-C_{29} may indicate a predominantly tree covered landscape (Aichner et al., 2010; Meyers, 2003). It should be noted that some overlap within the mid chain length alkanes *n*-C_{23} and *n*-C_{25}

200 is possible (Aichner et al., 2010; Meyers, 2003). The *n*-Alkanes proxies were calculated using the following equations:

ACL25–33 =$(25 \times C25 + 27 \times C27 + 29 \times C29 + 31 \times C31 + 33 \times C33)/(C25 + C27 + C29 + C31 + C33)$, (Poynter et al., 1989)

205 Tree vs. grass= $(C_{27}+C_{29})/(C_{31}+C_{33})$, (Aichner et al., 2010).

3.3 Regime disturbances by fire and herbivores

To determine past disturbance by fire, macroscopic charcoal particles were counted on samples of 2 cm^3 extracted at 1 cm contiguous intervals. Samples were bleached, wet-sieved through a 150-μm mesh and identified under a stereomicroscope

210 following the methodology described in Feurdean et al. (2017). Here we report only the results for total macro-charcoal particles. We calculated the macro-charcoal accumulation rate (CHAR, particles cm^{-2} yr^{-1}) by dividing the total macro-charcoal concentration by sediment deposition time (yr/cm). To determine past grazing activity, coprophilous fungi (*Sporomiella,* Sordaria-type and *Podospora*) were tallied during routine pollen counting (van Geel et al., 1980; Bakker et al., 2013). Percentages of coprophilous fungi were determined by adding their own sum to the total terrestrial pollen sum.

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4. Results

4.1 Chronology and sediment composition

The lithology of the core showed little variability throughout the profile and comprises clay, gyttja clay and sandy clay. The age-depth model indicates a rather constant sediment accumulation rate with a mean of 5 yr /cm and no evidence of hiatuses

220 (Fig. 2; S2). The OM as determined from LOI at 550°C varied between 3 and 10% with slightly higher values between 5000 and 3500 cal yr BP and over the past 2000 years (Fig. 3). Our selected geochemical detrital element, Zr proxy for erosion, showed the lowest values between 5500 and 3500 cal yr BP (up to 150 ppm) and greater, highly fluctuating values over the 2500 years (Fig. 3). The Fe: Mn ratio, our proxy for anoxic conditions in the lake, generally displayed large variability throughout the profile, although values were higher between 4000 and 3500 cal yr BP, around 3000 and between 2000 and

225 1500 cal yr BP (Fig. 3).

4.2 Landscape reconstruction from pollen

Three major periods of change in land cover and vegetation openness were detected over the last 6000 years at Lake Oltina based on the cluster analysis: open temperate deciduous broadleaf forest between 6000 and 4200 cal yr BP; the maximum

230 extent of broadleaf forest tree cover between 4200 and 2500 cal yr BP and the expansion of grassland between 2500 cal yr BP

to the present (Fig. 4). Results from the REVEALS model suggest that landscape openness was ca. 10-15% greater than the estimates derived from the raw pollen data. Overall, REVEALS indicate a greater proportion of *Carpinus orientalis*, *Tilia*, *Acer*, Rosaceae, Cerealia and Asteraceae, and a lower proportion of *Corylus avellana, Betula, Ulmus, Alnus, Fraxinus, Salix, Artemisia*, Chenopodiaceae than the raw pollen data (Fig. 4). *Quercus, Plantago lanceolata* and Poaceae show a largely similar
235 abundance in both the raw data and REVEALS estimates.

6000-4200 cal yr BP: Open temperate deciduous broadleaf forest or forest-steppe

The REVEALS estimate of tree cover fluctuated around 40%, compared to ~ 55% in the raw pollen percentages, and was primarily represented by *Carpinus orientalis, Quercus, Carpinus betulus, Corylus avellana, Tilia* and *Ulmus* (Fig. 4). The
240 REVEALS model predicts an almost equal proportion of total forb (*Artemisia,* Chenopodiaceae, Asteraceae, Rosaceae, Brassicaceae, *Plantago major*, *Thalictrum,* Caryophylaceae) and grass (Poaceae) in the herbaceous cover (Fig. 4). However, in the raw pollen percentages, forbs dominate the herbaceous assemblages (30%) whereas Poaceae constitutes ~ 20% (Fig. 4; A3). The Cerealia cover estimate fluctuates around ~ 20% in the REVEALS model and was below 5% in the raw pollen percentages. CHAR values were high between 6000 and 5000 cal yr BP and declined markedly thereafter (Fig. 3). The
245 abundance of coprophilous fungi (*Podospora, Sordaria* and *Sporomiella*), on the other hand, rose between 5000 and 4000 cal yr BP (Fig. 3; A1).

4200-2500 cal yr BP: Maximum extent of temperate deciduous broadleaf tree cover

Tree cover increased to its maximum extent in the profile (fluctuating around 55%) and was mostly represented by *Carpinus*
250 *orientalis* and *Quercus* with some occurrence of *Carpinus betulus, Corylus avellana* and *Tilia* (Fig. 4). The rise in *Carpinus orientalis* abundance is more evident in the REVEALS reconstruction (40%) than in the raw pollen percentages (20%). In the herbaceous cover, Poaceae declined the most but there were no marked changes in pollen of primary anthropogenic indicators (Cerealia; Fig. 4). Both, the abundance of CHAR and of coprophilous fungi decreased to one of the lowest in the profile (Fig. 3).

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2500-0 cal yr BP: Decline in Carpinus orientalis-Quercus broadleaf cover; the expansion of grassland/pasture and arable cover

The tree cover declined abruptly to ca. 20%; this was most evident for *Carpinus orientalis,* from 40% to 10% (Fig. 4). However, tree cover fluctuated strongly over the last 2500 years; with intervals of lower values (20%) between 2500 and 1700 cal yr BP,
260 and over the last 1000 years, and of increases (30%) between 1700 and 1000 cal yr BP (Fig. 4). The REVEALS estimate also suggests an increased proportion of grass (Poaceae), cultivated cereals (Cerealia and *Secale cereale*) and fobs. Among forbs, ruderal taxa Asteraceae, *Plantago lanceolata* and Rosaceae showed the most visible increase (Fig. 4; A1). CHAR values increased gradually from the beginning of this time interval and attained a maximum in the profile between 2000 and 1700 cal

yr BP, followed by the lowest values in the profile over the last 1000 years (Fig. 3). The abundance of coprophilous fungi was
265 particularly elevated between 2500 and 2000 cal yr BP and over the last 1000 years.

4.3 *n*-Alkane based lake ecosystem changes

The $(C_{27}-C_{29})/(C_{31}-C_{33})$ ratio in Lake Oltina varied between 0.63 and 5.99 and showed greatest values (2.84) between 4200 and
2000 cal yr BP and the lowest values between 5500-4200 cal yr BP (1.76) as well as over the past 2000 years (1.83; Fig. 3).
270 The ACL varied between 27 and 30 and shows an opposite pattern to the $(C_{27}-C_{29})/(C_{31}-C_{33})$ ratio.

5 Discussion

5.1 Forest steppe between 6000 and 4200 cal yr BP: maximum tree cover between 4200 and 2500 cal yr BP

The pollen-based quantitative land cover reconstruction shows an average tree cover of 40% between 6000 and 4200 cal yr
275 BP and a forest cover maximum of 50% between 4200 and 2500 cal yr BP in the surroundings of Lake Oltina (Figs. 4, 5). In
a pollen-based biome reconstruction, such a tree cover is likely to be indicative of a forest-steppe or open woodland forest type
(Marinova et al., 2018). This woodland consists of tree taxa of xerothermic character including *Quercus* (likely *Q. cerris, Q.
pubescens*) and *Carpinus orientalis,* along with temperate trees such as *Carpinus betulus*, *Acer, Tilia, Ulmus, Fraxinus*. The
shrub (Rosaceae, *Rosa canina, Sambucus, Prunus, Cornus*), grasses and forbs communities were abundant and composed of
280 a diverse mixture of mesophytic, xerothermic and halophilous taxa (Fig. A1). Coeval to the maximum extent in tree cover
between 4200 and 2500 cal yr BP there was also a rise in the abundance of *n*-alkanes with the shorter chain lengths (ALC) and
a higher $n(C_{27}+C_{29})/(C_{33}/C_{31})$ ratio, indicative of moister conditions and an increased contribution of tree-derived *n*-alkanes
(Meyers, 2003; Aichner et al., 2010). Analysis of the composition of lipid compounds in modern river sediment deposits along
the Danube River shows a predominantly local source of branched glycerol dialkyl glycerol tetraethers derived proxies
285 (Freymond et al., 2017). In line with this finding we presume that changes in *n*-alkane homologue abundance in our record
integrate vegetation changes in the lake, near the lake and more regionally in the lake catchment.

The maximum extent of tree cover parallels a slight Fe/Mn ratio increase, which may indicate the establishment of more anoxic
conditions (Naeher et al., 2013), possibly associated with a higher lake level or less turbulent conditions. More stable slope
conditions with low run off between 4200 and 2500 cal yr BP are indicated by low values of the lithogenic element Zr and
290 might support the hypothesis that increased anoxia may have resulted from less turbulent conditions in the lake. On a regional
scale, the 6000-4200 cal yr BP interval was characterised by contrasting climate conditions north and south of 45 degrees
latitude, due to differences in the dynamics of the storm tracks carrying moisture from the North Atlantic Ocean and
Mediterranean Sea (Persoiu et al., 2017). Whilst southern Europe lake levels were low prior to 4500 cal yr BP, those in central
Europe showed high stands during the same period (Magny et al., 2013). An opposite pattern is, however, visible after 4200
295 cal yr BP, when southern Europe lake levels increased whereas those from central Europe declined. Lake Oltina is situated at
45º N and thus at the transition between these contrasting southern and northern Europe changes in hydro-climatic conditions.
Our evidence of maximum expansion of the tree cover, and possibly an association with wetter conditions and a higher lake

level, after 4500 cal yr BP may indicate the response of tree cover to increased moisture availability in the region (Fig. 3).
Warmer conditions were reconstructed from stable isotopes in stalagmites in SW Romania (Dragusin et al., 2014), along with
300 an intensification of fluvial activity in several rivers in southern Romania and southern part of the Danube river at this time
(Bozilova and Tonkov, 1998; Filipova-Marinova et al., 2007; 2011; Howard et al., 2004; Persoiu, 2010). Coastal lakes along
the Black Sea were also at higher water levels at this time, whereas the Black Sea's level fluctuated strongly (Lamy et al.,
2006).

Macrocharcoal based reconstruction of biomass burning, and thus disturbance by fire, was low between 4200 and 2500 cal yr
305 BP at the time of greater forest cover and wetter climate conditions (Fig. 3; Diaconu et al., 2018). This fire–climate-vegetation
relationship is typical for a temperate environment, but contrast with the pattern found in environments with low vegetation
productivity, where increased moisture tends to enhance vegetation productivity and therefore fuel availability (Pausas and
Ribeiro 2013; Feurdean et al., 2020). Disturbance by herbivores, as inferred from the abundance of coprophilous spores in our
record, showed moderate values at the beginning of the record, but declined during the interval of forest cover increase (Fig.
310 3). This may point to some impact by grazing on the degree of forest openness. However, given the very large size of the study
lake, the long distance from the lakeshore to the coring point might have limited transportation of these spores and impact of
how representative their presence might be (Bakker et al., 2013).

5.2 Transition from forest steppe to cultural steppe over the last 2500 cal yr BP

315 Tree cover declined from 50% at 2500 cal yr BP to ~ 20% at 2200 cal yr BP (Fig. 5). Tree species composition retained a
xerothermic character, although *Carpinus orientalis* declined most strongly from 40% to 10% (Fig. 4). *C. orientalis* is a taxon
typical of hot and dry climatic and soil conditions (Sikkema and Caudullo, 2017). As climate conditions remained relatively
moist during this decline, anthropogenic rather than climatic causes are likely. The pollen-based decline in tree cover was
concurrent with a decreasing $n(C_{27}+C_{29})/(C_{33}/C_{31})$ ratio, characteristic of an increased contribution of grasses, further
320 suggesting a change in vegetation indicative of forest loss (Fig. 4). An average of 20% tree cover at 2200 cal yr BP is close to
the current tree cover in the surroundings of Lake Oltina (15%), which suggests the opening up of the forest steppe to a similar
extent as today. Anthropogenic conversion of broadleaved forests to agricultural land from 2500 cal yr BP onwards becomes
visible palynologically as an increase in the pollen of Cerealia (*Secale cereale*, *Triticum, Zea, Hordeum*), grassland (Poaceae),
pastoral and ruderal indicators (*P. lanceolata, Urtica, Rumex,* Chenopodiaceae, *Artemisia,* Asteraceae, Apiaceae; Figs. 4, 5;
325 A1). The levels of pollen of grazing indicators and nutrient-enriched soils (*Plantago. lanceolata, Urtica, Rumex),* as well as
coprophilous fungi, are particularly high after 2200 cal yr BP and may reflect more intensive animal husbandry. The proportion
of Cerealia is significantly greater in the REVEALS estimate (40%) than in the raw pollen percentages (5%). However, the
good match between the proportion of arable cover in the REVEALS and current land cover maps from CORINE for recent
times suggest that our REVEALS reconstruction best reflects that of cultivated land. Nevertheless, uncertainties in pollen-
330 based land cover reconstruction are common and connected to the availability and accuracy of the PPE, cropland management
and the general assumptions of the REVEALS model (Sugita et al., 2017; Hellman et al., 2009; Trondman et al., 2015;

Feurdean et a., 2017b). Biomass burning increased concurrently with the spread of pasture/grassland communities, which may indicate the use of fire for land use management (Fig. 3). However, fire activity fell to its lowest level in the profile in the last 1000 years, probably due to a decline in biomass availability associated with intensive land use and landscape fragmentation

335   typical of lowlands (Marlon et al., 2016; Feurdean et al., 2013; 2020). The timing of forest loss coincides with the peak number of archaeological finds in the Iron Age but is pre-dated by the abundant archaeological finds of the Bronze Age i.e., 4000 cal yr BP (Fig. 5). Interestingly, the typology of the houses in this area i.e., small houses three-quarters buried in the ground with one-quarter above ground comprising mud bricks walls, roofed with straw or reeds typical during the past 3000 years also reflects the limited availability of timber for building (Ailincăi, 2009). Historical records show that, due to its smaller size,

340   *Carpinus orientalis* was managed in coppice stands for household items, fuel production as firewood or charcoal (Goldsteinn et al., 1990; Atlas of European Tree Species, 2017) and this may have also been the cause of its marked reduction from 2500 cal yr BP at Lake Oltina. *Quercus* decline on the other hand, was more modest except for the last 1000 years. Historically, the aftermaths of the Slavic (first millennium AD) and Mongol (1224 AD) invasions could be a reason for a strong *Quercus* decline around this time (Matei, 1984; Epure, 2004). Oak was preferentially used for fortification in SW Romania (Krause et al., 2019;

345   Gumnior et al., 2020). Nevertheless, tree cover, and *Quercus* in particular, recorded episodic rises with the strongest being visible between 1700 and 1300 cal yr BP. This reforestation phase appears to coincide with the post-Roman decline in rural settlement and the subsequent re-growth of secondary forests (Roberts et al., 2018). However, selective oak preservation, due to its economic significance, may have also led to this pattern of *Quercus* increases, as documented over large areas in Europe (Garner et al., 2002; Feurdean et al., 2011; Jamrichová et al., 2017; Gumnior et al., 2020). Models of deforestation rates, using

350   a scenario that accounts for population history and technological advances, suggest that the extent of deforestation in the lower Danube basin increased continuously from 4000 cal yr BP and that this region was already deforested to a level comparable to today at the peak of the Roman Empire around 2000 years ago (Kaplan et al., 2009; Giosan et al., 2012). Although models generally underestimate the timing and magnitude of deforestation, onset of modelled-based deforestation in the lower Danube basin is earlier than our pollen-based reconstruction.

355   In-lake and catchment changes are also apparent in our record around the onset of forest loss. A slight increase in the Fe/Mn ratio, along with Zr concentrations between 2500 and 1500 cal yr BP may reflect soil erosion and detrital input into the lake associated with a diminished tree cover (Fig. 3). Southern European lake levels remained high at the time of deforestation, while those from central Europe (Magny et al., 2011; 2013) and central Romania declined (Feurdean et al., 2013), though others in this region increased (Magyari et al., 2009). Intensification in fluvial activity in several rivers in southern Romania

360   (Howard et al., 2004; Persoiu and Radoane , 2017), as well as on a wider scale in Central Europe (Wirth et al., 2013), has been reconstructed after 3000 cal yr BP, which could be another source of detrital delivery into the lake. In contrast, the Black Sea level lowered, which also suggests drier conditions in Eastern Mediterranean and over the Black Sea around the time of deforestation (Lamy et al., 2006), in line with the drier conditions in SW Romana found between 2000 and 1000 cal yr BP (Dragusin et al., 2014).

365

5.3 Comparison with other European forest steppe regions

Our quantitative record of vegetation indicates a higher than present tree cover across the landscape of the eastern Lower Danube Plain between 6000 and 4200 cal yr BP with an absolute maxima of 50% (60% raw pollen percentages) between 4200 and 2500 cal yr BP (Fig. 6, see Table 3 for reference and Fig. 1 for locations). The composition and structure of mid to late

370 Holocene vegetation of the eastern Lower Danube Plain resembled, to a large degree, that of other European forest steppe areas, although particularities also exist. Whilst in central eastern European forest steppe, *Quercus* and *Carpinus betulus* were the dominant tree species with a lower occurrence of *Tilia, Ulmus, Corylus* and *Pinus* (Magyari et al., 2010; Feurdean et al., 2015; Kuneš et al., 2015), on the Eastern European Plain, *Tilia* and *Quercus*, and in some places *Pinus,* were the dominant tree taxa (Kremenetski et al., 1995; Novenko et al., 2016, 2018; Shumilovskikh et al., 2018, 2019). Forests in the Black Sea region

375 also included thermophilus taxa i.e., *Quercus cerris*, *C. orientalis* (this study, Marinova et al., 2006; Tonkov et al., 2014) Remarkably, *Carpinus orientalis* was found to be significantly more abundant around the Black Sea coast i.e., Romania (20%), Bulgaria (>5%), or with only scattered occurrences in Ukraine, whilst it was absent from Central European forest steppe. Our pollen-vegetation calibration model shows that the adjusted abundance of *C. orientalis* is twice that recorded by its raw pollen percentages (Fig. 4).

380 Mid-Holocene landscape openness near Lake Oltina (ca. 55% pollen percentages) appears to have been in between that of the steppe in south-eastern Bulgaria (60-80%; Tonkov et al., 2014), the forest steppe of Ukraine (25%; Kremenetski et al., 1995; 1999) and that of the Eastern European Plain (20-55%; Shumilovskikh et al., 2018). However, landscape openness was greater than in other forest steppe sites from central eastern Europe, i.e., Romania (Feurdean et al., 2015; Tantau et al., 2006), Hungary (Willis et al., 1997; Willis, 2007; Magyari et al., 2010), Czechia and Slovakia (Pokorny et al., 2011, 2015; Hajkova et al.,

385 2013; Kuneš et al., 2015) where it varied between 10 and 35 % (Fig. 6). The composition of herbaceous plant cover included grasses (Poaceae) and a diversity of forbs thriving on a wide variety of habitats ranging from dry and saline soils (*Artemisia*, Chenopodiaceae, Asteraceae Compositae, Asteraceae Tubuliflorae) to dry and wet meadows *Filipendula, Galium, Anthemis, Aster*, Caryophyllaceae, *Euphorbia, Helianthemum, Hypericum*, Fabaceae, *Plantago lanceolata, P. major /P. media, Teucrium, Thalictrum* and *Verbascum;* Fig. 4; A31. Notably, however, the proportion of steppe and saline elements (*Artemisia*,

390 Chenopodiaceae) was greater at sites located in the Black Sea region, in agreement with greater temperature seasonality, lower precipitation as well as the occurrence of saline soils in this region.

The comparison with other sites in the region reveals a west to east gradient of both, the onset of deforestation and extent across the European forest steppe (Fig. 6). The timing of major anthropogenic ecosystem transformation in the Lower Danube Plain from about 2500 cal yr BP is close to that of other records in lowland areas in central eastern and south eastern Europe,

395 where it generally occurred after 3000 cal yr BP (Fig. 6). However, this is earlier than on the Eastern European Plain Europe, where it mostly occurred after 2000 cal yr BP. On the Thracian Plain, south eastern Bulgaria, anthropogenic deforestation was, however, noted already from 4000 cal yr BP (Connor et al., 2013). The anthropogenically-driven opening up of the forest steppe soon reached a similar extend as today in most regions which then remained open until the present day, although the climate conditions could have allowed the recovery of tree cover.

400

6 Conclusions

The pollen-based vegetation modelling applied here (REVEALS) provides the first, long-term quantitative reconstruction of land cover changes across the Lower Danube Plain (SE Romania) and in the SE Europe. In agreement with expert-based assessment of potential tree cover, this palaeoecological study demonstrates that the natural vegetation of the eastern Romanian

405 Plain under climatic conditions similar to today is indeed forest steppe /woodland. Enhanced moisture availability, mainly brought by southern Mediterranean storm tracks, led to a more extensive forest cover between 6000 and 2500 cal yr BP with a maximum of 50% between 4200 and 2500 cal yr BP. These woodlands were dominated by xerophilous and warm temperate tree taxa i.e., *Carpinus orientalis* and *Quercus* (perhaps *Q. cerris, Q. pubescens*). The forests of the Lower Danube Plain were intensively cleared and became as open as present day levels (around 20% tree cover) from the Iron Age (2500 cal yr BP. They

410 were replaced by agricultural land and pasture/semi-natural grasslands. Forest cover remained low throughout the last two millennia demonstrating the continuous anthropogenic pressure on the surrounding region. Given the dry character of the study region, deforestation may have additionally enhanced evaporation altering the moisture balance and further contributing to the tendency towards the aridisation of Lower Danube landscapes. The permanent loss of the tree cover is visible across a west-east gradient of the Central Eastern European forest-steppe region highlighting its sensitivity to anthropogenic impact. We also

415 show that both the extension and decline in forest cover determined by pollen, a well-established proxy for past vegetation change, is also reflected in the *n*-alkane record, which indicates their potential as a reliable record of tree versus grass cover changes in this region and therefore drier study sites in general where pollen analysis may not be possible. Our results can also be used to test land cover change scenarios in anthropogenic land use and land cover models, that generally underestimate the onset of deforestation, thought an earlier impact than in the reconstructions is also true.

420

Data sets

Accessibility Statement

All essential input data will be made open-access and available online in suitable repositories (Pangaea) upon publication.

425 **Author contribution**: AF design the study. AF, AD, AP and MB performed the fieldwork; RG, IT, AF pollen analysis; GF and EMN biomarkers; GF and SMH geochemistry; AD macrocharcoal; ST, AP and AF C14 measurements and age-depth model. RG, AN, AF REVEALS modeling. AF prepared the manuscript with contributions and input from all authors.

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Figure legends and embedded figures

Figure 1. Potential natural vegetation cover in Europe showing the extent of the European forest steppe region (after Bohn 2003; ©BfN, Bundesamt fur Naturschutz) the location of the study site and the other published sites used for comparisons. 1.

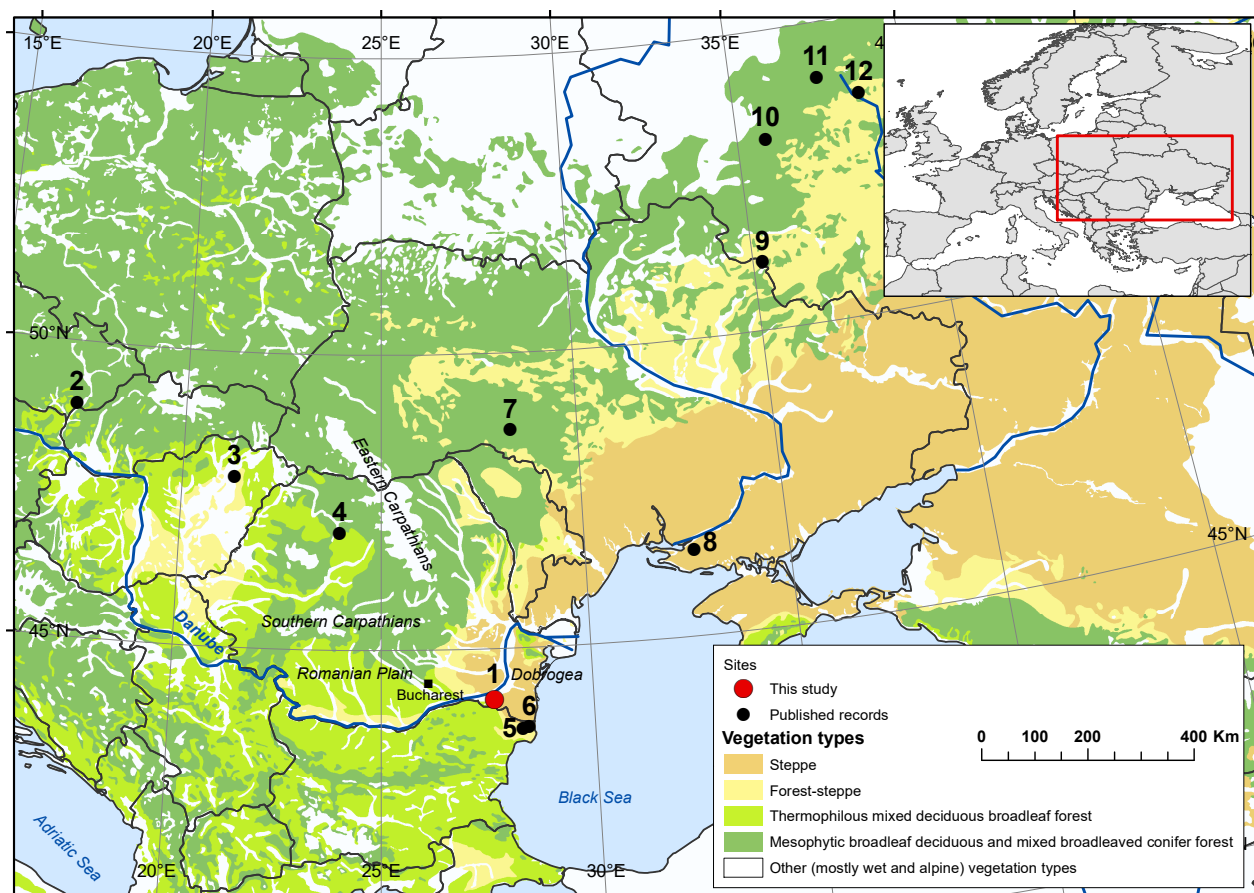
735   Lake Oltina (study site); 2. Lake Vracrov; 3. Sarló-hát; 4. Lake Știucii; 5. Durankulak-2; 6. Durankulak-3; 7. Dovjok; 8. Kardashinski; 9. Sudzha; 10. Selikhovo; 11. Isotechek; 12. Podkosmovo. For references see Table 3.

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Figure 2. Age depth model for Lake Oltina using a Bayesian approach (for more see S2).

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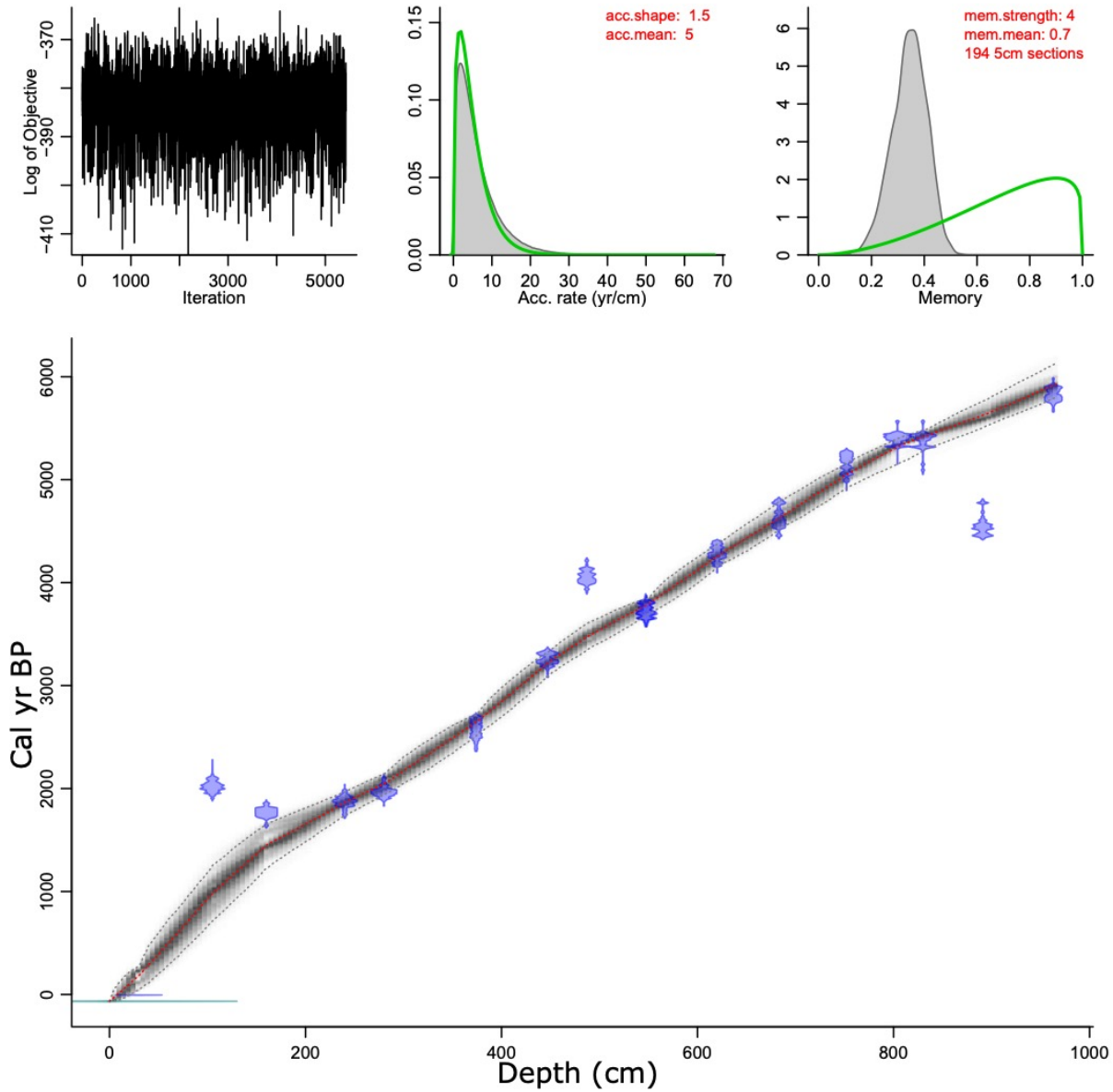
Figure 3. Integrative diagram showing in-lake ecosystems and catchment changes. Lake properties: volume magnetic susceptibly, organic matter content, and detrital elements (Zr and Fe/Mn ratio). Biomass burning as determined from the macro-charcoal record and grazing activity from coprophilous spores. Landscape cover determined from the arboreal pollen (AP) and the open land pollen percentages; ACL (Average Chain Length) and the ratio of $(n\text{-}C_{31} + n\text{-}C_{33})/(n\text{-}C_{27} + n\text{-}C_{29})$ as a

755 proxy for tree predominance in the landscape. Regional lake level fluctuations determined from the CA score at Lake Ledro, N Italy (45º N and Lake Preola, S Italy (37º N (Magni et al., 2013). Archaeological finds include settlements and cemeteries within a 20-km radius of Lake Oltina taken from Repertoriul Arheologic Național [Archaeological Repertorium of Romania]: http://ran.cimec.ro.

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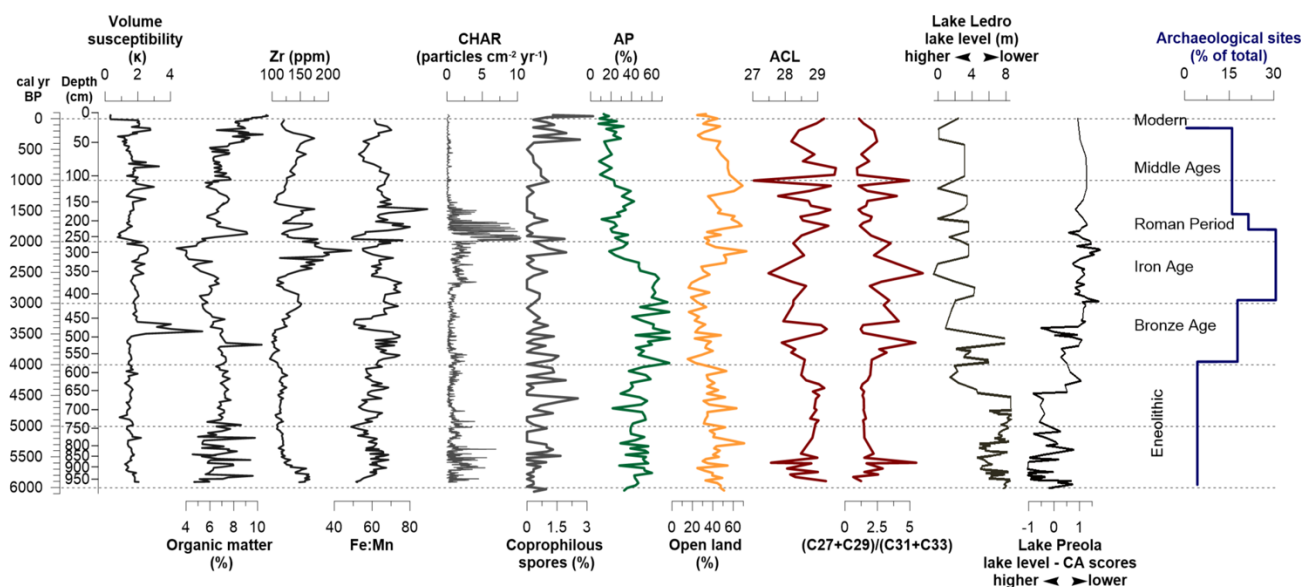
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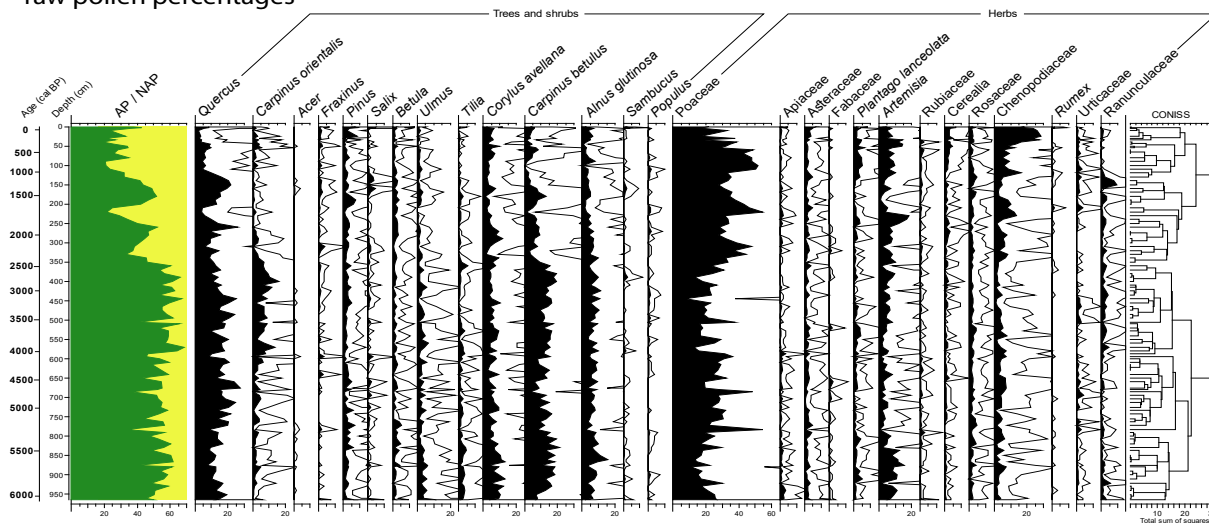
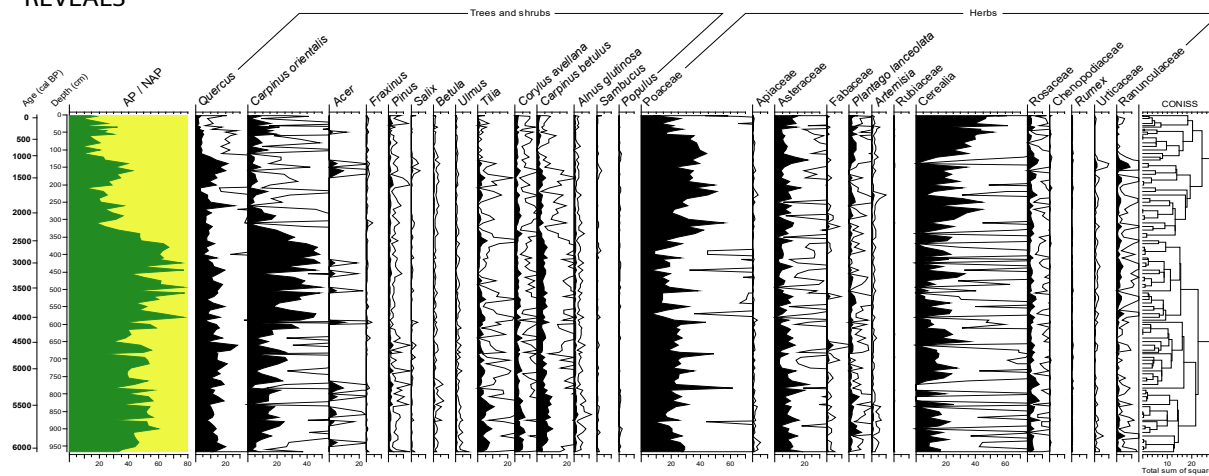
Figure 4. Raw pollen percentages (A) and estimated regional vegetation cover based on the REVEALS model (B) for 27 taxa including trees, shrubs and herbs at Lake Oltina.

Lake Oltina
raw pollen percentages

REVEALS

775 **Figure 5**. Comparative summary of the percentage vegetation cover estimates based on the REVEALS model and raw pollen percentages at Lake Oltina. Open land cover includes all non-arboreal pollen types, mostly indicators of pastures and grasslands. The Cerealia group include *Secale cereale*, *Triticum, Zea* and *Hordeum*. Archaeological finds as above.

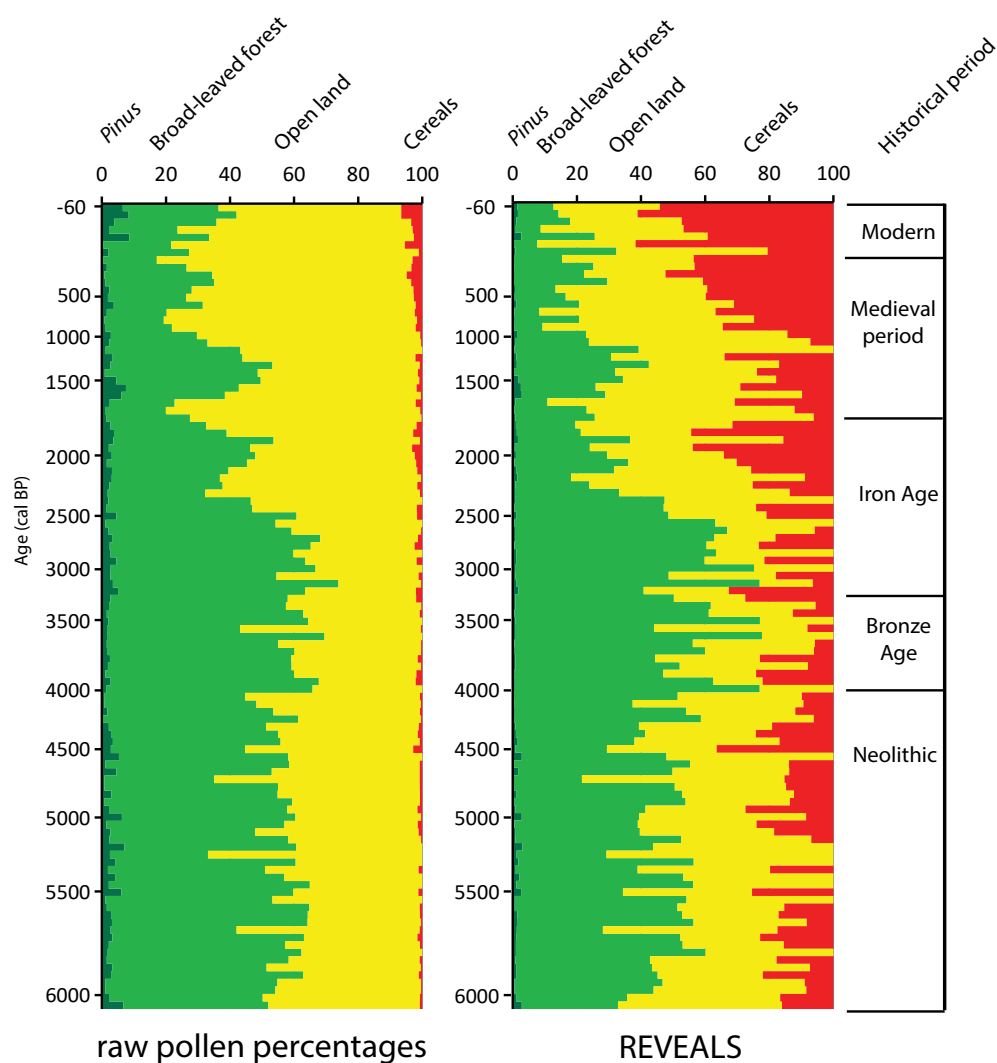



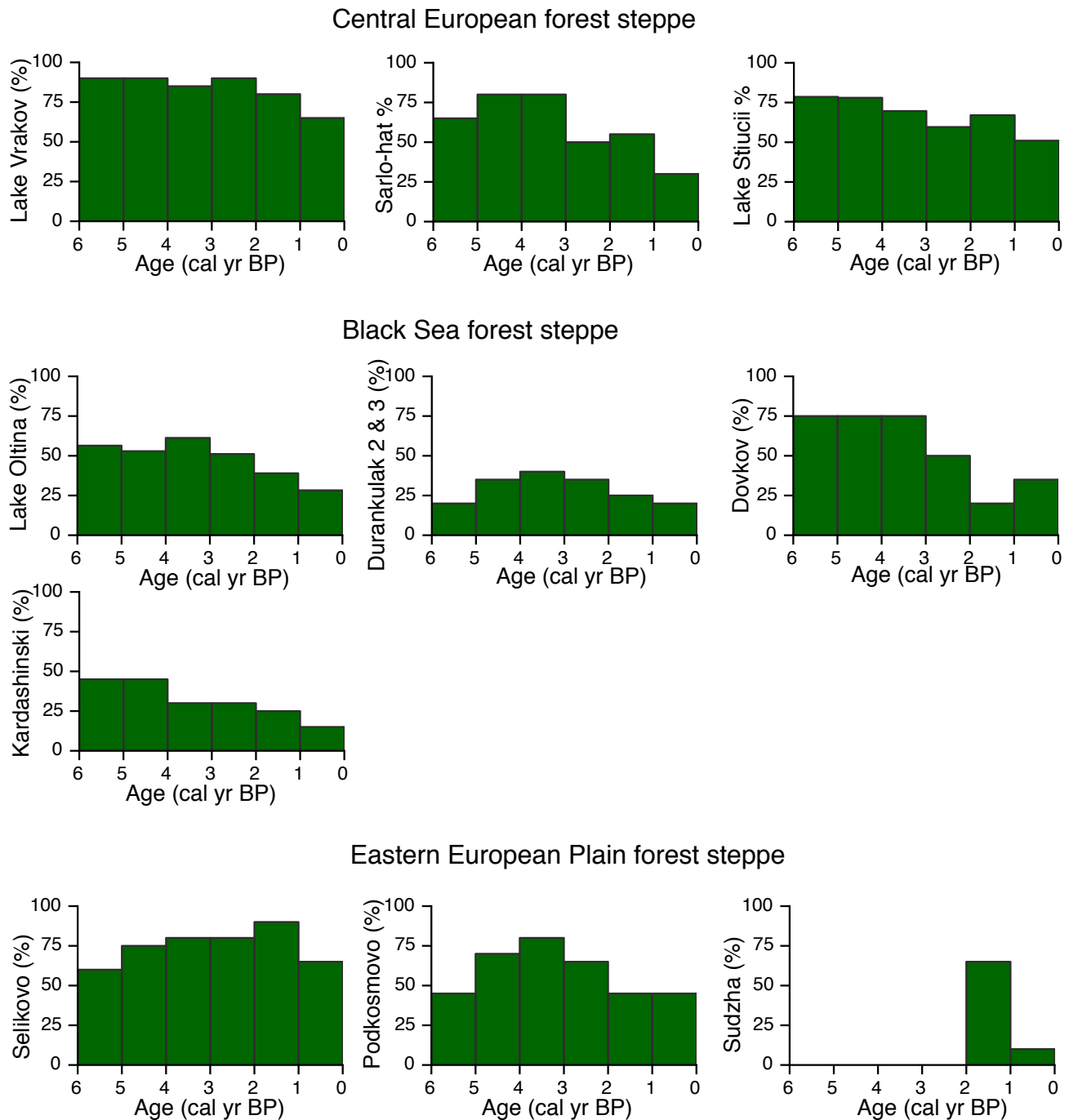
Figure 6. Arboreal pollen percentages illustrating temporal trends in deforestation in three different sub-regions along a west-
780 east transect across the European forest steppe region. For the location of individual sites see Figure 1 and Table 3.

Tables

Table 1. AMS ^{14}C measurements at Lake Oltina.

Lab. no.	Core	Depth (cm)	Mat. datedC^{14}	δ^{13}C
DeA-10928	1.1	30	Shell	880±19
DeA-11083	1.2	105	Bulk	2053±28
DeA-11085	1.2	160	Bulk	1832±27
DeA-11087	1.3	240	Bulk	1928±37
RoAMS 131.45	1.3	280	Shell	3016±30
RoAMS 128.45	1.4	374	Shell	3473±23
RoAMS 132.45	1.5	447	Shell	4042±24
RoAMS 366.45	1.5	487	Shell	4715±34
RoAMS 133.45	1.6	548	Plant macro	3459±31
RoAMS 356.45	1.6	547	Shell	4457±35
RoAMS 134.45	1.7	620	Shell	4856±25
RoAMS 364.45	1.7	683	Shell	5097±36
RoAMS 129.45	1.8	752	Shell	5476±25
RoAMS 135.45	1.9	804	Shell	5648±27
RoAMS 130.45	1.10	891	Shell	5055±30
RoAMS 363.45	1.10	926	Bulk	8886±41
RoAMS 361.45	1.10	963	Shell	6093±42

Table 2: Pollen productivity estimates relative to Poaceae and their respective fall speeds used in the REVEALS model. *standardized after Mazier et al. (2012).

a) Local pollen productivity estimates (PPE)

Taxon	PPE (Grindean et al., 2019)	Fall speed (m s^{-1})	Reference for fall speed
Quercus	1.10	0.035	Mazier et al. (2012)
Carpinus orientalis	0.24	0.042	Mazier et al. (2012)
Acer	0.30	0.056	Mazier et al. (2012)
Fraxinus	2.99	0.022	Mazier et al. (2012)
Poaceae	1.00	0.035	Mazier et al. (2012)
Apiaceae	5.91	0.042	Mazier et al. (2012)
Asteraceae	0.16	0.029	Mazier et al. (2012)
Fabaceae	0.40	0.021	Commerford et al. (2013)
Plantago lanceolate	0.58	0.029	Mazier et al. (2012)
Artemisia	5.89	0.014	Abraham and Kozakova (2012)
Rubiaceae	7.97	0.019	Broström et al. (2004)
Cerealia	0.22	0.06	Mazier et al. (2012)
Rosaceae	0.29	0.018	Mazier et al. (2012)

b) Literature-based pollen productivity estimates

Taxon	PPE	Fall speed (m s^{-1})	Reference
Pinus	2	0.031	Abraham et al. (2014)

Salix	2.31	0.022	Abraham et al. (2014)
Betula	2.62	0.024	Abraham et al. (2014)
Ulmus	6	0.032	Abraham et al. (2014)
Tilia	0.5	0.032	Abraham et al. (2014)
Corylus avellana	1.4	0.025	Abraham et al. (2014)
Carpinus betulus	3.55	0.042	Abraham et al. (2014)
Alnus glutinosa	4.2	0.021	Abraham et al. (2014)
Sambucus	1.3	0.013	Abraham and Kozakova (2012)
Populus	3	0.025	Matthias et al. (2012)
Chenopodiaceae	4.28	0.019	Abraham and Kozakova (2012)
Rumex	2.14	0.018	Mazier et al. (2012)
Urticaceae	10.52	0.007	Abraham and Kozakova (2012)
Ranunculaceae	1.96	0.014	Mazier et al. (2012)

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Table 3. Compilation of palaeoecological records along a west-east transect of the European Forest steppe. Key: Cz=Czechia; Hu-Hungary; RO-Romania; BG-Bulgaria; UK-Ukraine; RU-Russia.

Site	Country	Lat/Long	References
1. Lake Oltina	RO	44°09'N 27°38'E	This study
2. Lake Vracrov	CZ	48°58'N 17°11'E	Kunes et al., 2015
3. Sarló-hát	Hu	47°54'N 21°18'E	Magyari et al., 2010
4.Lake Stiucii	RO	46°58'N 23°58'E	Feurdean et al., 2015
5. Durankulak 2	BG	43°39'N 28°31'E	Bozilova & Tonkov ,1995
6. Durankulak 3	BG	43°39'N 28°31'E	Marinova, 2006
7. Dovjok	UK	48°45'N 28°15'E	Kremenetski ,1995
8. Kardashinski	UK	46°31'N, 32°37'E	Kremenetski ,1995
9. Sudzha	RU	51°08' N 35°46' E	Shumiloviskhk et al., 2018
10.Selikhovo	RU	53°13' N 35°46'E	Novenko et al., 2016
11.Isotechek	RU	54°41 N 37°30 E	Shumiloviskhk et al., 2018
12.Podkosmovo	RU	53°40 N 38°35'E	Novenko et al., 2014

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830 **Appendix A1.**

Figure A1. Full pollen diagram for Lake Oltina including all trees, shrubs and herbs.

Supplement

Supplement S1. Location of the study area (insert) and the distribution of surface sample sites used for the pollen-based calibration of the vegetation cover shown in the CORINE Land Cover (CLC) map from 2012. Source: CORINE land cover 2012 (CLC2012). For details see Grindean et al., 2019

Supplement S2. Lake Oltina chronology.