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Moisture availability versus grazing and burning as drivers of Holocene forest-grassland coexistence in Europe: A case study from open ecosystems of southeastern Romania

Angelica Feurdean[a,*], Diana Hanganu[b], Adrian Bălășescu[c], Andrei Diaconu[d], Mirjam Pfeiffer[e], Dan Warren[f], Mariusz Galka[g], Roxana Grindean[d], Simon M. Hutchinson[h], Irene Marzolff[a], Aurel Persoiu[i,j], Eszter Ruprecht[k], Ioan Tantau[d]

[a] *Department of Physical Geography, Goethe University, Altenhöferallee 1, 60438, Frankfurt am Main, Germany*
[b] *GEODAR Research Center for Geomorphology, Geoarchaeology, and Paleo-Environments, ICUB Research Institute of the University of Bucharest, Panduri 90, Bucharest, Romania*
[c] *Vasile Pârvan" Institute of Archaeology, Calea 13 Septembrie 13, Bucharest, Romanian Academy, Romania*
[d] *Department of Geology, Babes-Bolyai University, Cluj Napoca, Romania*
[e] *Institute for Applied Ecology, Rheinstrasse 95 D, 64295, Darmstadt, Germany*
[f] *Gulbali Institute for Applied Ecology, Charles Sturt University, Thurgoona, NSW, 2640, Australia*
[g] *Department of Biogeography, Paleoecology and Nature Conservation, Faculty of Biology and Environmental Protection, University of Lodz, Łodz, Poland*
[h] *School of Science, Engineering and Environment, University of Salford, Salford, UK*
[i] *Emil Racoviță Institute of Speleology, Romanian Academy, Cluj-Napoca, Romania*
[j] *Stable Isotope Laboratory, Ștefan cel Mare University, Suceava, Romania*
[k] *Hungarian Department of Biology and Ecology, Faculty of Biology and Geology, Babes-Bolyai University, Cluj-Napoca, Romania*

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ABSTRACT

Southeastern Europe is home to remnants of highly diverse open ecosystems, including grasslands and forest-steppe. To understand the impacts of climate changes, fire disturbance, and herbivory on forest-grassland coexistence in this region, we integrated new and published paleoecological data from two sedimentary records in southeastern Romania with information on herbivore population dynamics and dietary habits. Our findings indicate that fluctuations in forest-grassland cover closely mirrored changes in regional growing season moisture availability in the Black Sea region. During periods with increased moisture availability (e.g. 6000–3800 cal yr BP), diverse broadleaved forest dominated by *Quercus* expanded. Conversely, more drought-tolerant herbaceous cover increased during drier intervals (7200-6800 and 3800-2000 cal yr BP). We identified a critical tree cover of 25–40% at Mangalia Herghelie and 25–55% at Lake Oltina where neither forest nor grassland dominated. Stable forest states emerged above 40% tree cover and 55% respectively, while grassland-dominated states had tree cover below 25%.

Disturbances by fire and herbivores fluctuated over time, and were further influenced by human activity, which along with deforestation, altered the composition and extent of steppe and forest-steppe vegetation. High fire severity occurred during intermediate moisture conditions and tree cover (6800–5500, 3800–2800 cal yr BP), while low fire severity was observed when herbaceous biomass dominated (7200–7000, 2800–2000 cal yr BP) or under greater tree cover (5500–3800 cal yr BP). Herbivore dynamics shifted from large-bodied grazers in the Neolithic and early Eneolithic (7650–6550 cal yr BP; Prehamangia and Hamangia cultures) to a more diverse array of feeding types involving smaller domestic and wild herbivores along with sedentary agriculture during the flourishing Eneolithic (6550-5850 cal yr BP; Gumelnita culture), before returning to larger domestic grazers as well as omnivores in the Bronze and Iron Ages (3500–2000 cal yr BP). Large-bodied herbivores with selective diets (primarily grazers) had a more substantial effect on grasses compared to mixed feeders with bulk diets, whereas domestic herbivory was associated with increased apophyte abundance and diversity. Our findings underscore the essential factors for sustainable management of forest-grassland mosaics under changing climate

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* Corresponding author.
E-mail address: feurdean@em.uni-frankfurt.de (A. Feurdean).

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conditions with projected accelerating aridification. They also highlight the need for continued research to enhance our understanding of these biodiverse, sensitive open ecosystems to inform effective management strategies.

1. Introduction

European grassy ecosystems, including steppe, shrubland, and forest-steppe, exhibit a diverse range of vegetation compositions and structures (Dengler et al., 2014; Erdős et al., 2018, 2022; Rolecek, 2023). Traditionally, these ecosystems were considered to dominate regions too cold or too dry for tree growth and with poor soil conditions. This assumption aligns with classic successional theory, which posits that the distribution of potential natural vegetation types (PNV) is primarily determined by the interactions between climate and soil (Bohn et al., 2003). However, recent evidence challenges this view, as many grassy ecosystems thrive in warm and wet climates capable of supporting forests, as evidenced by the presence of forest patches and forestry plantations (Stevens et al., 2022).

An alternative explanation for the distributions of main vegetation types posits that open ecosystems may also be maintained by disturbances such as fire and herbivory, which alter the competitive balance between trees and grasses in favour of the latter (Pausas and Bond, 2020). These consumer-controlled open ecosystems can persist for millennia, if the disturbance regime prevails but may switch to closed forest if consumers are excluded from the system long enough to allow the growth of trees. Consequently, inaccurate identification of natural vegetation types can lead not only to unrealistic vegetation reconstructions (Chiarucci et al., 2010), but also to inappropriate management decisions, conservation practices and policies, including spatially misguided rewilding campaigns aimed at planting trees to mitigate climate change through enhanced plant-based carbon sequestration.

Our understanding of the effect of fire frequency and intensity on tree-grass balance primarily stems from studies in tropical grasslands (Pausas et al., 2017; Archibald et al., 2018; Bond et al., 2019; Stevens et al., 2022). Unlike tropical grasses, which have evolved high flammability strategies leading to high fire frequency and low severity, temperate open ecosystems exhibit far fewer fire-adapted traits (Ruprecht et al., 2013; Stevens et al., 2022). Recent charcoal-based reconstructions and expert assessments of global fire regime changes revealed that fire history trajectories in grassy ecosystems vary across continents, with knowledge being particularly limited in Europe (Leys et al., 2018; Karp et al., 2021; Sayedi et al., 2024). The few charcoal-based fire reconstructions from open ecosystems in Europe indicate a positive association between dry conditions and/or woodland openness and fire occurrence, and a decline in fire frequency as woody cover increases (Feurdean et al., 2013; Vincze et al., 2019; Lukanina et al., 2023). Additionally, fire-vegetation studies in modern environments show that fire frequency peaks in forest-steppes and savannas (tree cover 44–55%), which offer an optimal mix of coarse and fine fuel necessary to sustain fire spread (Whitlock et al., 2010; Pausas and Ribeiro, 2013; van Nes et al., 2018). This pattern has also been observed in palaeoecological records from Europe (Feurdean et al., 2020). Palaeoecological datasets further indicate that humans have substantially altered fire regimes in more open ecosystems to exploit fertile soils that were easier to clear and cultivate (Turner et al., 2008; Vannière et al., 2011; Feurdean et al., 2013; Leys et al., 2018). Efforts to differentiate between herb (fine) and wood (coarse) fuelled fires will lead to more accurate interpretations of past fire frequencies and severities in grass-woodland mosaics, and the effects of changing fire regimes on the composition of grass-dominated ecosystems (Leys et al., 2018; Feurdean et al., 2023).

Herbivores can maintain vegetation openness and can drive the climax state of vegetation succession towards a more open state (Pearce et al., 2023; Davoli et al., 2024). Grasses and forbs have developed adaptations to tolerate grazing pressure, therefore herbivores tend to disproportionately damage woody plants. However, this pattern is strongly influenced by the dominant herbivore's body size and dietary preferences, e.g. grazers, mixed feeders, and browsers (Staver et al., 2021; Davoli et al., 2024). The abundance, diversity, and body size of wild herbivores have markedly declined from the Late Glacial period to the present, leading to potential structural changes in vegetation composition (Nemeth et al., 2017; Karp et al., 2021; Pearce et al., 2023; Davoli et al., 2024). This decline in large wildlife has been paralleled by a progressive increase in the abundance and diversity of domestic herbivores. However, the impact of changes in herbivore composition and dietary preference on local vegetation structure have rarely been explored, especially in Europe (Staver et al., 2021; Davoli et al., 2024; Lundgren et al., 2024).

Southeastern Europe is home to a significant proportion of open ecosystems with exceptional biodiversity, including dry and mesic grasslands and forest-steppe vegetation (Ruprecht, 2006; Dengler et al., 2014; Feurdean et al., 2018; Erdős et al., 2018, 2022). The forest-steppe, a transitional zone between forest and grassland biomes, is characterized by highly variable tree cover (10–70%) that extends from the Carpathians to the Altai Mountains (Fig. 1) under mean annual precipitation between approximately 300 and 800 mm (Erdős et al., 2018).

To better understand the consequences of disturbances by fire and herbivores on the forest-grassland coexistence in southeastern Europe in a changing climate, we integrated new and published evidence from pollen, charcoal morphology, and coprophilous fungal spores from two sedimentary records in south-eastern Romania (Mangalia Herghelie and Lake Oltina), together with information on moisture availability during the growing season, herbivore abundance and dietary strategy obtained from databases. Firstly, we investigated tree cover's sensitivity to the reduction in moisture availability. We aimed to identify equilibrium points where neither woodland nor grassland dominates, but the two coexist. Secondly, we assessed the link between tree cover and fire frequency and severity and identified thresholds in tree cover at which the fire regime changed. Thirdly, we examined the impact of herbivore abundance on vegetation, specifically whether herbivores with browsing dietary preferences disproportionately damaged woody plants while grazers and mixed feeders impacted herbaceous plants. Lastly, we explored the human impact on the vegetation, mainly whether Neolithic farmers' agropastoralism and vegetation burnings restricted forest expansion during the moist early to mid-Holocene period.

2. Regional settings

The study sites, Mangalia Herghelie and Lake Oltina, are located in open ecosystems in southeastern Romania (Fig. 1). The Mangalia Herghelie wetland (43.838056°N, 28.583333°E, 5 m a.s.l., 100 ha) is a partly infilled coastal lagoon situated along the western Black Sea coast, near the town of Mangalia (Fig. 1). It was formed when a <50 m wide sand bar obstructed discharge from a small stream into the sea. This wetland evolved over a pre-existing doline, which developed within the underlying Sarmatian limestone (Constantinescu, 1995; Drăgușin et al., 2021). The catchment is poorly defined, and this wetland receives water primarily from surface runoff and a small ephemeral stream, both active only during heavy summer thunderstorms. Lake Oltina (44.158603°N, 27.635617°E, 7m a.sl., 3000 ha) is a fluvial lake on the Danube floodplain, located 100 km west of Mangalia, in the forest-steppe zone of the Lower Danube Plain (Fig. 1; see Feurdean et al., 2021).

The potential natural vegetation at Mangalia Herghelie is steppe of

Pontic-Balcanic origin (Bohn et al., 2003), which has been extensively converted into arable land and pasture. There are also small, protected areas such as Obanu Mare and Padurea Hagieni hosting steppe species. According to CORINE Land Cover (CLC) data, 91% of the land cover within a 50 km radius around the wetland comprises arable land, 6% pasture and other natural grasslands, and 3% forest (Copernicus Land Monitoring Service, 2024). Common thermophilus broadleaved tree species include *Quercus pedunculiflora*, *Q. pubescens*, *Q. cerris*, *Carpinus orientalis*, *Fraxinus ornus*, *Acer tataricum.* Meadow steppe species, mostly confined to protected areas, include species of *Stipa*, *Poa*, *Potentilla*, *Achillea* and other Asteraceae (for a detailed list of species see SI). At Lake Oltina, the potential natural vegetation is forest-steppe with largely similar species composition as presented at Mangalia Herghelie. However, currently, the area surrounding the lake includes 78% arable land and orchard, 8% pastures and other natural grasslands, and 14% forest (Grindean et al., 2019; Feurdean et al., 2021).

The climate of the region is warm-temperate continental, characterized by cold and dry winters and hot summers (Köppen–Geiger class Dfa). The mean annual temperature is ca. 11 °C, with a mean January temperature of ca. 1 °C and a mean summer temperature of 25 °C. Annual precipitation is about 400 mm. The geology of the region comprises Sarmatian limestones covered by late Quaternary loess deposits, with soils primarily represented by Haplic and Luvic Chernozems and Phaeozems (IUSS WRB, 2006).

3. Materials and methods

3.1. Core collection, lithology and chronology

At Mangalia Herghelie, two sediment profiles were extracted in 2017 and 2023. The first sediment profile, totalling 450 cm, was taken using a Livingstone piston corer in spring 2017 from the wetland's marginal beach side at a water depth of 120 cm. The second sediment profile, totalling 300 cm, was retrieved with a Russian corer in summer 2023 at a water depth of 190 cm, approximately 100 m towards the centre from a reed mat developed at this point. The chronology was established based on 11 radiocarbon AMS (accelerator mass spectrometry) measurements in the marginal profile and on five from the central profile (SI Table 1). The radiocarbon age estimates were calibrated to calendar years BP using the Bacon software (Blaauw and Christen, 2011) with the IntCal20 data set of Reimer et al. (2020). The results revealed a peat hiatus spanning the last 2000 years in the marginal profile (2017) and approximately 3000 years in the central profile (2023), the latter identified after a radiocarbon date of 137 ± 16 years at a depth of 30 cm (SI Fig. 1a and b). These hiati are likely the result of dredging of the lake in the 1980s to maintain an open water body for birds. Therefore, the palaeoecological analyses were performed on the marginal core, with samples only taken from the top 30 cm of the central core.

At Lake Oltina, the core collection, chronology, pollen, and coprophilous analysis were previously described by Feurdean et al. (2021). In this study, we updated the age-depth model from IntCal13 to

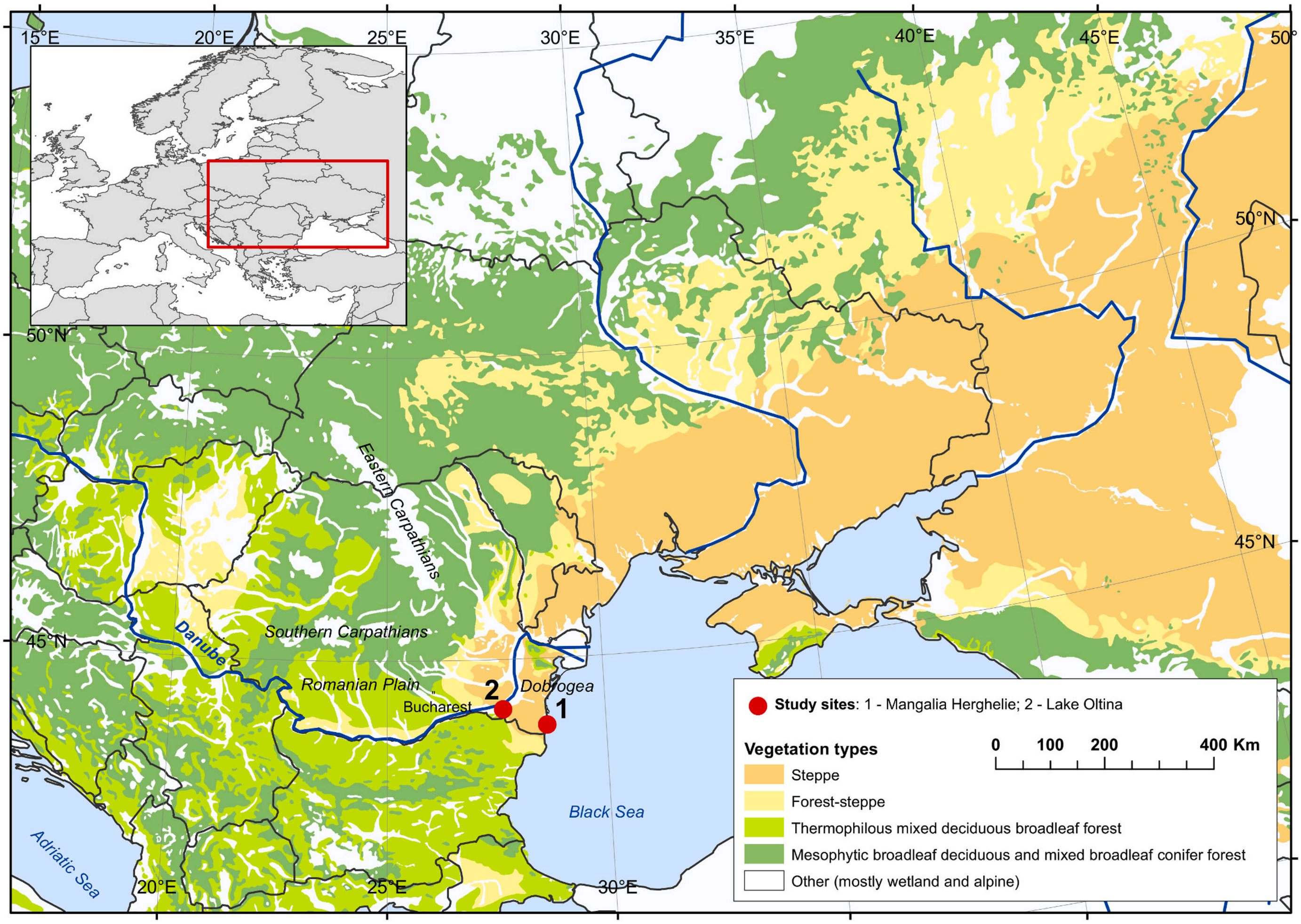


Fig. 1. Potential natural vegetation in Europe highlighting the extent of open ecosystems (insert map) including steppe and forest-steppe (adapted from Bohn, 2003; BfN, Bundesamt für Naturschutz). The locations of the two study sites in southeastern Romania, Mangalia Herghelie (1, steppe) and Lake Oltina (2, forest-steppe) are also indicated (redrawn after Feurdean et al., 2021).

the IntCal20 data set of Reimer et al. (2020) while keeping all other original settings (SI Fig. 1c) and present the new methodology on charcoal morphologies.

3.2. Geochemical elements and plant macrofossils

To determine wet-to-dry shifts in wetland conditions at Mangalia Herghelie, we used the Ca/Zr ratio (entire profile) and the Fe/Mn ratio (>7000-6500 cal yr BP), where Mn values were above the detection limit (Naeher et al., 2013). The Ca/Zr ratio indicates carbonate

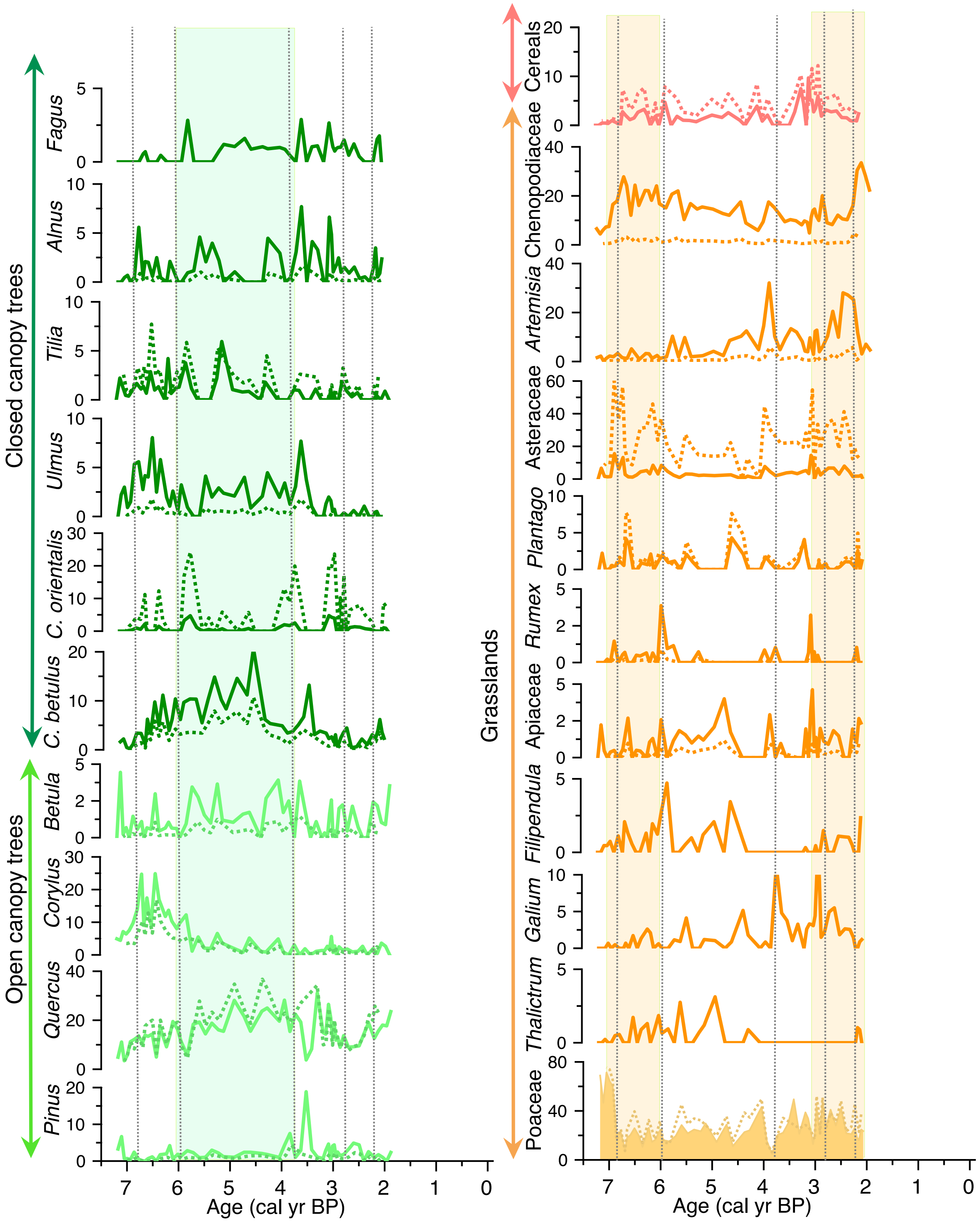


Fig. 2. Comparative raw pollen percentages (solid line) and estimates based on the REVEALS model (dashed line) for selected taxa at Mangalia Herghelie. The cereals group includes Poaceae >40 µm, *Secale cereale*, *Triticum/Avena*, and *Hordeum*. Woody taxa are categorized into light-demanding and closed-canopy types. Vertical dashed lines denote the main pollen zone as determined by CONISS. The coloured rectangles highlight the main vegetation phases, with green indicating periods of more developed tree cover and orange, more abundant grasslands, particularly drought-tolerant forbs. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

precipitation versus detrital input, whereas the Fe/Mn ratio serves as a proxy for redox conditions; both relate to changes in local hydrological conditions (SI Fig. 2). Elemental geochemical concentrations were measured using a non-destructive Niton XL3t 900 X-ray fluorescence analyser (FPXRF), employing NCS DC73308 as a certified reference material to ensure accuracy. The analytical procedure followed Hutchinson et al., (2016).

Plant macrofossils were analysed from sediment samples with a volume of approximately 10 cm^3 (SI Fig. 3). The samples were rinsed using warm water over 0.20 mm mesh screens. The composition of vascular plants was determined based on carpological remains and vegetative fragments using available identification keys (Velichkevich and Zastawniak, 2006).

3.3. Pollen based land cover reconstruction

We used pollen analysis to determine past vegetation cover and composition. Sediment preparation at Mangalia Herghelie largely followed the protocol of Bennett and Willis (2001). The pollen grains were identified using the atlases by Moore et al., (1991); Reille (1995), and Beug (2004), and online databases. 150 to 300 terrestrial pollen grains were counted at most levels, due to poor pollen concentration but generally well-preserved pollen. Levels with counts below 150 pollen grains were recorded at 487-481 cm, 367-351 cm, 335-237 cm, 221-180 cm, and the top sample. Pollen percentages were calculated based on the terrestrial pollen sum (Fig. 2). The proportion of wetland taxa (Cyperaceae and *Typha*) was calculated relative to their pollen sum and the terrestrial pollen sum.

To determine the degree of forests openness, we categorized the trees into light demanding, shade-intolerant (*Pinus sylvestris, Betula, Populus, Quercus, Corylus, Fraxinus ornus, Sorbus,* and *Salix*), and closed-canopy *(Ulmus, Carpinus betulus, C. orientalis, Acer, Fagus sylvatica, Fraxinus excelsior, Alnus, Picea abies)* taxa following the classification by Pearce et al. (2023). Herbaceous taxa were categorized into grasses (Poaceae) and forbs (flowering plants, not grasses). In the biomisation procedure, an increased proportion of pollen from forbs, e.g., Amaranthaceae/Chenopodiaceae, *Aster, Artemisia*, and Asteraceae, is interpreted as an indication of an enlargement in drought-tolerant habitats (Marinova et al., 2018). Therefore, the increased proportion of these taxa relative to other forbs, e.g., *Filipendula, Galium, Thalictrum,* Apiaceae, etc., in our record was interpreted as an expansion of drought-tolerant vegetation, however, they also indicate ruderal habitats. Cultural indicators included taxa of arable fields such as pollen of Cerealia and weeds (*Agrostemma githago, Centaurea cyanus*, and Papaveraceae), and grazing indicators (*Plantago lanceolata, Plantago* spp, *Urtica, Rumex*) following Deza-Araujo (2022). CONISS analysis applied on the terrestrial pollen record was used to determine the main changes in pollen stratigraphy (SI Fig. 4).

We employed the Regional Estimates of Vegetation Abundance from Large Sites (REVEALS) model (Sugita, 2007) to quantitatively reconstruct vegetation cover at Mangalia Herghelie following the methodology detailed for Lake Oltina in Feurdean et al. (2021). However, unlike the previous study, we opted for a literature-based pollen productivity estimate (PPE) of 1.85 for Cerealia instead of the local estimate of 0.22, as the latter appears to overestimate the cereal cover (Table S2). To ensure consistency and comparability between the reconstructions at both sites, we also re-ran the REVEALS model at Lake Oltina using the literature-based PPE of 1.85 for Cerealia (Table S2). The pollen–vegetation relationship depends on the size and type of the sedimentary basin (e.g., lake or bog) and differences in pollen productivity and dispersal characteristics between taxa (Sugita, 1994, 2007). Both wetland and lake models assume that atmospheric deposition is the primary pollen transport pathway to the basin. Atmospheric deposition was likely the main pathway for pollen entering Mangalia Herghelie wetland; however, for Lake Oltina, pollen may also be delivered through runoff. Despite the uncertainties associated with assuming atmospheric pathways and constant pollen productivity over space and time, the REVEALS model has yielded reliable estimations of vegetation cover (Hellman et al., 2007; Soepboer et al., 2008; Mazier et al., 2012).

3.4. Disturbances by fire

3.4.1. Charcoal morphologies and morphometrics as indicators of fuel and fire type

To determine past fire disturbances, we conducted macroscopic charcoal analysis on 2 cm^3 samples extracted at 1 cm contiguous intervals at both sites. Sample preparation involved bleaching and wet sieving through a 160 μm mesh. Identification of charcoal morphotypes followed methodologies outlined by Feurdean et al. (2017) complemented Enache and Cumming (2006); Jensen et al., (2007); Courtney-Mustaphi and Pisaric (2014); Feurdean (2021) and Feurdean et al. (2023). Charcoal morphotypes were categorized into four types: 1) grass (Poaceae) leaves; 2) herbs (mainly stems from forbs and Poaceae); 3) broadleaves associated with deciduous trees and forbs; and 4) wood (Fig. 3). We separate the charcoal fractions in four classes (SI Fig. 5) then grouped these categories into two size classes (150–500 μm and >500 μm) to infer more local versus distal fire events (Adolf et al., 2018; Florescu et al., 2018). To calculate the influx of charcoal morphotypes and size classes (particles cm^{-2} yr^{-1}), we divided their respective concentration (particles cm^3) by the deposition time determined from the age-depth models (yr cm^{-1}).

We estimated the frequency and severity of fire episodes by analysing charcoal peaks derived from macrocharcoal values using the method of Higuera et al. (2009). The CHAR time series were first interpolated to constant time intervals (Cinterpolated) of 10 yr at Mangalia and 6 yr at Oltina, using a robust LOWESS smoother (400 years). Subsequently, we decomposed the total CHAR component into CHAR background (Cbackground) and CHAR peaks (Cpeak), reflecting local fire episodes. A Gaussian mixture model with a globally defined threshold was used to discern noise-related fluctuations from charcoal peaks, as this choice maximized signal-to-noise index SNI (Higuera et al., 2009; Kelly et al., 2011). Charcoal values exceeding the 99th percentile threshold of the modelled noise distribution were identified as potential fire episodes, and their frequencies were smoothed using a 1000-yr window width. Fire frequency (FF) was determined by counting the number of charcoal peaks within a 1000-yr time window. The methodology for extracting charcoal peaks was originally designed for forest ecosystems, which are characterized by high-intensity fires and longer return intervals. In contrast, grassland fires occur more frequently and with lower intensity, producing less charcoal. Therefore, our statistical reconstruction of the fire regime may be biased towards detecting high-severity fires and longer return intervals.

3.4.2. Recent fire regime reconstruction with satellite imagery

To evaluate how well charcoal morphologies reflect the type of fuel availability and fire severity at local (2 km radius) and local to regional (10 km radius) scales around the two sites (Fig. 4), we extracted fire occurrence data from 2001 to 2022 using the MODIS/Aqua + Terra Thermal Anomalies/Fire locations product (MCD14ML) distributed by Fire Information for Resource Management System (FIRMS, 2024). To identify the primary vegetation types where these fires occurred, we used CORINE Land Cover (CLC) data managed by the Copernicus Land Monitoring Service (Copernicus Land Monitoring Service, 2024).

3.5. Disturbances by herbivores

3.5.1. Coprophilous fungal spores

To determine past herbivore activity, we counted the abundance of predominantly coprophilous fungal spores (*Sporormiella, Sordaria, Podospora*, and *Delitschia*) during pollen analysis (van Geel et al., 2006; Shumilovskikh et al., 2022; van Asperen et al., 2020). Although the *Arnium* type is primarily coprophilous we considered this spore

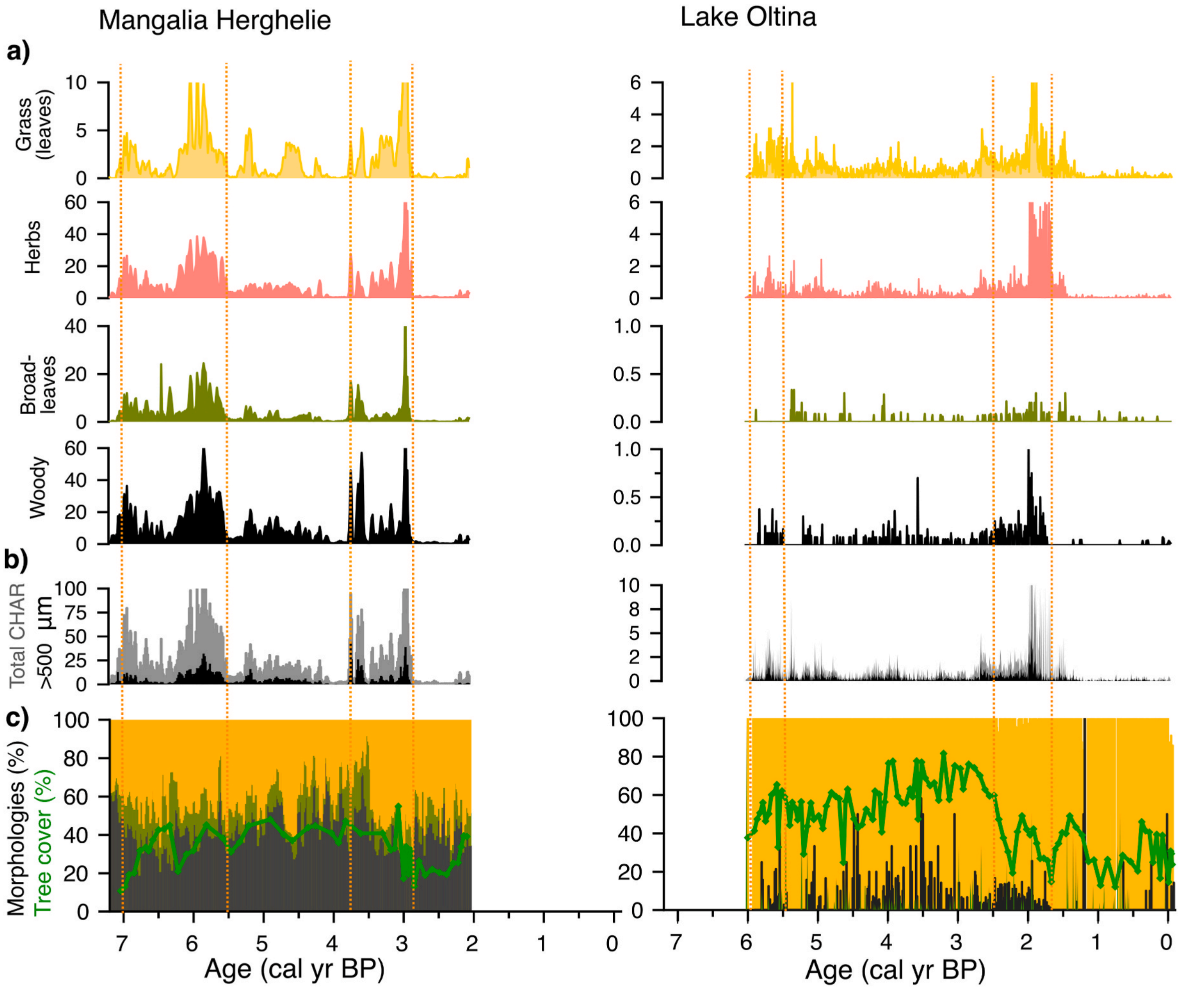


Fig. 3. a) Influx of charcoal morphologies (#/cm^2/yr) categorized into four types: grass leaves, herbs (stems of forbs and grasses), broadleaves (deciduous trees and forbs) and woody material. b) Total charcoal influx (>150 µm) and particles larger than 500 µm. c) Charcoal morphologies as percentages (using the same colour scheme as in the influx chart, with dark orange representing the sum of all grass and forb remains), alongside tree pollen percentages (green diamond line), illustrating the relationship between the abundance of woody fuel (tree pollen percentages) and woody charcoal. Vertical lines mark the major temporal changes in charcoal morphologies. The exceptionally high values of total CHAR at Mangalia Herghelie, reaching 180 #/cm^2/yr are not displayed to more clearly illustrate the general trends in the charcoal influx. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

separately due to its high and strongly fluctuating values over time. Additionally, *Arnium* was found to be a less common coprophilous taxa in recent dung samples (Richardson et al., 2001). The abundance of coprophilous fungal spores is represented both as percentages and influx. Percentages were calculated relative to their sum added to the terrestrial pollen sum, while influx was calculated relative to the *Lycopodium* spores (1 tablet) added (Fig. 5).

3.5.2. Herbivory from databases

We extracted data on herbivore occurrences from archaeozoological databases and relevant literature (Bălăşescu, 1997; Bălăşescu et al., 2005, 2015; Bălăşescu and Radu, 2021; El Susi, 2001; Haimovici and Ureche, 1968; Haimovici and Bălăşescu, 2006; Manhart, 1998; Moise, 2001; Vasilescu-Ureche and Haimovici, 1976; Voinea et al., 2023). The data collection focused on a 50–85 km radius around Mangalia Herghelie, the approximate source of regional pollen rain, extending up to 100 km due to scarcity of remains. We concentrated the archaeozoological analysis on Mangalia Herghelie, where sufficient coprophilous fungal spores were present due to the core's proximity to the basin margin. We quantified the abundance of domestic versus wild herbivore communities relative to the total number of herbivores and assessed the abundance of individual taxa within the domestic and wild categories. Wild boar and pig were included in the herbivore analysis as they can cause substantial damage to vegetation. Herbivore diet types (grazer, browser, and mixed feeder) were derived from HerbiTraits (Lundgren et al., 2020), and their abundances were calculated relative to the total herbivore finds.

3.6. Statistical analysis

To explore the response of forest and grassland cover and composition to environmental drivers we employed variable importance by permutation (VIP) applied to generalized additive models (GAMs; Wood, 2011). The proxy used as response variables included tree cover and the abundance of dominant woody taxa (*Quercus, Carpinus betulus, C. orientalis, Corylus avellana*), total grassland cover, and separately the abundance of grasses (Poaceae) and forbs, represented by their REVEALS-based percentages. The proxies used as predictors were growing season moisture availability, represented by δ^{13}C (‰) from Sofular cave, northern Turkey; fire severity, defined by charcoal influx (#/cm^2/yr), as this correlates highly with wood charcoal influx); herbivory, represented by the percentages of coprophilous fungal spores; and human impact, defined as the percentages of cultural indicators. These proxies differ in the spatial resolution they represent. For example, the REVEALS model reconstructs vegetation cover at a regional scale of up to 100 km (Sugita, 2007). Macroscopic charcoal

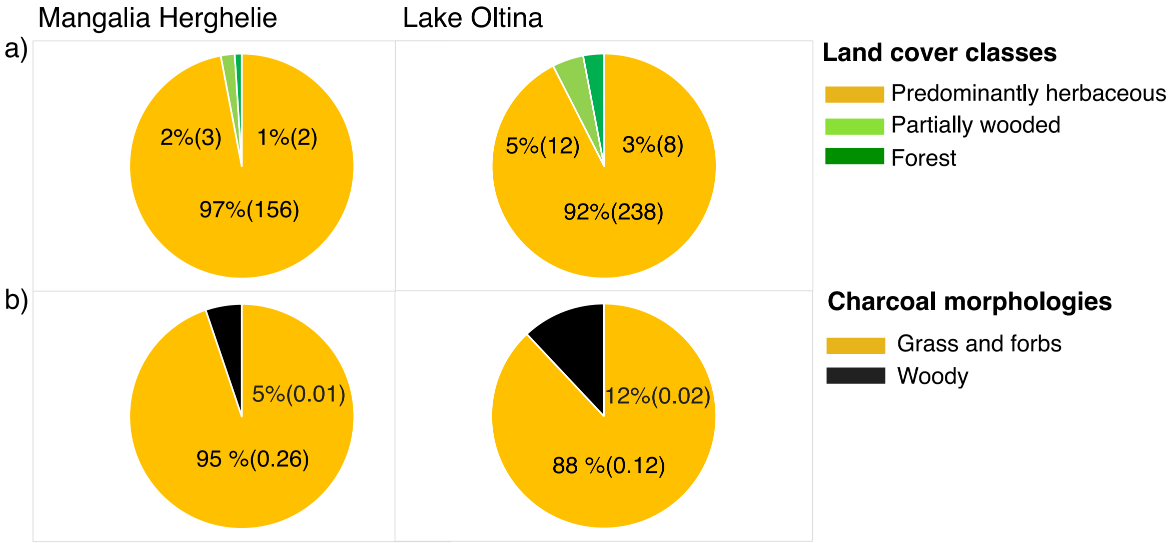


Fig. 4. a) Satellite-based fire occurrences between 2001 and 2022, both in percentage and absolute number of fires (in brackets), across land cover classes within a 10 km radius of each site. These are grouped into predominantly herbaceous (agricultural and wetlands), partially wooded (orchards, vineyards, and transitional woodlands), and forest categories. b) Charcoal morphologies from surface sediment samples show the dominant fuel types, with herbaceous materials (grass and forbs) and woody charcoal represented as percentages and influx (in brackets).

reflects fire events on a more local scale. Wood charcoal particles are typically deposited within approximately 2 km of the fire source, while grass charcoal mainly disperses up to 10 km. However, smaller quantities of both charcoal types can travel as far as 100 km (Vachula and Rehn, 2023). In contrast, dung spores generally serve as highly localised indicators of grazing activity (Baker et al., 2016), though they can also be long transported by air and water. Note that proxy data do not always linearly correspond to the actual changes they represent. For instance, variations in $\delta^{13}C$ or charcoal levels do not scale linearly with the amplitude of changes in moisture availability or fire severity, which may affect the strength of the relationship between predictors and the response variable.

The GAMs estimate the shape of the relationships between predictors and response variables, distinguishing between gradual and abrupt responses, while VIP analyses assess the importance of each predictor in fitting the data (Fig. 6; Table 1a, b). VIP analyses were constructed using percent of deviance explained. To model the relationships between predictors and response variables, we used a Gaussian distribution with an identity link function. Models were fit using restricted maximum likelihood (REML), as implemented in the 'mgcv' package in R. Model fit and validity were assessed by comparing residuals of the empirical model to those produced by simulated data from using the DHARMa R package (Dunn and Smyth, 1996; Hartig, 2017), which provides diagnostic tools to ensure model assumptions and quality. All the statistical analyses were performed in R 4.1.1 (R Core Team, 2023).

4. Results

4.1. Lithology, chronology, and local wetland conditions of the Mangalia Herghelie site

The age-depth model of the marginal profile at Mangalia Herghelie indicated a constant sediment accumulation rate, averaging 10 years/cm (SI Fig. 1a). Lithology and plant macrofossil analyses revealed the deposition of marine clay between 550 and 477 cm (>7200-7080 cal yr BP) and gyttja clay between 477 and 474 cm (7080-7050 cal yr BP), with no preserved plant remains in these units. Between 474 and 470 cm (7050-7000 cal yr BP) coarse detritus gyttja accumulated, whereas from 470 to 100 cm (7050-2000 cal yr BP), the deposition of a homogeneous peat layer composed of undetermined herbaceous plants and Cyperaceae (mainly *Cladium mariscus*) indicated stable hydrological conditions (Fig. 7, SI Fig. 3).

Lower Ca/Zr ratios, indicative of less evaporative (wetter) conditions, occurred between 6700 and 6500, 6250-6000, 4800-3500, and 3200-2000 cal yr BP (Fig. 7). Additionally, high Fe/Mn ratio, indicating anoxic (wet) conditions, were observed at >7000 cal yr BP and 6700-6500 cal yr BP (SI Fig. 2). Increased water levels at 6550, 5900, and 3700 cal yr BP are shown by the sporadic presence of *Chara* oospores and by the peak in *Typha* pollen around 7000 cal yr BP (SI Figs. 2 and 4). Conversely, higher Ca/Zr ratios, indicating drier conditions, were recorded between 6900 and 6700, 6500-6250, 6000-4800, and 3500-3200 cal yr BP, which were further supported by lower Fe/Mn ratio.

4.2. Pollen based land cover reconstruction

No pollen was preserved below 487 cm (>7200 cal yr BP) at Mangalia Herghelie, and pollen counts were low between 7200 and 7050 cal yr BP. The REVEALS model and raw pollen data showed similar values in landscape openness (non-arboreal pollen) and *Quercus* at Mangalia Herghelie, while at Lake Oltina, REVEALS predicted 10–15% greater openness (Fig. 6). In comparison to the raw data at Mangalia Herghelie, REVEALS generally predicted higher proportions of *Carpinus orientalis, Tilia, Acer*, Rosaceae, Cerealia and Asteraceae, and lower proportions of *Corylus avellana, Carpinus betulus, Betula, Ulmus, Alnus, Fraxinus, Salix, Artemisia*, and Chenopodiaceae (Fig. 2). Cluster analysis at Mangalia Herghelie identified major vegetation shifts at 6800 and 3800 cal yr BP, with smaller changes occurring at 6000, 2800, and 2200 cal yr BP (SI Fig. 4). The main vegetation changes in each of these zones are described below.

4.2.1. Zone 1, 7200-6800 cal yr BP: low tree-high herbaceous cover

At the beginning of the record, pollen-based vegetation reconstruction indicated a low woody cover (20%), primarily consisting of *Corylus avellana*, *Quercus*, *Betula*, *Pinus*, *Tilia*, *Ulmus*, and *Alnus* (Figs. 2 and 7; SI Fig. 4). The dominant *Pinus* pollen is Diploxylon type (likely originating from *P. sylvestris,* thought possible also *P. peuce;* see Hanganu et al., 2023*)*, with Haploxylon type (probably *P. cembra*) showing scattered occurrences. Open vegetation was dominated by Poaceae (70%), with a smaller proportion of forbs, particularly *Aster*. Low percentages of cultural (cereals) and grazing indicators (e.g. *Plantago lanceolata*), were also

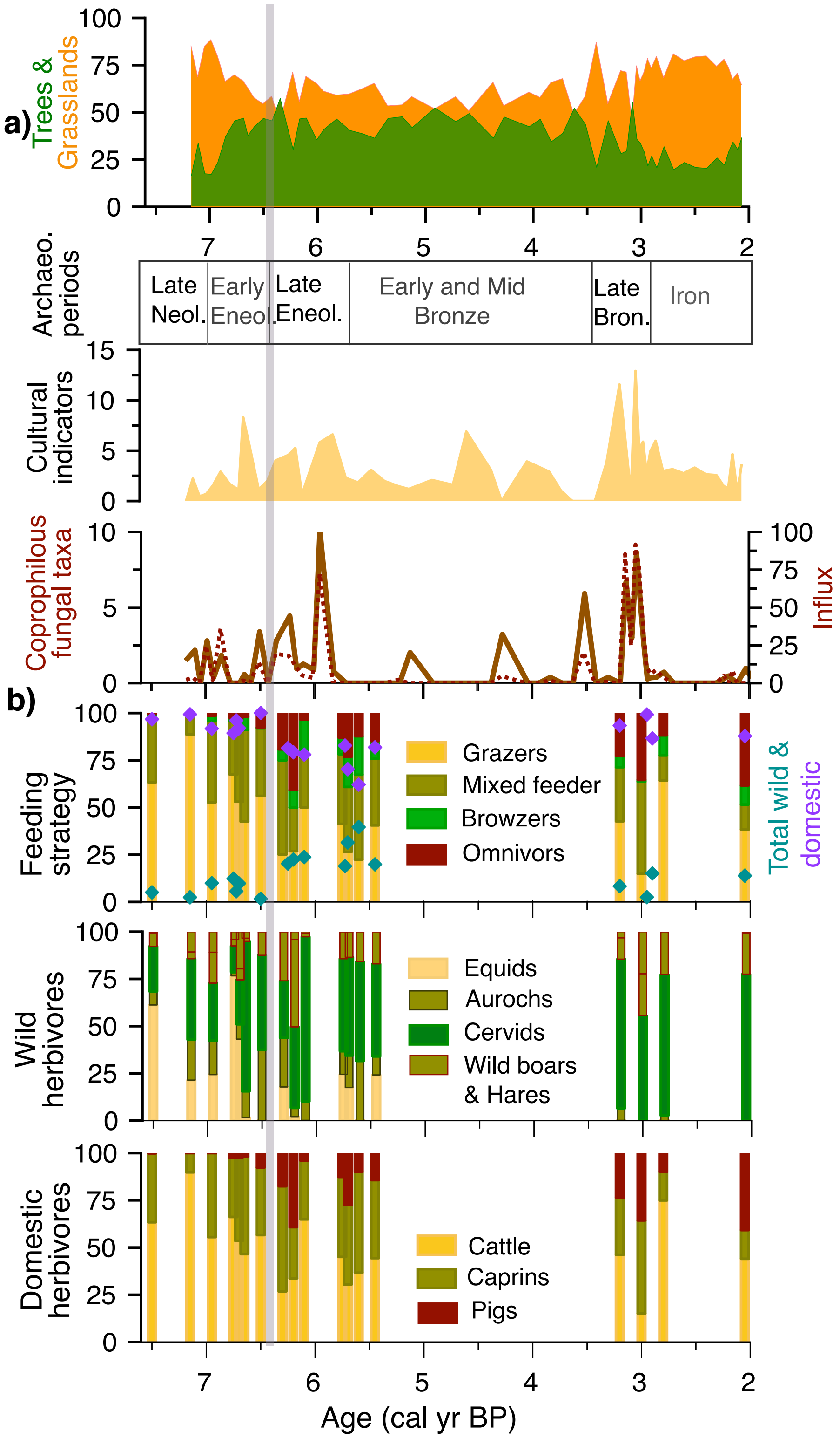


Fig. 5. a) Temporal changes in pollen indicative of grasslands and tree cover alongside cultural indicators (arable and pastureland) and coprophilous fungal taxa (*Sporormiella, Sordaria, Podospora, Delitschia*) as percentages and influx (#/cm^2/yr dashed line). b) Temporal shifts in the main herbivore types based on feeding guilds during different archaeological periods also highlighting the contributions of domestic and wild herbivores (diamonds). Archaeological periods are also marked. Mid/late Neolithic includes Prehamangia and Hamangia (7650-7000 cal yr BP) cultures, Early Eneolithic includes Hamangia culture and Late Eneolithic (flourishing Eneolithic) includes Gumelnita culture (6550-5850 cal yr BP). The vertical grey bar indicates a dietary shift from large-bodied herbivores with selective diets (primary grazers) to a more diverse feeding type involving smaller domestic and wild herbivores.

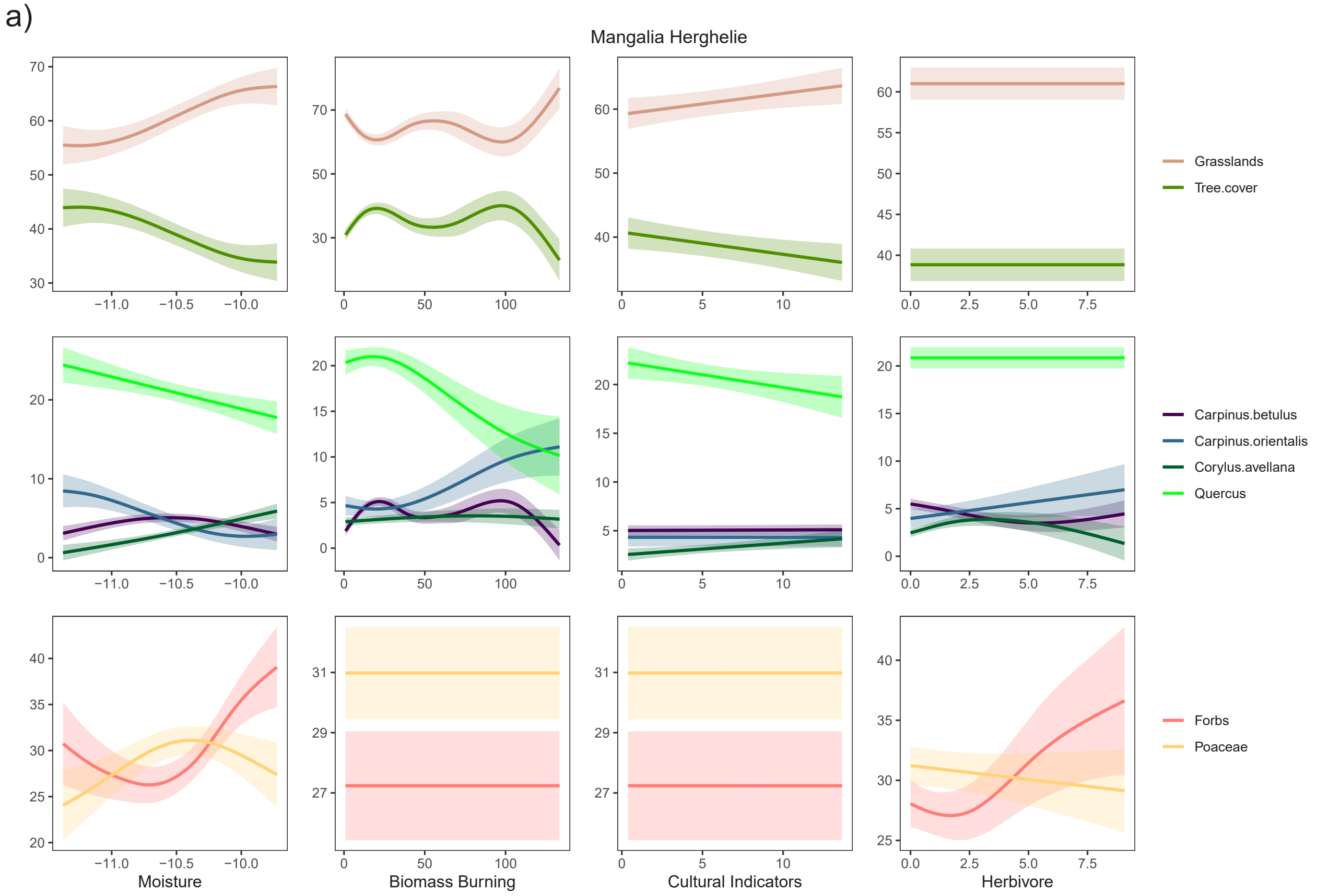


Fig. 6. Generalized additive models showing the relationships between tree cover and grasslands as well as separately on individual tree taxa, grass and forb (dependent variables, y-axis) with key factors such as moisture, fire, human impact, and herbivore (x-axis) at Mangalia Herghelie a) and Lake Oltina b). Tree and grass cover are represented by their pollen percentages. Moisture availability is determined by δ^{13}C, where increases in δ^{13}C (more negative) values denote a change towards lowering moisture availability, fire by charcoal influx (#/cm^2/yr), anthropogenic impact by pollen percentages of cultivated and grazed plants and herbivores by percentages of coprophilous fungal taxa.

recorded. Sedge graminoids (Cyperaceae) showed percentages around 15%.

4.2.2. *Zone 2, 6800-3800 cal yr BP: increasing tree cover*

Woody cover increased rapidly, peaking at 35–50% between 6800 and 3800 cal yr BP. This included a mix of open- (35%, including *Quercus, Corylus avellana*, and *Betula*) and closed-canopy taxa (10%, including *Carpinus betulus, C. orientalis, Tilia,* and *Ulmus*). The proportion of Poaceae decreased, while those of forbs, particularly of drought tolerant type (Chenopodiaceae, Asteraceae, *Aster)* increased between 6800 and 6000 cal yr BP (zone 2a). Grazing and cultivated indicators showed rising values between 6600 and 5900 cal yr BP. Around 6000 cal yr BP, *Corylus avellana* declined, while *Quercus*, *Betula* and closed canopy tree taxa (*Carpinus betulus, Fagus sylvatica*) increased (zone 2b). In respect of herbaceous taxa, the proportion of Poaceae and forbs e.g., *Thalictrum, Galium, Filipendula*, and Apiaceae rose, while more drought tolerant forb types declined, particularly between 6000 and 4200 cal yr BP. Cyperaceae peaked between 5000 and 4200 cal yr BP (SI Fig. 4). The abundance of cultural indicators declined and remained low between 5900 and 3800 cal yr BP.

4.2.3. *Zone 3, 3800-2800 cal yr BP: declining tree cover-increasing herbaceous cover*

Tree cover, particularly *Quercus,* along with *Carpinus betulus* declined from ca. 45% at 3800 cal yr BP to 25% at 2800 cal yr BP. *C. orientalis* showed highly fluctuating values but overall rose. Herbaceous cover consisted of an equal mix of Poaceae and forbs (25–30%); Cyperaceae were also abundant (20%). Cereals (12%) and grazing indicators (10%) reached maximum values in the profile between 3200 and 2900 cal yr BP (Fig. 7).

4.2.4. *Zone 4, 2800-2000 cal yr BP and the last 200 years: low tree cover-dominance of herbaceous vegetation*

Tree cover, particularly *Quercus* increased to 35% between 2200 and 2000 cal yr BP (zone 4a). Herbaceous taxa were represented by a mix of Poaceae and forbs, with *Artemisia,* Chenopodiaceae, and Asteraceae, showing the most increase, while the proportion of cultural indicators declined. The top pollen samples (approximately the last 200 years) showed a tree cover of around 10%, dominated by *Quercus*, with a slight increase in *C. betulus* (zone 4b). The abundance of cereals and forbs, particularly of drought tolerant and/or ruderal types (Chenopodiaceae, *Artemisia*) and Asteraceae increased markedly (Fig. 7; SI Fig. 4).

4.3. *Fire severity identification from charcoal morphologies and satellite images*

4.3.1. *Recent fire identification*

Satellite-derived fire data (FIRMS MODIS) indicated that between

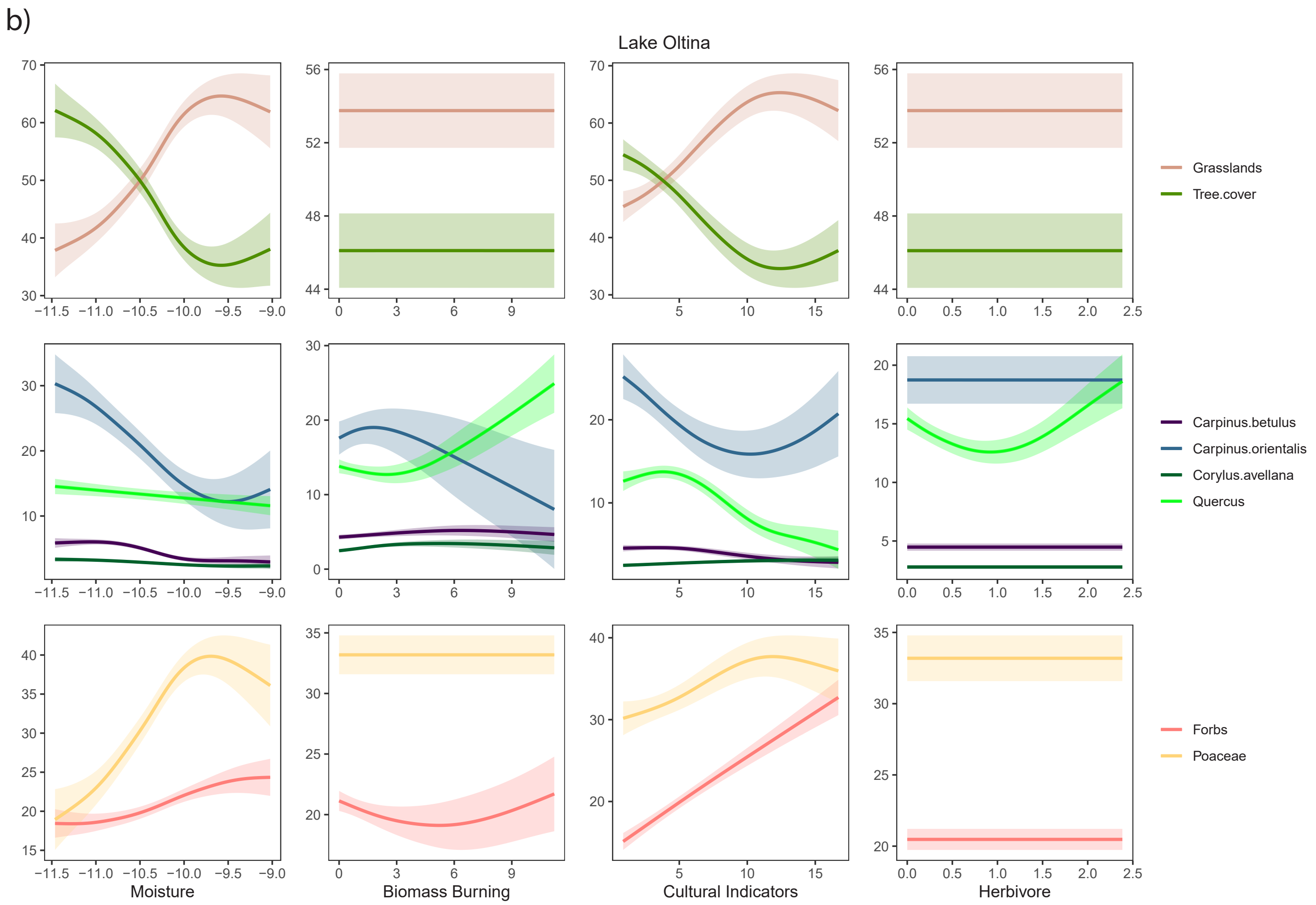


Fig. 6. (*continued*).

Table 1a
Results for generalized additive models of the relationship between vegetation types to various independent drivers at Mangalia Herghelie and Lake Oltina (values in brackets) sequences. The significance of each modelled parameters is given by p values ***p < 0.0001: **p < 0.001; *p < 0.1.

Models	P -values			
Vegetation	**Moisture**	Biomass burning	Cultural indictors	**Herbivore**
Tree cover	0.0026 ** (<0.0001***)	0.0063** (0.751	0.1058 (<0.0001***)	0.6957 (0.407)
Quercus	0.0424* (0.0804.)	0.0145 * (0.005**)	0.1310 (<0.0001 ***)	0.3853 (0.0079) **
C. betulus	0.0248* (6.92e ***)	6.92e ***(0.112)	0.2899 (0.0040 **)	0.0089** (0.4635)
C. orientali	0.0088** (0.0002 ***)	0.0358 *(0.1804	0.9998 (0.0210*)	0.1437 (0.571)
Corylus avellana	0.0005*** (0.0085 **)	0.2178 (0.022*)	0.0987. (0.0485*)	0.0636. (0.9497)
Grassland cover	0.0011** (<0.0001 ***)	0.0064** (0.748)	0.1115 (<0.0001***)	0.708 (0.394)
Poaceae	0.107 (<0.0001 ***)	0.583 (0.7343)	0.516 (<0.0118*)	0.246 (0.7268)
Forbs	0.0013* (0.0065 **)	0.7441 (0.1543)	0.6193 (<0.0001***)	01455 (0.5518)

2001 and 2022 there were 5 fires at Mangalia Herghelie and 25 fires at Lake Oltina within a 2 km radius. Within a 10 km radius, Mangalia Herghelie experienced 163 fires, while Lake Oltina recorded 259 fires (Fig. 4). All fires occurring within a 2 km radius of the study sites were in herbaceous-dominated land cover classes, such as arable lands, pastures, managed grasslands and wetlands (latter class only at Lake Oltina). Within a 10 km radius, agricultural fires accounted for 97% (156) of fires around Mangalia Herghelie and 92% (238 agricultural and wetland fires) around Lake Oltina, with the remaining fires occurring in orchards, vineyards, transitional woodlands, and deciduous forests (Fig. 4). Analysis of surface charcoal samples revealed that 95% of charcoal morphologies at Mangalia Herghelie and 88% at Lake Oltina originated from herbaceous plants, with only 5% and 12%, respectively derived from wood (Fig. 4).

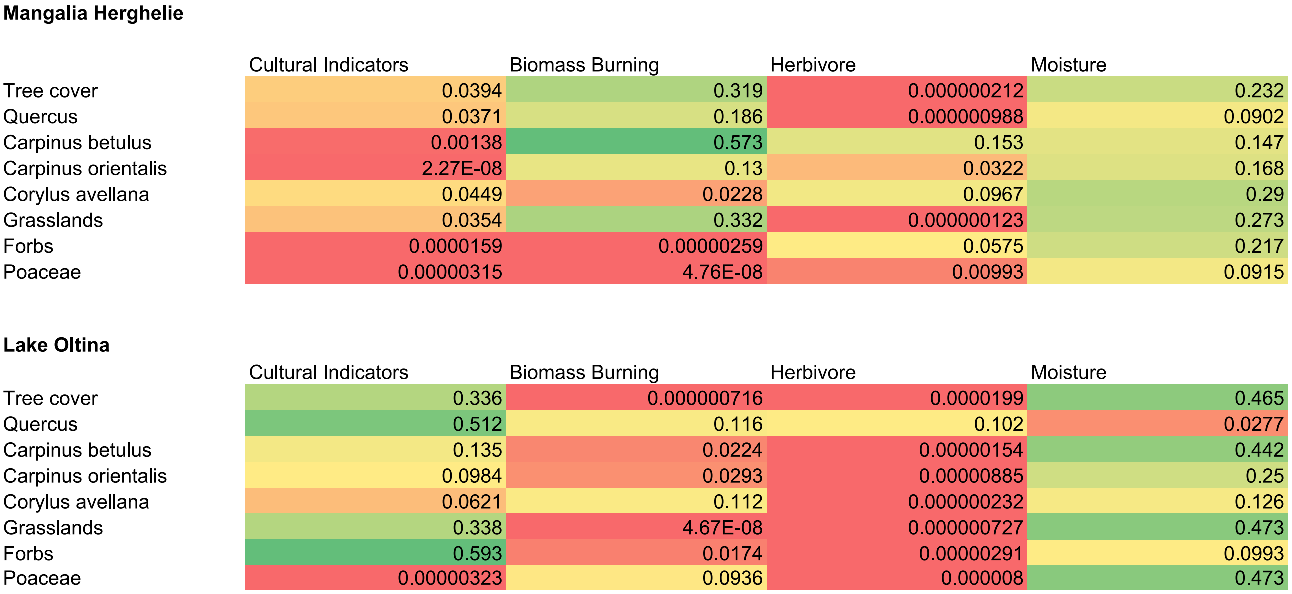
4.3.2. *Past fire identification*

The charcoal records indicate that Mangalia Herghelie had significantly more particles than Lake Oltina (mean 25.4 vs. 1.1 particles/cm^2/yr) with a higher proportion of larger particles and wood morphologies (Fig. 3; SI Fig. 5). There is strong co-variability among morphotypes at both sites (Fig. 3), with the strongest correlation observed between grasses and forbs (r = 0.89 Mangalia Herghelie; r = 0.7 Lake Oltina). Broadleaved morphologies exhibited a slight stronger association with pollen of tree (r = 0.38, p = 0.015) than with forbs (r = 0.28, p = 0.036) at Mangalia Herghelie but no significant association with either was found at Lake Oltina. The wetland-type basin of Mangalia Herghelie and its marginal coring location favoured the deposition of larger, heavier (wood) and less aerodynamic (leaf) charcoal forms. In contrast, the larger Lake Oltina (1000 ha), likely limited the deposition of charcoal, especially less aerodynamic particles, at its centre, despite capturing more fire events due to a larger charcoal source area.

At Mangalia Herghelie, the average fire frequency was 6 fires/1000 years. Overall, high charcoal abundance was observed between 7000-5500 and 3800-2800 cal yr BP, with peak charcoal accumulation,

Table 1b

Results for the variable importance by permutation (VIP) showing the importance of each modelled parameters.



Mangalia Herghelie

	Cultural Indicators	Biomass Burning	Herbivore	Moisture
Tree cover	0.0394	0.319	0.000000212	0.232
Quercus	0.0371	0.186	0.000000988	0.0902
Carpinus betulus	0.00138	0.573	0.153	0.147
Carpinus orientalis	2.27E-08	0.13	0.0322	0.168
Corylus avellana	0.0449	0.0228	0.0967	0.29
Grasslands	0.0354	0.332	0.000000123	0.273
Forbs	0.0000159	0.00000259	0.0575	0.217
Poaceae	0.00000315	4.76E-08	0.00993	0.0915

Lake Oltina

	Cultural Indicators	Biomass Burning	Herbivore	Moisture
Tree cover	0.336	0.000000716	0.0000199	0.465
Quercus	0.512	0.116	0.102	0.0277
Carpinus betulus	0.135	0.0224	0.00000154	0.442
Carpinus orientalis	0.0984	0.0293	0.00000885	0.25
Corylus avellana	0.0621	0.112	0.000000232	0.126
Grasslands	0.338	4.67E-08	0.000000727	0.473
Forbs	0.593	0.0174	0.00000291	0.0993
Poaceae	0.00000323	0.0936	0.000008	0.473

woody morphotypes, and large charcoal particles occurring at 7000-6800, 6250-5500, 3800-3500, and 2900-2800 cal yr BP (Figs. 3 and 7; SI Fig. 5). Charcoal accumulation and fire frequency decreased to 2 fires/1000 years between 5500-3800 and 2800-2200 cal yr BP.

At Lake Oltina, the highest charcoal accumulation and fire frequency were recorded between 6000 and 5500 (19 fires/1000 years) and 2400-1500 cal yr BP (25 fires/1000 years), during which grass and forb morphologies predominated, but wood and leaves also reached their highest proportions (Figs. 3 and 7; SI Fig. 5). Between 4700 and 2700 cal yr BP, charcoal accumulation and fire frequency declined to 10 fires/1000 years, accompanied by a slight decline in wood morphologies. The exceptionally high peak in charcoal and woody morphologies at 1800 cal yr BP, along with high detrital geochemical input, suggests charcoal transport by Danube water discharge into the lake (Feurdean et al., 2021). No large fire episodes occurred in the past millennium, and woody morphotypes nearly disappeared.

4.4. *Coprophilous fungal spores at Mangalia Herghelie*

The analysis of coprophilous fungal spores, including *Sporormiella*, *Sordaria*, *Podospora*, *Delitschia*, and the predominantly coprophilous *Arnium*, revealed distinct temporal patterns in herbivore presence (Fig. 5, SI Fig. 4). Between 7200 and 5800 cal yr BP, coprophilous fungal spores particularly *Sordaria* and *Podospora* were abundant, both in terms of percentage and influx, with a pronounced peak between 6500 and 5900 cal yr BP. From 5800 to 3500 cal yr BP, spore abundance remained low, with only sporadic peaks around 5200 and 4300 cal yr BP. The abundance of coprophilous fungal spores, mostly *Podospora* increased again around 3500 cal yr BP, reaching a peak between 3200 and 2900 cal yr BP (Fig. 5; SI Fig. 4). *Arnium* showed a different pattern; reached higher levels around 6800, between 5500 and 4500 cal yr BP, and from 3000 to 2800 cal yr BP (Fig. 5; SI Fig. 4). This may be linked to different ecological preferences that are not necessarily related to dung.

4.5. *General additive models*

The VIP analyses indicate that at Mangalia Herghelie, moisture availability and fire had the strongest influence on vegetation (Table 1b). In contrast, at Lake Oltina moisture availability and cultural indicators were the most important factors. The relationships between vegetation cover and various environmental factors, as determined by generalized additive models (GAMs), are detailed below (Fig. 6a and b).

4.5.1. *Moisture availability*

Model results indicated a significant positive relationship between tree cover and increased moisture availability at both sites (Fig. 6a and b, Table 1a,b). A significant positive relationship was also observed for *Quercus, Carpinus betulus, C. orientalis,* while this relationship was negative for *Corylus avellana.* In contrast, grassland cover showed a significant negative relationship with increased moisture at both sites. When separated into forbs and Poaceae, forbs exhibited a significant negative relationship with moisture at both sites, and Poaceae at Lake Oltina.

4.5.2. *Fire*

At Mangalia Herghelie, tree cover showed a significant positive relationship with both low to intermediate and extremely high CHAR values (Fig. 6 a, Table 1 a,b). *Carpinus betulus* and *C. orientalis* exhibited statistically significant positive responses to rising CHAR, whereas *Quercus* showed a negative response. At Lake Oltina, *Quercus* and *Corylus avellana* demonstrated a statistically significant positive response to CHAR, while *Carpinus betulus* showed a similar, but statistically insignificant, trend (Fig. 6b–Table 1a,b). Grassland cover showed a positive response to intermediate and high CHAR values, though this relationship was statistically significant only at Mangalia Herghelie.

4.5.3. *Cultural indicators*

Tree cover, *Quercus*, *Carpinus orientalis*, and *Carpinus betulus* showed a negative correlation with cultural indicators, though this was statistically significant only at Lake Oltina (Fig. 6a and b, Table 1b). In contrast, *Corylus avellana* along with grassland cover, forbs and Poacea exhibited a positive response to cultural indicators, with significance also observed only at Lake Oltina. The more substantial effect of cultural indicators on tree cover at Lake Oltina results from their higher abundance at this site. However, using the relative abundance of pollen from cultural indicators as a predictor variable for the dominance of woody taxa, also inferred from pollen, implies some circularity.

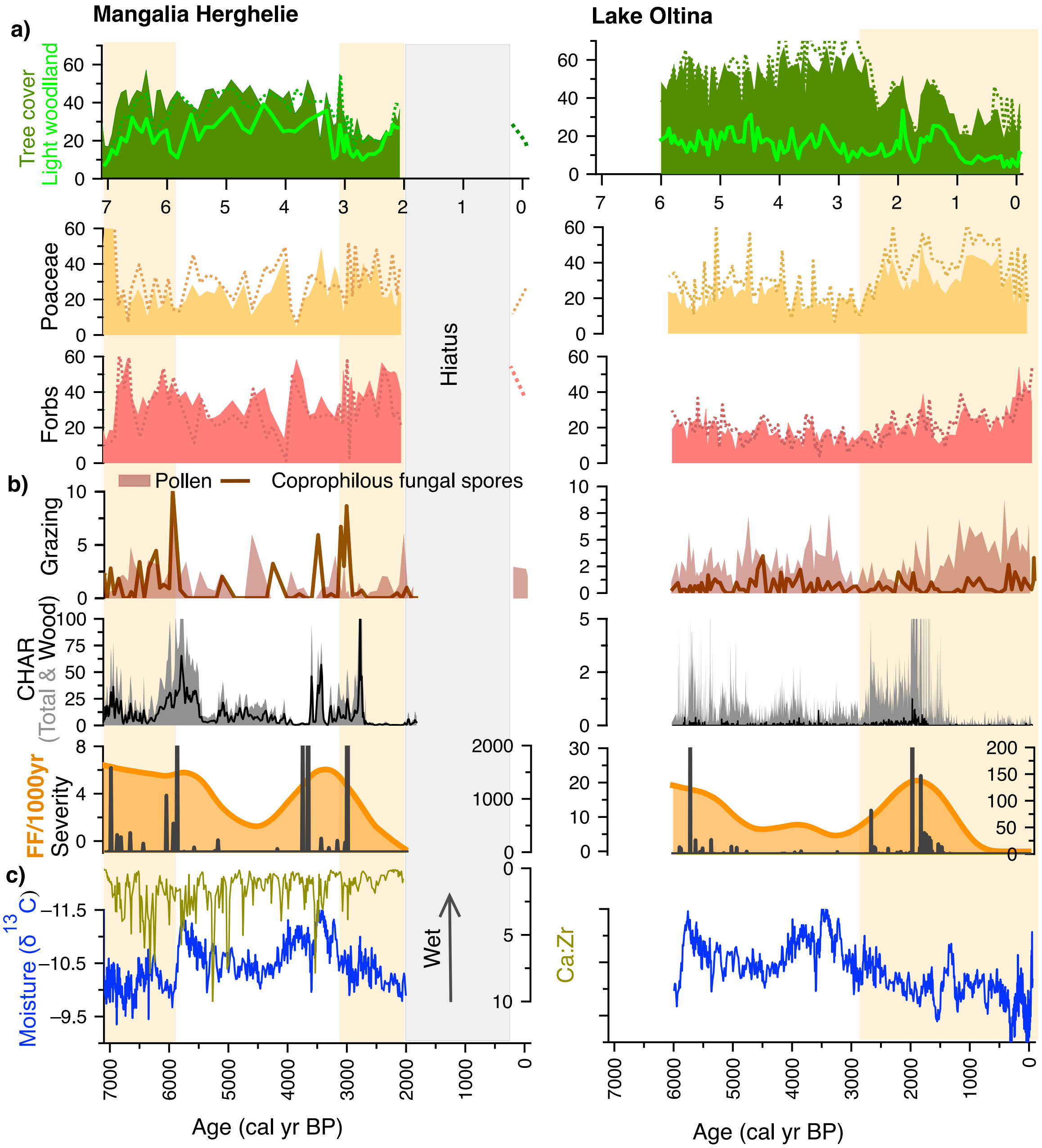


Fig. 7. Integrated summary of key environmental changes: a) Main land cover changes, including total tree and light-demanding tree taxa, forbs, and grasses (Poaceae) inferred from pollen percentages (solid line) and the REVEALS model (dashed line). b) Disturbance by herbivory from coprophilous fungi and pollen. Disturbance by fire from total CHAR values (biomass burning) as well as charcoal peak magnitudes and woody morphologies (fire severity). c) Local hydrological conditions at Mangalia Herghelie inferred from the Ca:Zr ratio, along with regional moisture availability (spring to fall) indicated by carbon δ^{13}C from Sofular Cave, northern Türkiye (Fleitmann et al., 2009; Göktürk et al., 2011). Arrows indicate the direction of increased moisture availability; with lower, less negative δ^{13}C values and lower Ca: Zr ratio associated with wetter conditions. Periods of regionally low moisture conditions are marked in orange. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.5.4. *Herbivore*

Only *Carpinus betulus* at Mangalia Herghelie and *Quercus* at Lake Oltina showed a statistically significant negative relationship with increasing coprophilous fungal taxa (Fig. 6a and b, Table 1a,b). Additionally, *Carpinus orientalis* and *Corylus avellana* exhibited a positive trend with increasing coprophilous fungal taxa at Mangalia Herghelie (Fig. 5). No significant associations were found between grasslands and coprophilous spores at either site. However, forbs displayed a significant positive relationship with increasing coprophilous fungal taxa at Mangalia Herghelie.

5. Discussion

5.1. *Moisture driven forest-grassland dynamics*

Fluctuation in soil moisture availability is a key driver of the dynamics between forests and grasslands in Eurasian open ecosystems (Erdős et al., 2022). Climate reconstructions for the Black Sea region and Romania reveal significant variability in precipitation throughout the Holocene. Between approximately 7500 and 6000/5500 cal BP, high precipitation during the autumn and winters (Persoiu et al., 2017; Warken et al., 2024) but lower during the growing season (Göktürk et al., 2011), resulted in reduced plant-available moisture. Growing season moisture availability was high between 6000 and 3500 cal BP, gradually decreasing thereafter (Fleitmann et al., 2009; Göktürk et al., 2011). We found significant variability in tree cover during the mid and late Holocene and a strong positive correlation between increased plant moisture availability (declining δ^{13}C values in speleothems) and tree cover (Fig. 7). At Mangalia Herghelie, tree cover primarily dominated by light-demanding taxa, *Quercus*, *Corylus avellana*, *Betula*, and *Pinus* along with closed canopy species (*Carpinus betulus*, *C. orientalis*, *Tilia*, *Ulmus*, *Fraxinus*, *Alnus*, and *Fagus sylvatica*) increased rapidly from 20% to 45% around 6800 cal yr BP. The abundance of *Carpinus betulus* and *Betula* was particularly pronounced during periods of high plant moisture availability, between 6000 and 4500 cal yr BP (Figs. 2 and 6). Lake Oltina also showed higher woodland cover (max. 50%) between >6000 and 2500 cal yr BP (Feurdean et al., 2021, Fig. 3). Although growing season moisture was regionally low between 6800 and 6000 cal yr BP, tree cover expanded locally, possibly aided by higher winter precipitation and subsequent water storage in the soil and increased snowmelt in the spring. Ca/Zr and Fe/Mn ratios at Mangalia Herghelie additionally suggest local wet conditions between 6700-6500 and 6250-6000 cal yr BP (Fig. 7). Increases in tree cover including mesic tree species, were also observed from ca. 6500-6000 cal yr BP in the north-western Black Sea region (Ganz et al., 2024; Lukanina et al., 2023; Tonkov et al., 2014; Filipova-Marinova, 2007; Bozilova and Tonkov, 1998) and from 5500 cal yr BP in the Eastern Mediterranean–Black Sea Caspian Corridor (Connor et al., 2013; Cruz et al., 2024), pointing to a broad pattern of forest expansion influenced by regional moisture increase.

A pronounced decline in tree cover down to 25% was observed at Mangalia Herghelie from 3800 cal yr BP and at Lake Oltina from ca. 2800 cal yr BP (Figs. 2 and 7). Although these declines in tree cover occurred asynchronously at the two sites, they correspond with a progressive regional decrease in moisture availability during both cold and the growing seasons (Fleitmann et al., 2009; Dragusin et al., 2014; Warken et al., 2024). Additionally, dry wetland conditions were noted based on Ca/Zr ratios at Mangalia Herghelie between 3500 and 3200 cal yr BP (Fig. 7). Tree species composition also shifted during this period. *Carpinus orientalis* appeared to replace *C. betulus* and, to some extent, *Quercus* species (Figs. 2 and 7). *C. orientalis* is more drought-tolerant than *C. betulus* and the thermophilous and xerophilous *Quercus* species, such as *Q. robur*, *Q. pubescens*, and *Q. pedunculiflora*. The pollen record does not distinguish individual *Quercus* species, however, more mesic species, such as *Q. robur*, could have been replaced by xerophilous species. Additionally, *C. orientalis* has a high regenerative capacity, mainly through resprouting in disturbed habitats, and it is fire-resistant (San Miguel-Ayanz et al., 2016). We also observed an expansion in grassland cover associated with decreasing moisture availability (as indicated by high δ^{13}C values in speleothems; Fig. 6). A mix of grasses, sedges, and forbs (*Thalictrum*, *Galium*, *Filipendula*, Apiaceae) developed under a wide range of moisture conditions, while during drier periods most notably between 6800 and 6000 cal yr BP and 2500-2000 cal yr BP, more drought-tolerant forbs (*Aster*, *Artemisia*, Asteraceae, Chenopodiaceae) expanded.

Human activity also contributed to the reduction of tree cover and the transformation of naturally open vegetation into cultural landscapes ~ 3800 years ago. This is demonstrated by the elevated abundance of cultural indicators, fire activity, and the contrasting response curves of trees (negative) and grasslands (positive) to these indicators (Figs. 2, 6 and 7). The lowest tree cover was observed around 2400 cal yr BP, coinciding with the establishment of the Greek colony and harbour of Callatis, now the modern town of Mangalia (Repertoriul Archeologic National). Thus, the demand for wood for construction may have further reduced the tree cover in the surrounding landscape. On a larger spatial scale, across the lower Danube Plain and Dobrogea, human-driven deforestation is evident in pollen records from at least 3900 years ago, with intensification occurring from 3200 cal yr BP (Hanganu et al., 2023; Tonkov et al., 2014; Bozilova and Tonkov, 1998), whereas vegetation models suggest progressive deforestation starting around 4000 cal yr BP (Giosan et al., 2012).

Present-day landscapes around the Romanian shores of the Black Sea are predominately treeless, with forest patches dominated by *Quercus* species (*Q. pubescens, Q. pedunculiflora, Q. robur, Q. cerris*) and *Carpinus orientalis* confined to protected areas. Our moisture–tree cover model identified a critical state, where forest and grassland reached an equilibrium at 25–40% tree cover at Mangalia Herghelie and 25–55% at Lake Oltina. A more stable, forest-dominated state was reached above 40% tree cover at Mangalia Herghelie and 55% at Lake Oltina, while a grassland-dominated state was typical below 25% tree cover (Figs. 6 and 7).

5.2. *Fire driven forest-grassland coexistence*

5.2.1. *Fuel type, fire severity and frequency from charcoal morphologies*

The quality and quantity of charcoal produced by wildfires vary significantly, depending on the characteristics of the vegetation consumed and fire temperature. Compared to surface fires, which consume fine fuels such as forbs and grasses, and dead litter, high-intensity crown fires destroy more biomass and produce more charcoal particles, particularly those with woody characteristics (Conedera et al., 2009). Wood-derived morphologies with rounded shapes and higher density tend to deposit closer to the wildfire origin than grass-derived particles with elongated shapes (Vachula and Rehn, 2023). The charcoal morphological assemblages in the core surface primarily contain grass and forb morphologies, consistent with predominant fire occurrence in herbaceous-dominated vegetation inferred from satellite images (Fig. 4). Additionally, the strong temporal co-occurrence of grass with forb in both records conforms with low charcoal production from fine fuels, particularly grass found in experimental burning (Umbanhowar and McGrath, 1998; Hudspith et al., 2018; Feurdean, 2021; Feurdean et al., 2023). Therefore, we propose that higher levels of charcoal and large particles size and a greater proportion of woody morphologies relative to fine fuel identifies a mixed to high-severity fire in the forest-grassland mosaic.

At Mangalia Herghelie, we mostly identified fires within the forest-grassland mosaic with a frequency of 6 fires/1000 years (~1 fire every 170 years). We recorded elevated fire severity and frequency between 7000 and 6800 cal yr BP, 6250-5500 cal yr BP, 3800-3500 cal yr BP and 3000-2800 cal yr BP (Figs. 3 and 7). A lower fire frequency (2 fires/1000 years) and fires predominantly affecting surface vegetation, were typical between 5500 and 3800 cal yr BP and 2800-2200 cal yr BP. Lake Oltina experienced a higher mean fire frequency of 30 fires/1000 years (~1 fire every 33 years) but lower severity than Mangalia Herghelie, potentially also reflecting a larger site capturing more fire events and a lower proportion of bulky, woody particles. Fires of high severity occurring in the forest-grassland mosaic were largely synchronous with those at Mangalia i.e., 6000 and 5000 cal yr BP and 3000 and 1800 cal yr BP, with fires predominantly consuming fine fuel during the remaining periods. The few fire regime reconstructions from open ecosystems in Europe report fire intervals during the Holocene ranging from 150 to 500 years (Feurdean et al., 2013; Vincze et al., 2019; Lukanina et al., 2023), which are much longer than the fire intervals at Lake Oltina but comparable with those at Mangalia Herghelie.

5.2.2. *Fire-vegetation-climate feedback*

Wildfires can influence forest-grassland dynamics and species composition the converse can also occur (Archibald et al., 2018). We observed an association between tree and grassland cover and fire severity; however, this relationship is statistically robust only at Mangalia Herghelie (Figs. 6 and 7). Tree cover reached its highest values (40–45%) under low fire severity, with a second peak associated with extremely severe fire events (Figs. 3 and 5). *Carpinus betulus*, *C. orientalis* (at Mangalia Herghelie) and *Corylus avellana* (at Lake Oltina) known fire resprouters (Tinner et al., 2005), showed a significant positive response to increased fire severity (Fig. 6). Although *Quercus* regeneration also occurs in areas disturbed by fire (Bobiec et al., 2018), its strong negative association with fire severity at Mangalia Herghelie may reflect a stronger combined effect of droughts, fire events and herbivory on the Black Sea coast.

We observed a higher grassland cover (60–70%) under fire severities extending from low to extremely high. However, grasses showed no apparent response to fire, whereas the forb abundance appears to increase in response to severe fires (only at Lake Oltina (Fig. 6). Many herbaceous species from fire-prone ecosystem exhibit rapid-flammability strategies and post-fire regeneration traits (Pausas et al., 2017). However, in non-fire-prone ecosystems, as those from the studied region, species exhibit exaptation traits, which are broader regeneration strategies after severe disturbances caused by herbivores or other agents (e.g., fire). Experimental burning on temperate herbaceous species has shown that fire reduces recruitment from seeds, particularly in species of Poaceae and Asteraceae (Ruprecht et al., 2013). Further, a review of prescribed burning experiments in European grasslands demonstrate that the effect of fire is strongly dependent on the applied fire frequency, season, and extent (Valkó and Deák, 2021). However, both studies were conducted at very small spatial and short temporal scales, highlighting the need for extended studies in both time and space.

We suggest that the fire–vegetation relationship can be explained by feedback mechanisms linking fuel composition and structure with climate conditions. Low fire severity but highly variable frequency in grassland-dominated landscapes (7200-7000 and 2800-2000 cal yr BP) may have been driven by low fuel availability. In contrast, increased fire frequency and severity within the forest-grassland mosaic during intermediate moist conditions favourable for tree expansion (6800-5500 cal yr BP and 3800-2800 cal yr BP) were likely triggered by augmented fuel loads and connectivity (Figs. 3 and 6). However, as moisture and tree cover became elevated (5500-3800 cal yr BP), the probability of ignition and fire spread visible as a reduction in both severity and frequency, decreased, due to more shaded conditions and the reduced availability of flammable grass biomass. At Mangalia Herghelie, we found that fire severity peaked at approximately 40% tree cover (Fig. 6). This finding corroborates studies in savanna ecosystems, where wildfire activity rises sharply when tree cover falls below around 40% (van Nes et al., 2018), and in the broadleaved forest zone of central-eastern Europe as tree cover drops below 50% (Feurdean et al., 2020).

5.3. Herbivore abundance and feeding guilds as drivers for vegetation change: A case study at Mangalia Herghelie

Fluctuations in coprophilous fungal spores in our sedimentary sequence provide valuable insights into herbivore population dynamics and their impact on vegetation. Archaeofaunal remains suggest that wild and domestic herbivores coexisted throughout the studied period, likely exerting a combined influence on the vegetation. However, the relative importance of different herbivores and their dietary preferences varied significantly over time. The pollen record from Mangalia Herghelie indicates the presence of grazing-associated plants such as *Plantago lanceolata*, *Plantago* spp., and *Rumex* spp., along with coprophilous fungal taxa (*Sordaria*, *Podospora* and *Sporormiella*), and cereals from the start of the record at 7200 cal yr BP, peaking between 6600 and 5900 cal yr BP (Figs. 2 and 7; SI Fig. 4). Archaeofaunal remains suggest that during the Neolithic and early Eneolithic (7650-6550 cal yr BP, Prehamangia and Hamangia cultures), animal husbandry dominated, with domestic herbivores (cattle – *Bos taurus* 62%, caprine – *Ovis aries/Capra hircus* 36%) comprising 93% of animal remains consumed by human settlers (Fig. 5). Wild species (7%) included equids (*Equus ferus* and *Equus hemionus* 38%), cervids (*Cervus elaphus* and *Capreolus capreolus* 36%), and aurochs (*Bos primigenius* 12% (Bălășescu et Radu, 2021; Haimovici and Bălășescu, 2006; Manhart, 1998; Voinea et al., 2023).

Around 6500–6700 cal yr BP, coinciding with the transition to the flourishing Eneolithic period (6550-5850 cal yr BP) represented by the Gumelnița culture, a shift towards more sedentary agriculture and greater use of woodland resources occurred (Bălăşescu et al., 2005; Moise, 2001; Manhart, 1998; Bălășescu et al., 2015; Voinea et al., 2023, submitted; Balasse et al., 2016). This is evidenced by increased cereal pollen (Fig. 2), a decline in the consumption of domestic herbivores and a corresponding rise of wild herbivores (20–40%; Fig. 5b). Notable is also the increased consumption of caprine (45%) and pigs (*Sus domesticus* 17%) among domestic herbivores, and of cervids (52%), wild boar (Sus scrofa, 22%), and aurochs (20%) among wildlife. This faunal change indicates a transition from grasslands and forest-steppe environments - typical habitats for equids and cattle - during the mid-Neolithic, to shrublands and woodlands - typical habitats for cervids, aurochs, wild boar, goats, and sheep - during the flourishing Eneolithic. This environmental shift is further supported by an increase in woodland carnivores (e.g., wild cats – *Felis silvestris*, lynx – *Lynx lynx*, marten – *Martes martes*) (Demay et al., 2021).

Importantly, this shift in herbivore composition also signified an alteration in feeding guilds, which likely influenced plant composition and structure. Large-bodied grazers such as equids and cattle (61%) and mixed feeders (35%), present during the Neolithic, changed to a more diverse array of feeding guilds and body sizes in the flourishing Eneolithic that included grazers (36%), mixed feeders (36%), omnivores (17%), and browsers (11%). Browsing herbivores (aurochs and cervids) tend to disproportionately damage woody plants, while grazers (equids and cattle) target palatable grasses and forbs (Lundgren et al., 2020; Staver et al., 2021; Pearce et al., 2023). Mixed feeders (sheep and goats) adjust their diet, browsing on shrubs, particularly under dry conditions with limited grass biomass. Our models show a trend of negative response of *Quercus* and *Carpinus betulus* to herbivory at Mangalia Herghelie (Fig. 6), possibly indicating their response to increased abundance of browsers and mixed feeders (Figs. 2 and 5). Although pig consumption increased around 6500 cal yr BP, carbon and nitrogen isotope analysis suggests that, unlike the early Neolithic when pigs were herded, during the Gumelnița culture, they were kept closer to settlements (Balasse et al., 2013; 2017) and may have had a lower impact on woodlands. Poaceae abundance declined alongside an increase in generally less palatable forbs, such as *Artemisia, Aster,* and other Asteraceae, during periods of intensified herbivore activity (Figs. 2 and 7). However, palatability varies among species within these forbs (Damiran, 2005), which we cannot differentiate taxonomically based on pollen.

The period between 5900 and 3800 cal yr BP saw restrained herbivory activity in both palaeoecological and archaeofaunal evidence, coinciding with the most developed woodland cover (Fig. 5). During this time, human settlers increased their consumption of wild herbivores associated with woodland habitats and browsing guilds, particularly cervids (El Susi, 2001). However, by the late Bronze Age (around 3500 cal yr BP) and especially during the Iron Age (3200-2800 cal yr BP), coprophilous fungal taxa mainly represented by *Sordaria,* and grazing pollen indicators rose to levels comparable to those of the Neolithic, while woodland cover declined markedly (Figs. 4 and 7, SI Fig. 4). Domestic herbivores (over 90%) with diverse feeding guilds: large-bodied grazers (40%, cattle), mixed bodied feeders (25%, caprine), and omnivores (28%, pigs), and wildlife (10%), consisted of smaller-bodied browsers (62%, cervids) and omnivores (22%, wild boars) dominated the Bronze and Iron Age assemblages (Fig. 5; Manhart, 1998; Bălășescu, 1997; Bălășescu et al., 2015; Vasilescu-Ureche and Haimovici, 1976). Herbivore activity linked to human management practices appeared to have also impacted tree cover, particularly that of *Quercus*, and the abundance of Poaceae (Figs. 5 and 7).

To sum up, our results reveal distinct shifts in herbivore dynamics and their impacts on vegetation over time. During the Neolithic, grazing was predominantly carried out by large-bodied grazers and mixed feeders. This pattern shifted to a more diverse array of feeding types involving smaller domestic and wild herbivores in the flourishing Eneolithic. By the Bronze and Iron Ages, there was a notable increase in grazing by large-bodied domestic grazers as well as omnivores. These changes correlate with a rise in the diversity and abundance of cultural indicators, suggesting that herbivory, particularly by domestic animals positively impacted apophyte and adventive abundance and diversity. Large-bodied herbivores with selective diets (primarily grazers) appeared to have a more substantial effect on grass compared to mixed feeders with bulk diets. It is important to note that the low taxonomic resolution for grass and forb identification in pollen data limits our ability to fully reconstruct changes in species composition.

6. Conclusions

Our study of long-term interactions between moisture availability, fire, and herbivory in the Black Sea region's open ecosystems reveals that soil moisture is the primary driver of tree cover and dominant tree species abundance. This highlights the critical role of water as a key driver of woody cover in these ecosystems. We identified a critical state, where forest and grassland reached an equilibrium at 25–40% tree cover at Mangalia Herghelie and 25–55% at Lake Oltina. More resilient woodland states emerged above 40% tree cover at Mangalia Herghelie and 55% at Lake Oltina, while a grassland-dominated state was typical below 25% tree cover.

Disturbance by fire and herbivore varied between the two sites, likely also influenced by taphonomic factors such as basin size. A nonlinear relationship between fuel composition and moisture availability was observed. Fire severity and frequency increased during intermediate moisture periods, promoting tree expansion (6800–5500 and 3800–2800 cal yr BP), while reduced fire severity and variable frequencies occurred during periods of higher soil moisture favouring tree dominance (5500–3800 cal yr BP) or lower moisture favouring herbaceous dominance (7200–6800 and 3200–2000 cal yr BP). Herbivore dynamics shifted from large-bodied grazers and mixed feeders during the Neolithic to diverse feeding types with smaller domestic and wild herbivores in the flourishing Eneolithic, returning to large-bodied domestic grazers as well as omnivores in the Bronze and Iron Ages. Herbivory by domestic animals coincided with increased abundance and diversity of apophyte species.

Current low annual precipitation, prolonged droughts, and projected acceleration of aridification may hinder natural tree recovery and reforestation efforts, particularly for native species such as *Quercus* (*Quercus pedunculiflora*, *Q. pubescens*, *Q. cerris*), *Carpinus orientalis*, and *Fraxinus ornus*. Disturbances from fire and grazing could further impede tree recovery, especially for *Quercus* species. The complex interactions among these drivers underscore the need for further research to better understand past dynamics and future coexistence of diverse forest and grassland ecosystems in Europe.

CRediT authorship contribution statement

Angelica Feurdean: Conceptualization, Methodology, Formal analysis, Data curation, Visualization, Writing – original draft, Project administration, Funding acquisition. **Diana Hanganu:** Methodology, Formal analysis, Writing – review & editing. **Adrian Bălășescu:** Methodology, Formal analysis, Writing – review & editing. **Andrei Diaconu:** Methodology, Formal analysis, Writing – review & editing. **Mirjam Pfeiffer:** Methodology, Formal analysis, Writing – review & editing. **Dan Warren:** Methodology, Formal analysis, Writing – review & editing. **Mariusz Galka:** Methodology, Formal analysis, Writing – review & editing. **Roxana Grindean:** Methodology, Formal analysis, Writing – review & editing. **Simon M. Hutchinson:** Methodology, Formal analysis, Writing – review & editing. **Irene Marzolff:** Methodology, Formal analysis, Writing – review & editing. **Aurel Persoiu:** Methodology, Formal analysis, Writing – review & editing. **Eszter Ruprecht:** Conceptualization, Writing – review & editing, Conceptualization, Formal analysis, Writing – review & editing. **Ioan Tantau:** Formal analysis, Writing – review & editing.

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Declaration of competing interest

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

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The text and the figures are the work of the authors. However, the lead author used chatGPT to check the language and readability of the submission. After using this service, the lead author reviewed and edited the content as appropriate.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2024.109153.

Data availability

The dataset used in the paper is provided in the Supplementary Material.

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