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A multi-proxy approach to mid-5th millennium BCE human-plant relationships at Ploča Mičov Grad, Lake Ohrid☆

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ABSTRACT

On-site and near-site analyses from Ploča Mičov Grad, Lake Ohrid (North Macedonia) provide complementary perspectives on the mid-5th millennium BCE pile-built lakeshore settlement and local vegetation dynamics within a sheltered bay. Through a synthesis of archaeobotanical, dendroarchaeological and palaeoecological evidence, we consider the relationship between human activity (particularly foraging, timber selection and cultivation) and local vegetation changes during the settlement phase, against the background of the longer term palynological record. The archaeobotanical dataset from the lakeshore settlement's cultural sequence shows that the plant food system incorporated a broad spectrum of crops and collected fruits and nuts, many of which are reflected in the palynological record. The near-site palynological and on-site archaeobotanical records together suggest that human activities, including systematic foraging, encouraged the growth of rosaceous plant foods such as almond, possibly through protection and/or management of woodland edges. The complementary dendrochronological analyses of the wooden pile construction elements attest to woodland structure and timber selection practices, with a preference towards large-diameter timbers for construction. Analysis of the arable weed flora associated with archaeobotanical crop remains indicates that autumn-sowing was practiced and that cultivation was intensive and, as confirmed by the palynological data, small-scale. Arable plots and/or wheat processing activity likely occurred near to the settlement. The archaeobotanical, dendroarchaeological and palaeoecological analyses offer independent and complementary lines of evidence for the nature of plant-centred activities by the mid-5th millennium BCE community over a period of around a century.

1. Introduction

Different environmental archaeological datasets such as macrobotanical assemblages, pollen spectra and preserved timbers provide distinct but complementary evidence of past plant-human relationships. Each approach has its own potential and challenges in terms of scope and resolution (Pişkin et al., 2018). Due to excavation limitations or preservation biases, it is rare that we can deploy these multiple environmental approaches together to provide an integrated perspective on prehistoric biocultural environments and human activities. Wetland sites present the opportunity to integrate complementary evidence from numerous waterlogged environmental datasets, including (un)charred macrobotanical remains, pollen and wood, enabling a richer understanding of prehistoric human and plant activities (Behre and Jacomet, 1991; Jacomet, 2004; Valamoti, 2023). In the southern Balkans, a key region for early European farming, the vast majority of prehistoric agricultural sites are situated in drylands, with comparatively little data regarding plant-human relationships in wetland ecosystems (Allen and

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Gjipali, 2014; Antolín et al., 2020; Hafner et al., 2021; Sabanov et al., 2024; Valamoti, 2023).

This paper takes an integrated approach to explore human-plant relationships at the multi-phase, pile-built lakeside settlement of Ploča Mičov Grad, on the eastern shore of Lake Ohrid (North Macedonia), by combining evidence from archaeobotany, dendroarchaeology and palaeoecology with a particular focus on the mid-5th millennium BCE phase. Together, these datasets provide independent and complementary insights into woodland and agricultural activities, including foraging, timber selection and cereal cultivation. Palaeoecological sediment cores were extracted in close proximity (10–30 m) to the excavation area within the pile field at Ploča Mičov Grad. The palaeoecological record spans approximately eight millennia from c. 11000 to 3000 cal BCE, tracking vegetational changes before, during and after the settlement occupation phases, and within approximately 3–5 km of the site (Brechbühl et al., 2023). Agricultural activities emerged between 5500-4700 cal BCE according to palaeoecology and by around 5750-5700 cal BCE according to directly dated archaeobotanical remains (Brechbühl et al., 2023; Holguin et al., 2024). Subsequent occupation occurred during several periods in both the 5th and 2nd millennia BCE, documented through pottery, stone tools, bones, wood and archaeobotanical remains (Bolliger et al., 2023; Hafner et al., 2021; Holguin et al., 2024; Reich et al., 2021; Reich et al., 2025). The mid-5th millennium BCE phase is exceptionally well preserved, with numerous wooden construction components and a substantial archaeobotanical assemblage that accumulated between c. 4555-4373 to 4437-4241 cal BCE based on the radiocarbon dating of short-lived plant remains (Holguin et al., 2024). These modelled start and end date ranges align well with the earliest dendrochronologically identified phase (felling dates from 4469 to 4383 cal BCE), lasting a minimum of 87 years and likely up to c. 150 years (Bolliger et al., 2023). The on-site archaeobotanical and dendroarchaeological datasets provide evidence for human-plant activities, from plant food practices to timber selection, centred at the lakeside settlement, while the near-site palaeoecological record reflects broad local vegetation dynamics across millennia. Together, these datasets contribute evidence from across different temporal and spatial scales.

Neolithic food systems in the southern Balkans included the collection of a diverse range of 'wild' edible plants such as grapes, pears, acorns, terebinth nuts, elderberries and cornelian cherries (Antolín et al., 2020; Beneš et al., 2018; Filipović et al., 2018; Valamoti, 2015, 2023). All of these plants have been identified in the archaeobotanical record at Ploča Mičov Grad (Holguin et al., 2024). Food plants can be challenging to classify archaeologically, as palatability and edibility are social concepts, defined by cultural practices as well as by human physiology (Bishop et al., 2014; Ertuğ, 2009; Johns, 1994; Milner, 2009; Valamoti, 2015, 2023). However, many aspects of the archaeobotanical record at Ploča Mičov Grad suggest that fruits and nuts were deliberately collected and brought to the site for food or for fodder, craft, medicine or other reasons (see Holguin et al., 2024). Here, we do not attempt to consider all possible food plants, but rather focus on key taxa that are abundant both in the palaeoecological and archaeobotanical record. We combine the archaeobotanical and palaeoecological evidence with the dendroarchaeological data to examine interwoven human-woodland interactions. Relationships between prehistoric people and plants evolved through the collection of these wild plant foods, alongside other woodland activities such as felling, as part of a complex, dynamic network of relationships (van der Veen, 2014). As plants adapted and responded to human activities, their changing distributions and abundances would have created new opportunities and encounters for prehistoric communities, in turn influencing human behaviours, perhaps encouraging increased investment and potentially care, through protection and management practices.

At Ploča Mičov Grad, foraging for local plants complemented the cultivation of a wide spectrum of cereals (dominated by einkorn and emmer) and pulses (including bitter vetch, lentil and pea) (Holguin et al., 2024). While Neolithic arable habitats in southeast Europe have been broadly characterised as small-scale, long-lived and labour-intensive 'garden-like' plots (Bogaard and Halstead, 2015; Halstead, 2018; Vaiglova et al., 2014, 2020, 2023), analyses have primarily concentrated on dryland environments in this region. Research centred upon lakeshore Neolithic settlements in the Alpine foreland suggests that dry and wet landscapes afforded similar intensive management practices in central Europe (Jacomet et al., 2016; Styring et al., 2016). However, the agroecology of wetland, upland zones in south-east Europe is still largely unexplored. Brechbühl et al. (2023) argue that the abundance of cereal pollen and associated disturbance-loving taxa in near-site palaeoecological cores, compared with the absence of these signals in cores further out in the lake, indicates that arable agriculture at the site of Ploča Mičov Grad was likely small-scale and intensive. The use of fire to manage land suggested by the high levels of microscopic charcoal could also relate to agricultural land use (Brechbühl et al., 2023). Here, we add evidence from the archaeobotanical dataset from Ploča Mičov Grad to interrogate these interpretations from the palaeoecological analysis. To do this, we first use crop processing analysis to test the hypothesis that seeds of herbaceous plants associated with crop material are arable weeds, before analysing the weed assemblage to provide insights into crop sowing times and management intensity. By understanding the nature and intensity of cultivation, we can gain a deeper understanding of various human-plant interactions from routine weeding activities (Bogaard et al., 2018a, b; Stroud et al., 2023) to the transformation of space (i.e. plot creation and permanence) and the formation of new biocultural environments such as a disturbed woodland-edge habitats, rich with edible fruits and nuts.

2. Materials and methods

2.1. The site of Ploča Mičov Grad

The submerged prehistoric site of Ploča Mičov Grad (Плоча Мичов Град, 40.994°N, 20.798°E) is located upon the eastern shore of Lake Ohrid (North Macedonia), at the foot of the Galičica mountain range within a sheltered bay (Fig. 1 b). Situated at a mean water table altitude of 693 m a.s.l., Lake Ohrid is one of the largest (358 km^2) and deepest lakes (290 m) in southern Europe (Matzinger et al., 2006; Panagiotopoulos et al., 2014). Temperatures, particularly during the summer, were likely slightly higher during the 5th millennium BCE than in the present-day, and the winters likely cooler (Tóth et al., 2015; Thienemann et al., 2017; Samartin et al., 2017). Precipitation was likely reduced during the summer and increased during the winter as a consequence of higher summer insolation and lower winter insolation (Tzedakis, 2007). Köppen-Geiger climate classification characterises the area today as warm-summer mediterranean climate, 'CSb' (Fig. 1 a, Kottek et al., 2006).

The site was first studied in the 1990's and 2000's (Kuzman, 2013). A large-scale multidisciplinary field campaign took place in 2018 and 2019. During this campaign, 799 archaeological wood samples were collected from an excavation trench of nearly 100 m^2 of the pile field for dendrochronological analyses and 6 sediment cores were extracted on-site and off-site for archaeobotanical and palaeoecological analyses (Fig. 1; Bolliger et al., 2023; Brechbühl et al., 2023; Hafner et al., 2021; Holguin et al., 2024; Reich et al., 2021, 2025).

2.2. Previous dendroarchaeological analyses

The dendrochronological analysis resulted in the construction of multiple tree-ring chronologies ("mean curves") from different wood taxa: oak, pine, juniper, hornbeam, hop-hornbeam and ash (Bolliger et al., 2023). The tree-ring chronologies were anchored on a calendar time-scale through modelling (wiggle-matching) series of radiocarbon dates made on tree-rings. Three major construction phases were identified based on the dendrochronological results – around 4400 cal BCE,

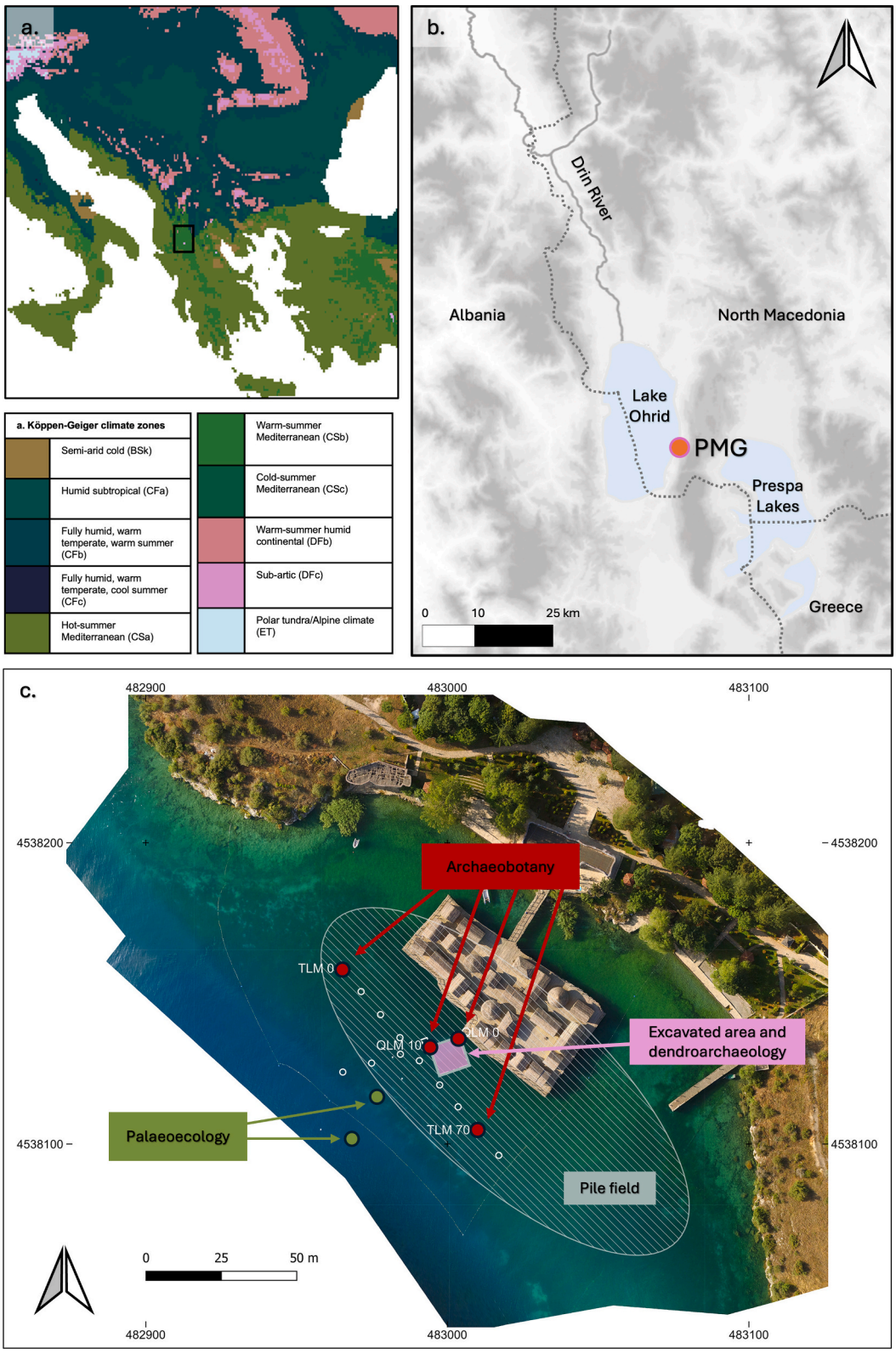


Fig. 1. The location of the site of Ploča Mičov Grad (PMG). At the interface of different climate zones (a), Ploča Mičov Grad is situated on the eastern side of Lake Ohrid (North Macedonia) in a sheltered bay at the foot of the Galičica mountain range (b). The black rectangle in a. matches the area shown in b. In c, the approximate extent of the site (hatched oval) lies under a pile-dwelling village reconstruction. The location of the excavated area and the archaeobotanical and palaeoecological sediment cores is indicated (Orthophoto: G. Milevski and J. Reich, CRS: EPSG 32634, Hafner et al., 2021). For a, Köppen-Geiger climate classification after Kottek et al. (2006) downscaling after Rubel et al. (2017) © Climate Change & Infectious Diseases Group, Institute for Veterinary Public Health, Vetmeduni Vienna, Austria. For b, elevation data from USGS Global Multi-resolution Terrain Elevation Data.

1800 cal BCE and 1200 cal BCE – with several sub-phases within each. These likely represent the principal periods of occupation, but the extent of the unexcavated parts of the pile field (> 8000 m^2) suggest that additional phases may exist beyond the sampled area (c. 100 m^2). The earliest dendrochronologically documented settlement in the excavated area is represented by 150 dated piles, with felling dates ranging from 4469 to 4383 cal BCE, with a precision of the radiocarbon-modelled end-date range of c. ± 15 cal years (Bolliger et al., 2023). The span of 87 years between the earliest and latest felling date marks the minimum duration of this phase. A later phase around 4170 BCE is indicated by few dated piles (n=4). Importantly, the 5th millennium BC archaeological layers largely correspond to the timeframes established through dendrochronological analysis (Reich et al., 2025; Reich, in prep), demonstrating a clear relationship between layer composition and construction activity. This period is variously described as Late Neolithic, Final Neolithic, Eneolithic and Chalcolithic in regional chronologies of the Balkans.

2.3. Previous palaeoecological analyses

Two cores were extracted from the lake bed near to the site for palaeoecological analysis; the one closest to the pile field is OHR19-5/6 and the one closest to the lake centre OHR19-3/4. Samples were analysed for pollen and microscopic charcoal (Fig. 1 c). Together the sediment cores cover approximately 8000 years of vegetational changes from about 11000 to 3000 cal BCE, based on an age-depth model of 22 radiocarbon dates from plant macroremains (two of the samples were rejected as outliers and considered contamination). The 6th and 5th millennium BCE deposits were only preserved in the core closer to the settlement (OHR19-5/6). The pollen core was divided into six statistically significant pollen zones with cultural indicators beginning in OHR-4b (5550–5350 cal BCE) and increasing in OHR-5 (5350–4150 cal BCE, Fig. 2). Methodological details and results were published in Brechbühl et al. (2023).

2.4. Previous archaeobotanical analyses

Four cores, extracted through an organic cultural layer (up to c. 1.5 m thick) associated with the site, were the focus of the archaeobotanical analysis (Fig. 1 c). Archaeobotanical sampling, wash-over, quantification and identification methods are detailed in Holguin et al. (2024). Samples were taken based on stratigraphic layers (when present) or as spits of approximately 6 cm. In total, 98 samples were taken across the four cores. The mid 5th millennium BCE phase (n=81 samples) formed between 4555–4373 and 4437–4241 cal BCE (94.5%, start and end date ranges) according to the radiocarbon dates on plant macroremains (with one basal sample giving a slightly earlier date of 4705–4541 cal BCE). There was also a minor 6th millennium BCE and minor 2nd millennium BCE phase. The mid-5th millennium BCE archaeobotanical assemblage was dominated by glume wheat chaff and the remains of edible fruits and nuts, suggesting that it was midden-like, composed of refuse from domestic activities (Holguin et al., 2024).

2.5. Synthesis of the dendroarchaeological, archaeobotanical and palaeoecological analyses

This paper focuses on the mid-5th millennium BCE settlement phase identified in the archaeobotanical and dendroarchaeological datasets. The mid-5th millennium BCE settlement phase aligns with the end of the OHR-5 statistical zone in the palaeoecological record. Key taxa that were found in at least two of the analyses were identified and broad trends of vegetation dynamics in the palaeoecological core were established by determining whether pollen percentages were generally increasing, constant or decreasing prior to occupation, during occupation and

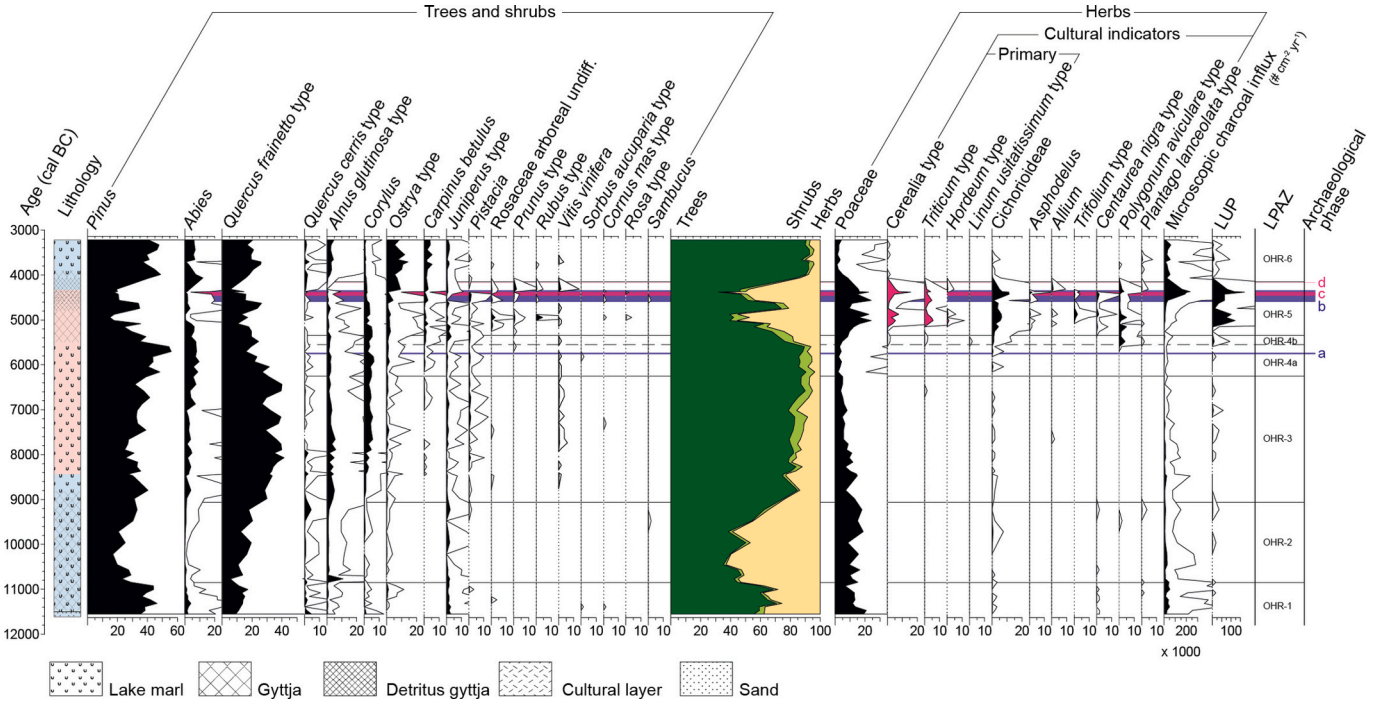


Fig. 2. Key palaeoecological results. For the lithology, blue shading highlights data gained from core OHR19-5/6 and red shading core OHR19-3/4. Pollen percentages that are shown as empty curves show a 10x exaggeration. The pollen percentage curves of primary cultural indicators (e.g. Cerealia types) are filled bright pink. LUP = Land Use Probability. The LPAZ (Local Pollen Assemblage Zones) show the 6 statistically significant zones (OHR-4 was further divided into two non-significant subzones based on cultural indicators and arboreal decline). The purple horizontal highlights refer to archaeological phases identified in the archaeobotanical record, while the pink horizontal highlights refer to phases identified dendrochronologically. Archaeological phases A: early 6th millennium BCE archaeobotanical agricultural evidence; B: the main archaeobotanical mid-5th millennium BCE settlement phase; C: the main dendroarchaeological mid-5th millennium BCE settlement phase; and D: a few dendrochronologically dated piles were assigned to 4170 BCE.

following occupation (Fig. 2). Nomenclature follows *Flora Europaea* for crops (Tutin et al., 1980) and *World Flora Online* (WFO, 2024) for all other taxa.

Earlier activity was detected in both the palaeoecological (c. 5550–4850 cal BCE) and the archaeobotanical datasets (c. 5790–5722 to 5755–5714 cal BCE), likely marking the start of local agricultural clearance, but the numbers of plant macroremains were very low (Holguin et al., 2024). A few samples (n=4) from the archaeobotanical dataset also date to the 2nd millennium BCE (1878–1688 cal BCE), which aligns with the second dendrochronological identified settlement phase at around 1800 cal BCE. When relevant, these earlier or later phases are briefly considered for comparative purposes.

2.6. Analyses of arable weeds in the archaeobotanical assemblage

In this study, several analyses were applied to the possible arable weeds. Herbaceous plants which grow naturally in wetland or aquatic environments such as *Phragmites australis* (the common reed) were excluded from all analyses in this paper, as they likely accumulated within the deposit through natural pathways. As the organic layer was relatively homogenous with few clear stratigraphic layers, the merging of data from adjacent samples was in some cases considered appropriate. The sedimentary profiles were examined to determine the confidence of identified stratigraphic layers and the similarity of sample composition was assessed through correspondence analysis and a depth-constrained cluster analysis (Supplementary Materials). Based on stratigraphic information and compositional similarity, after merging, 60 samples/sample groups remained. Further details of sample merging are provided in the Supplementary Materials.

2.7. Crop processing analysis

Some herbaceous taxa were possibly arable weeds harvested with the crops. To assess the relationship between the potential weed flora and crop processing stages, a discriminant analysis was conducted following Jones (1984, 1987). Based on comparison with an ethnographic model from the processing of cereals and pulses in Amorgos, Greece (Jones, 1984), three physical characteristics of weed seeds (size, aerodynamics and 'headedness' i.e. the tendency to remain enclosed in a capsule following threshing) are used to discriminate between weeds associated with four different stages in crop processing — winnowing by-products, coarse-sieving by-products, and fine-sieving by-products and fine-sieve products (Jones, 1984, 1987).

Only seeds can be included in this analysis; other herbaceous plant parts, such as capsules, were removed from the dataset. Only samples/merged sample groups with over thirty potential weed seeds were included in the analysis. To assess the impact of preservation on the assemblage, we compare the results of three different analyses: (1) the full dataset, (2) only charred macroremains and (3) all uncharred and charred herbaceous taxa if they sometimes occur in charred form. The third analysis is the main form considered here; details of the first two can be found in the Supplementary Materials. Forty-four samples (/merged sample groups) and 35 taxa were included in this analysis. The R-package CropPro (Stroud et al., 2025) was used to perform the analyses and to visualise the data in R (version 4.3.2 2023-10-31, R Core Team, 2021).

2.8. Weed species habitat association, life history and seasonality

The habitat association, life history and seasonality of the possible weed taxa were identified using Ellenberg et al. (1992) and Rothmaler (1995). Both the whole dataset and only the charred dataset are considered. As this analysis considers the presence of different taxa across the mid-5th millennium BCE assemblage rather than individual counts, there is no need to consider the paired dataset (all uncharred and charred taxa if they occur sometimes in charred form) as this dataset, by definition, is identical to the only charred dataset in terms of presence/absence. More information can be found in the Supplementary Materials.

The habitat association and life history of potential weed taxa can help distinguish fixed-plot cultivation (with more annuals and taxa associated with disturbed places) from shifting cultivation (with more perennials and more woodland taxa) (Bogaard, 2002). In addition, crop sowing times can be inferred from the seasonality (flowering times and durations) of the weed taxa (Bogaard et al., 2001).

2.9. Functional weed ecology

To compare the nature of arable agriculture at Ploča Mičov Grad to modern traditional agrosystems, functional weed ecology was used. The R-package WeedEco was used for the data analysis and visualisation (Stroud et al., 2023). The package's Model 2 was used which included modern arable weed survey data from Haute Provence (France), Asturias (Spain), Evvia (Greece) and oasis and rainfed terrace fields in Morocco (Bogaard et al., 2016, 2018a, Jones et al., 1999, 2000). The high- and low-input regimes are discriminated on the basis of four functional traits (mean specific leaf area, ratio of leaf area to thickness, canopy height and canopy diameter). The high-input regimes (Moroccan oases, Evvian gardens and Asturian gardens) included weeding and manuring (Bogaard et al., 2016, 2018a; Stroud et al., 2023). The low-input regimes were the Moroccan rain-fed terraces, Evvian fields and Haute Provence fields. The functional trait data for the relevant species were taken from a trait database linked to the 'WeedEco' package (Stroud et al., 2023; Hodgson et al., 2023). Again, only samples/merged sample groups with over 30 seeds of herbaceous taxa (identified to species with known functional traits) were included in the analysis, meaning that the final analysis included 34 samples and 22 species. The archaeobotanical samples (or merged sample groups) were entered as unknown cases into the classification phase of the analysis. The function classifies samples as 'low-input' based on the presence of weeds with lower soil fertility attributes or conversely as 'high-input' dominated by weeds with attributes associated with higher soil fertility. As for the crop processing analysis, we assessed the impact of preservation by comparing results from 1) the full dataset, (2) only charred macroremains and (3) all uncharred and charred herbaceous taxa if they sometimes occur in charred form. The third analysis is considered the final analysis. Details of the first and second analyses can be found in the Supplementary Materials.

3. Results

3.1. Comparison Between Palaeoecological, Archaeobotanical And Dendroarchaeological Results

During the mid-5th millennium BCE occupation phase, there was a significant decrease in arboreal pollen types, with pine (*Pinus*), fir (*Abies*), deciduous oak (*Quercus frainetto* and *Q. cerris* types), alder (*Alnus glutinosa* type) and hazel (*Corylus*) pollen percentages markedly declining, suggesting extra-local deforestation. All of these taxa were also identified in the archaeobotanical record, with finds of pine needles (in addition to rare pinecone fragments and one pine seed), fir needles, oak/acorn nutshell fragments, alder seeds (as well as a single alder cone) and hazelnut shell fragments frequent (Table 1; Fig. 2). Oak and pine were common taxa selected for the wooden construction piles, in addition to juniper (*Juniperus* sp.) and hop-hornbeam/hornbeam (*Ostrya/Carpinus* sp.; Fig. 3a; Bolliger et al., 2023). Juniper and hop-hornbeam were also present in the archaeobotanical record. However, the pollen percentages of these disturbance-adapted trees followed different trajectories to the other arboreal taxa, fluctuating rather than declining during the settlement occupation period. In particular, *Ostrya* type pollen percentages increased following the settlement occupation, as the forests re-established with disturbance-adapted taxa gaining

Table 1
Comparison between the palynological, archaeobotanical and dendroarchaeological results for arboreal, fruit shrub and cultivated taxa that occur in the mid-5th millennium BCE. Similar taxonomic categories between the three datasets are aligned. For each, trends in pollen percentages increasing +, decreasing −, or fluctuating +/- before, during and after the mid-5th millennium BCE occupation (the second opening phase in the palaeoecological record) are indicated. X signals taxa that were not present or present only in very low numbers. Brackets show less pronounced/uncertain changes e.g. (+/-). For the trends before occupation, the pollen numbers before and after the earlier (early 6th millennium BCE) settlement phase are taken into consideration.

Palynological taxa	Archaeobotanical taxa	Wooden construction elements (piles)	Pollen-inferred vegetation dynamics		
			Before	During	After
Pinus sylvestris type	*Pinus* sp.	*Pinus* sp.	+	−	+
Abies	*Abies alba* Mill.		+	−	+
Quercus frainetto type *Quercus cerris* type	*Quercus* sp.	*Quercus* sp. section *Quercus* (e.g *Q. pubescens, Q. frainetto, Q. petraea* etc.)	+	−	+
Alnus glutinosa type	*Alnus glutinosa* (L.) Gaertn.	*Alnus* sp. (rare)	+	−	+
Corylus	*Corylus avellana* L.		+	−	−
Ostrya type (inc. *Carpinus orientalis*)	*Ostrya carpinifolia* Scop.	*Ostrya carpinifolia /Carpinus betulus /orientalis*	+/-	+/-	+
Juniperus type	*Juniperus* cf. *oxycedrus* L.	*Juniperus excelsa/ foetedissima/oxycedrus*	(+/-)	−	+
Pistacia	*Pistacia terebinthus* L.		+/-	+	−
Rosaceae arboreal undiff.	*Rosa* spp. *Malus* sp. *Pyrus/Sorbus* sp. *Prunus* cf. *amygdalus* Batsch *Rubus fruticosus* agg. *Rubus idaeus* L.		X	+	−
Prunus	*Prunus* cf. *amygdalus* Batsch *Prunus spinosa* L.	Possible	X	+	−
Rubus	*Rubus fruticosus* agg. *Rubus idaeus* L.		X	+	−
Vitis vinifera	*Vitis vinifera* subsp. *sylvestris*		(+/-)	+	−
Sorbus aucuparia type	*Pyrus/Sorbus* sp.		X	X	X
Cornus mas type	*Cornus mas* L.				
Rosa type	*Rosa* sp.				
Sambucus	*Sambucus* spp.				
Cerealia type	As for *Hordeum* and *Triticum*		X	+	−
Triticum type	*Triticum monococcum* L. *Triticum dicoccum* Schrank ex Schübl. *Triticum timopheevii* sensu lato (Zhuk.) Zhuk. *Triticum durum* Desf. /*aestivum* L. *Triticum aestivum* L.		X	+	−
Hordeum type	*Hordeum vulgare* L. *Hordeum distichon* L.		X	(+)	−
Linum usitatissimum type	*Linum usitatissimum* L.		X	X	X

importance.

Acorn, hazelnut and juniper are three of many edible tree/shrub fruits and nuts abundant in the archaeobotanical record (Fig. 4) which match types found in the palaeoecological record. *Vitis* pollen was present variably preceding occupation and markedly increased towards the end of the occupation phase, before returning to a lower level. *Pistacia* pollen percentages increased slightly during the settlement phase, although their percentages fluctuated consistently over the prior millennia. Both wild grape pips (*Vitis vinifera* subsp. *sylvestris*) and terebinth nutshells (*Pistacia terebinthus*) were common features of the archaeobotanical samples. The percentages of Rosaceae arboreal undiff., *Prunus* type and *Rubus* type pollen were very low prior to OHR-5 (c. 5350 cal BCE), increased substantially during the mid-5th millennium BCE occupation and declined thereafter. These pollen types correlate with many edible fruits found in abundance within the archaeobotanical record including rosehip (*Rosa* spp.), apple and pear/rowan (*Malus* and *Pyrus/Sorbus*), almond (*Prunus* cf. *amygdalus*), blackberry (*Rubus fruticosus*) and raspberry (*Rubus idaeus*). The category of Rosaceae arboreal undiff. includes all pollen that resembles tree/shrub Rosaceae but could not be identified further. Pollen grains of *Rubus, Prunus, Rosa, Pyrus, Sorbus* and *Malus* are all identifiable to genus. However, it is possible that they are included in 'Rosaceae arboreal undiff.' if diagnostic features were unclear. While *Pyrus/Sorbus* was a common component of the mid-5th millennium BCE archaeobotanical record, only two pollen grains of *Sorbus* were identified in contexts earlier than the mid-5th millennium BCE phase in zones OHR-1 and OHR-4a.

Prior to OHR-5, cereals were almost absent in the pollen record, with the exception of a small percentage of *Triticum* type (wheat) pollen in OHR-3 (c. 6500 cal BCE) and of Cerealia and *Triticum* type in OHR-4b. Cerealia type, *Triticum* type and *Hordeum* type pollen percentages increased at the beginning of OHR-5. Cerealia type and *Triticum* type pollen percentages peaked again during the main mid-5th millennium BCE occupation phase (the second half of OHR-5). However, *Hordeum* type pollen percentages were low during this phase. Abundant chaff remains of the glume wheats, einkorn (*Triticum monococcum*), emmer (*Triticum dicoccum*) and Timopheev's wheat (*Triticum timopheevii*), were recovered in the archaeobotanical assemblage alongside some barley (*Hordeum distichon* and *Hordeum vulgare*, both six- and two- row barley, and each as both hulled and naked varieties; for chaff identification criteria, see (Charles et al., 2026) and some bread wheat (*Triticum aestivum*). Several pulse crops (bitter vetch, *Vicia ervilia*, lentil, *Lens culinaris* and pea, *Pisum sativum*). While flax (*Linum usitatissimum*) was common in the mid-5th millennium BCE archaeobotanical assemblage, only one *Linum usitatissimum* type pollen grain was identified in the OHR-4b zone (c. 5500 cal BCE).

4. Results of the arable weed analyses

4.1. Crop processing analysis results

Crop processing analysis (Jones, 1984, 1987) was used to assess the likelihood that the herbaceous macroremains were arable weeds and as

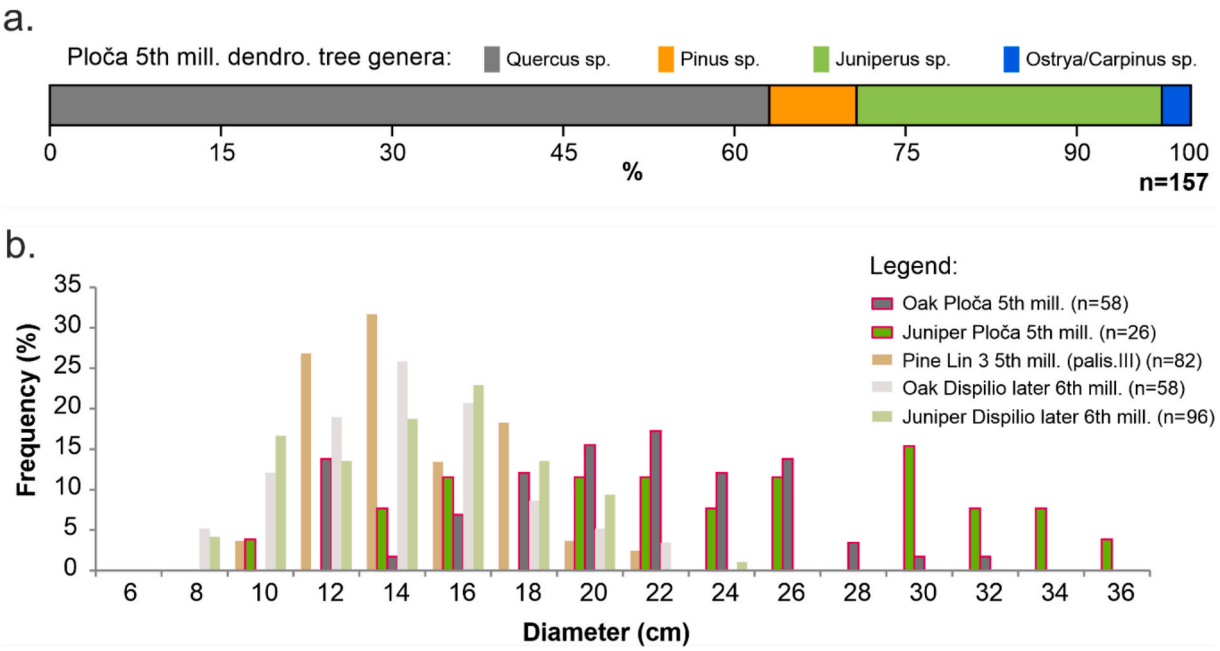


Fig. 3. Ploča Mičov Grad 5th millennium BCE tree genera and between-site comparison of vertical piles diameters. **a.** 5th millennium BCE tree taxa composition of the dendrochronologically and ^{14}C-dated wooden posts from Ploča Mičov Grad; **b.** Ploča Mičov Grad compared with material from two other sites: (1) palisade III from the contemporaneous site Lin 3 across the lake (Albania) (Yermokhin et al., 2025); (2) oak and juniper piles from later 6th millennium BCE Dispilio (Greece) (c. 5311–5140 BCE) (Maczkowski et al., 2024a,b). Ploča Mičov Grad oaks lack sapwood and waney edge, Lin 3 piles are contemporaneous but composed of different species with preserved waney edge, Dispilio piles are chronologically older by c. 600/700 years and have low preservation of sapwood among oaks. Dispilio samples are from the whole excavated area, whereas Lin 3 samples are limited to one palisade in order to have comparable sample sizes between the sites.

such compatible with the associated crop remains (particularly the glume wheat chaff) in terms of processing stage (Fig. 5 and 6). The results of all three analyses – (1) the full weed dataset and (2) only charred macroremains and (3) uncharred and charred macroremains if the taxa were at least sometimes present in charred form – were broadly similar with the samples classified primarily as fine-sieving or winnowing by-products (Supplementary Materials).

Dataset 3 (the final analysis) included uncharred taxa if also found in charred form (35 different taxa and 44 samples). When adding the Ploča Mičov Grad archaeobotanical samples as unknown cases following the extraction of the discriminant function (using the 'LDAcrop.pro' function in the CropPro package, Stroud et al., 2025), they were classified as the by-products of winnowing (n=23, 52.27%) or fine sieving (n=21, 47.73%). Most samples were closely grouped with no clear patterns based on depth or core (Fig. 5). Given this outcome was compatible with the crop composition (i.e. the amount of glume wheat chaff; Holguin et al., 2024), the assemblage was considered suitable for further weed ecological analyses.

4.2. *Weed species habitat association, life history and seasonality results*

The herbaceous assemblage (Fig. 6) contained 53 different species and 4 small species groups (small ecologically similar groups of 2 or 3 species, henceforth taxa). Twenty-five of these taxa were found charred or both charred and uncharred across the assemblage.

Agricultural or ruderal land was a key habitat for many taxa (c. 80% of all taxa; Fig. 7). A small percentage of taxa were associated with grasslands, woodlands and freshwater/marshlands. The majority of taxa were annuals (c. 70% of all taxa). Annuals are often found in high percentages in long-lived plots as opposed to recently cleared plots as in a shifting cultivation regime, which are instead dominated by perennials and include woodland perennials (Bogaard, 2002).

A range of flowering time/duration categories relevant to the inference germination season and crop sowing time are present, from short/early to long- and late-flowering. The short/early-flowering taxa are typically autumn-germinating and tend to be removed by tillage in spring-sown fields. The occurrence of multiple short/short flowering taxa is therefore a strong indicator that at least some autumn sowing was practised. Late- and long-flowering taxa flourish in spring-sown fields but can also occur in autumn-sown fields, especially with disturbance during the growing season due to activities such as hand-weeding (Bogaard et al., 2001).

4.3. *Functional weed ecology results*

As with the crop processing analysis, to explore the impact of potential taphonomic biases affecting the weed assemblage, two preliminary analyses were performed with (1) the full weed dataset and (2) only charred material. The first analysis aligned the majority of samples with high-input regimes, while the second had insufficient data (too few samples with small numbers of weed seeds; Supplementary Materials, Fig. S7 and S8). Details of the first two preliminary analyses can be found in the Supplementary Materials. The third/final analysis included all weed seeds except those taxa only preserved in an uncharred state across the assemblage (see Supplementary Materials for further details of taxa exclusion and inclusion).

The final analysis included 22 weed seed types (Supplementary Materials, Table S4) and 34 sample/merged sample groups (with >30 weed seeds). The discriminant scores ranged from -1.670 to 3.511 (with an average 0.796 Fig. 8). In total, 30 of the samples were classified as 'high-input' and 4 as 'low input'. There was slight grouping by core or by depth (e.g. samples from core QLM0 had slightly lower values, while samples from QLM10 had slightly higher values), but samples from all cores overlapped. The analysis output tables can be found in the Supplementary Materials (Table S5).

5. Discussion

The synthesis of on-site archaeobotanical, on-site dendroarchaeological and near-site palaeoecological records from Ploča Mičov Grad



Fig. 4. Arboreal, fruit and nut macroremains from Ploča Mičov Grad. All macroremains are uncharred seeds unless specified. A. *Rubus fruticosus* agg.; b. *Vitis vinifera* subsp. *sylvestris*; c. *Quercus* sp. nutshell base; d. *Pyrus/Sorbus* sp.; e. *Malus* sp.; f. *Juniperus* cf. *oxycedrus*; g. *Prunus* cf. *amygdalus* (almost complete) nutshell; h. *Alnus glutinosa* cone; i. *Pistacia terebinthus* whole nutshell and j. *Corylus avellana* nutshell fragment. All scales are 1 mm.

presents a rare opportunity to investigate mid-5th millennium BCE activities in an upland, wetland lake basin in south-east Europe using a multi-proxy approach. These complementary datasets enable the reconstruction of human-plant interactions, including foraging, timber selection and cultivation, associated with the earliest dendrochronologically dated settlement phase of the lake-dwelling site of Ploča Mičov Grad. Using evidence taken at different resolutions, and reflecting complementary spatial and temporal scales, this multi-stranded approach allows for a robust understanding of biocultural activities centred at the lakeshore settlement and the site's relationship with local vegetation dynamics.

5.1. Forests and woodlands

The decrease in arboreal pollen during the mid-5th millennium BCE likely reflects land-use and clearance activities by the lakeshore community of Ploča Mičov Grad. Oak was the favoured wood for the pile structures (Fig. 3) and so its decline in the pollen record is (at least in part) associated with clearance activities for construction (Hafner et al., 2021; Bolliger et al., 2023) as well as for agricultural activities (Brechbühl et al., 2023). The subsequent rapid recovery of the forest following the settlement phase, with a high contribution of disturbance-adapted species, underlies the resilience of the forest to prehistoric activity (Brechbühl et al., 2023).

While non-fruit/nut arboreal remains were rare in the archaeobotanical assemblage, many tree/shrub fruits and nuts were present which, based on their high numbers and occasional charring across the archaeobotanical assemblage, were likely collected for food, craft, medicine and/or other uses (Holguin et al. 2024). Many correspond to arboreal types seen in the pollen record, such as acorn, hazelnut, terebinth, grape and juniper. While hazel and oak decline in the pollen record during the settlement phase, juniper, grape and terebinth show

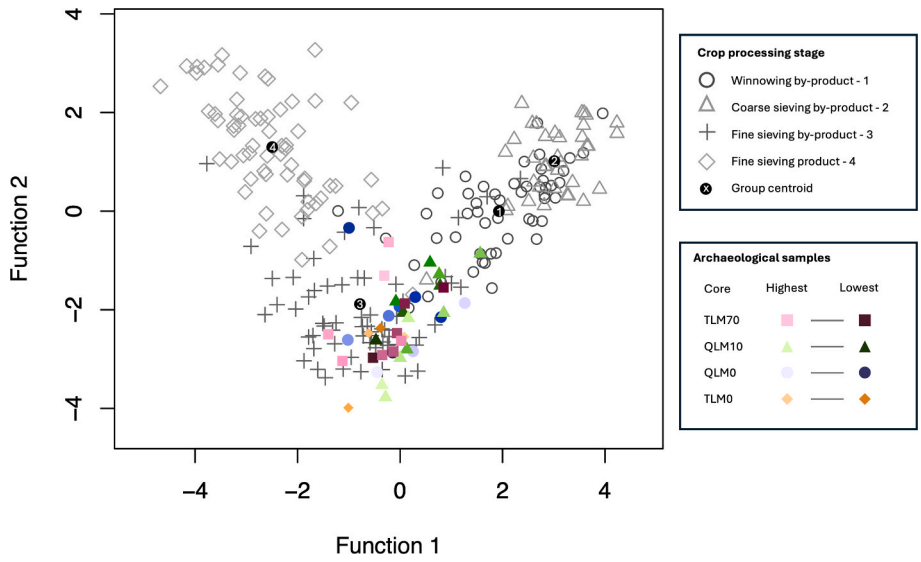


Fig. 5. Crop processing analysis of the possible weed seeds (including uncharred taxa if also found in charred form). The archaeological samples are coded by core with the shade reflecting the depth of the samples (the darkest colours found at the base of the sedimentary sequence). The modern data points are shown in greys with numbered group centroids in black. The plot of function 2 and 3 can be found in the Supplementary Materials (Fig. S6).

variable (and often low) pollen percentages from c. 8000 cal BCE (Brechbühl et al., 2023), suggesting that their populations were influenced by climatic changes or human activity at different points over time. All of these species have been identified (albeit many rarely) from Neolithic sites in North Macedonia, Albania and northern Greece (e.g. Allen and Gjipali, 2014; Antolín et al., 2020; Beneš et al., 2018; Kotzamani and Livarda, 2018; Marinova and Ntinou, 2018; Valamoti, 2023; Valamoti, 2004). The rarity of these finds in published archaeobotanical assemblages is likely, at least in part, due to contextual and preservation biases at dryland sites discriminating against fruit and nut macroremains, since charred remains overwhelmingly reflect food plants such as crops stored and consumed year-round (Antolín and Jacomet, 2015; Bogaard and Halstead, 2015; Valamoti, 2015, 2023). Exceptionally well-preserved assemblages from dryland sites such as Dikili Tash (northern Greece) suggest that fruit and nut collection and storage was likely more widespread and systematic than routinely assumed (Valamoti, 2015; 2023). The taphonomic complexity is underlined by the archaeobotanical dataset from Ploča Mičov Grad as the majority of fruit and nut remains were recovered uncharred and so would be absent on dryland sites (Holguin et al., 2024).

There is a clear relationship between the level of human activity and local abundance (as inferred from the pollen record) of the Rose family (Rosaceae) which thrived during human occupation. Prior to and following occupation, Rosaceae arboreal and *Prunus* pollen percentages were low or absent. However, during the main settlement phase at Ploča Mičov Grad, there was a marked increase in rosaceous pollen percentages (Brechbühl et al., 2023). Very high numbers of Rosaceae taxa, particularly almond, blackberry, raspberry, wild apple, pear/rowan and rosehip, were present in the archaeobotanical assemblage, likely as systematically collected resources.

Almond is the main *Prunus* identified in the archaeobotanical record. Based on morphological characteristics, this is likely *Prunus amygdalus* (a species whose natural distribution is largely confined to south-west and central Asia and is today widely cultivated (Browicz and Zohary, 1996)), although *Prunus webbii*, a similar species native to the Mediterranean could not be completely excluded (Supplementary Materials). In southern Greece, almond wood charcoal (e.g. Asouti et al., 2018) and nutshell fragments (e.g. Hansen, 1991; Sarpaki, 2013) have been identified from prehistoric sites. However, there is only rare evidence of almond in Neolithic archaeobotanical assemblages from northern Greece, Albania and North Macedonia (Allen and Gjipali, 2014; Antolín et al., 2020; Beneš et al., 2018; Marinova and Ntinou, 2018; Valamoti, 2023). At Ploča Mičov Grad very low percentages of *Prunus* pollen first occur in the palynological record from about 5600 cal BCE, not long after the earliest evidence for human activity (c. 5750 cal BCE according to archaeobotanical evidence; Holguin et al., 2024). The first *Prunus* pollen percentages are also linked to the first occurrence of *Triticum* type and *Linum usitatissimum* type pollen (Brechbühl et al., 2023). *Prunus* and *Triticum* type pollen both increase towards the end of the 6th millennium BCE and peak in the mid-5th millennium BCE (Fig. 2). A similar pattern is observed in the archaeobotanical record at the nearby sites of Lin 3 (Albania, 10 km away across Lake Ohrid) and Dispilio (Greece, approximately 90 km southeast of Lake Ohrid on Lake Kastoria). At both sites almond was absent in the early 6th millennium BCE archaeobotanical assemblages, but appears in limited quantities by c. 5400-5200 cal BCE at Dispilio and in the early/mid 5th millennium BCE at Lin 3 (Ballantyne, Ergun and Gkatzogia *per comms*). While it remains possible that almond was already present in the area (invisible in the palynological and archaeobotanical records), the broadly coeval appearance of the earliest evidence for human activity (both in the archaeobotanical and palaeoecological records) and the *Prunus* pollen suggests its introduction to the Lake Ohrid locality in the 6th millennium BCE. The common peaks of *Prunus*, Rosaceae, *Triticum* type and *Hordeum* type pollen in the mid-5th millennium BCE indicates settlement activity (likely through collection of nuts and broad disturbance) encouraged the growth of *Prunus* and Rosaceae populations.

This observation leads us to consider whether almonds (and all other edible fruits and nuts for that matter) were to some extent tended, managed or cultivated. At Knossos (Crete), cultivation of (wild) almond has been suggested due to the number of nutshells recovered from the Early Neolithic II levels (Sarpaki, 2013), but evidence is currently inconclusive (Valamoti, 2023). Research into early viticulture suggests that some form of fruit tree management and cultivation occurred during the Neolithic, marking the beginnings of domestication processes (Pagnoux et al., 2021; Valamoti, 2015). Early management practices could include pruning, pollarding, coppicing and grafting (Bathe, 2018). The finds of *Vitis* charcoal at Dikili Tash, paired with evidence for stored and pressed grapes, have been interpreted as incipient cultivation with management practices such as pruning (Valamoti, 2015). Other archaeological evidence for tree management (in this case, pollarding) includes the finds of cut young branches recovered from Late Neolithic (c. 4350–2450 cal BCE) lakeshore pile-dwellings in the northern Alpine



Fig. 6. Mid-5th millennium BCE cereal and weed macroremains from Ploča Mičov Grad. All macroremains are uncharred seeds unless specified. A. glume wheat spikelet fork, b. *Triticum monococcum* charred spikelet fork, c. *Triticum dicoccum* charred spikelet fork, d. *Triticum timopheevii* charred spikelet fork, e. two charred rachis segments of *Hordeum vulgare* (hulled), f. *Silene* sp., g. *Petrorhagia* sp., h. *Valeriana dentata*, i. *Campanula* sp., j. *Heliotropium europaeum*, k. *Capsella bursa-pastoris*, l. *Chenopodium album*, m. *Glebionis segetum*, n. charred *Euphorbia* cf. *helioscopia*, o. *Hypericum perforatum* and p. *Malva* cf. *sylvestris* mericarp. All scale bars are 1 mm.

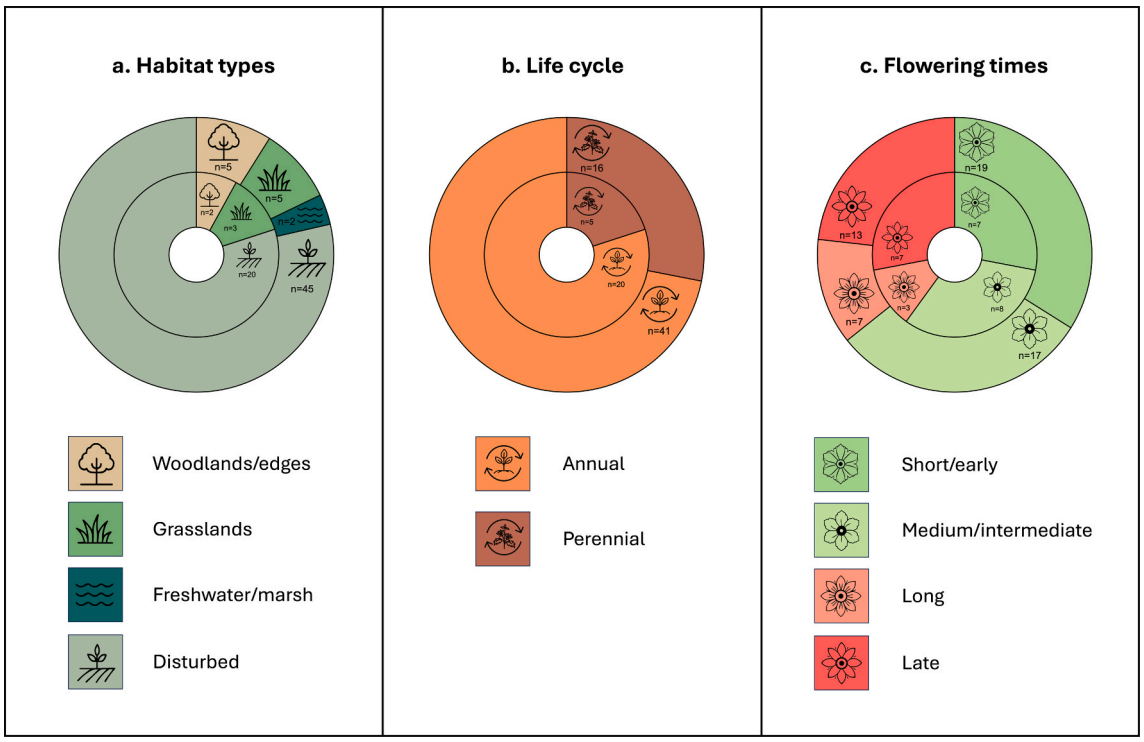


Fig. 7. Nested pie charts showing the proportions of different habitat types, life cycles and flowering times/durations (seasonality) across the weed assemblage. The external pie includes all taxa in the assemblage. The internal pie is a sub-set of the data showing only taxa that were preserved charred in the assemblage. N = number of taxa.

Foreland (Favré and Jacomet, 1998; Waller et al., 2012). With current evidence from Ploča Mičov Grad, the extent to which the farmers were tending, managing or cultivating fruit and nut trees remains unclear. However, the similarity of the *Prunus,* Rosaceae and cereal pollen percentage patterns for more than one millennium between 5500 and 4200 BCE suggests a very close relationship between human activities and these plant populations (Fig. 2, Brechbühl et al., 2023). Ongoing analysis of wood charcoal from the settlement area will contribute to this discussion (Ntinou et al., in prep).

Systematic and opportunistic foraging was part of an ever-evolving relationship between humans, fruit and nut trees and biocultural landscapes more broadly. Some fruits and nuts may have been collected near to the settlement at the woodland margins – for example, acorns, cornelian cherries and rowan fruits grow in the oak-dominated closed forests near to the lakeshore today (693 m a.s.l.). Other taxa likely motivated foragers to travel deeper into woodlands, up the sides of the Galičica mountain chain and near to the timberline, such as juniper which dominates local modern shrublands at higher elevations up to 1650 m a.s.l. Brechbühl et al. (2023). Foragers likely followed pre-existing animal tracks or created new trails through the biocultural landscape, encountering new plants and returning to known or preferred stands, attractive for their accessibility, abundance, particularly desirable fruit/nut qualities such as size and taste or for other social reasons (Bell, 2020; Davies et al., 2005; Valamoti, 2015). Naturally, these trails would have been dynamic, re-routing and expanding in response to vegetational shifts and community needs. Loose twigs from the woodland floor or cut branches might have been used to bend high branches or to shake and dislodge inaccessible fruits and nuts (Mabey, 2001; Burrows, 2005; Bishop et al., 2014). Collection followed seasonal cycles with increased foraging opportunities in the late summer and autumn. Fruits and nuts could have also been stored for future consumption or use, adding resilience to food systems year-round. However, at Ploča Mičov Grad the limited number of charred items suggests that fruits and nuts were primarily consumed in season (Holguin et al., 2024).

Complementing these botanical data, dendroarchaeological analyses of the wooden pile structures at Ploča Mičov Grad provide further insight into woodland dynamics and timber selection practices. Oak timbers from the 5th millennium BCE have a range of ring number and diameters, characterised by older trees with many rings, suggesting the exploration of various stands and a relatively undisturbed forest with a variety of age classes. The oaks are accompanied by juniper trunks with diameters over 30 cm (Fig. 3b). The range of tree rings in the mid 5th millennium BCE is wider than those from the 2nd millennium BCE layers which consist of a remarkably uniform group of oak piles with similar diameters, ring numbers, high initial growth rates and closely grouped growth initiation dates around 1460 cal BCE (Bolliger et al., 2023). This pattern in the 2nd millennium BCE suggests a synchronous regeneration event and may reflect woodland succession following earlier exploitation, consistent with a managed woodland system. This interpretation is further supported by the biological capacity of oak to regenerate after cutting or burning, unlike some conifers, such as pine, which do not resprout. Such regenerative traits make oak particularly suitable for repeated use in systems like coppice forestry, as documented in comparable sites north of the Alps (Horvat et al., 1974; Billamboz, 2014; Bleicher and Staub, 2023). The differences between the 5th and 2nd millennium BCE timber characteristics may point to: (1) a shift in resource availability by the Bronze Age, potentially due to prior over-exploitation of more accessible stands, (2) the general availability/predominance of old growth stands around the site in the 5th millennium BCE and/or (3) a deliberate selection of robust, long-lived species for construction purposes during the 5th millennium BCE. The fact that these large timbers were not split, although they could have been, supports the interpretation of availability of choice for material (3), rather than a forced reliance on oversized or suboptimal material due to scarcity. Alternatively, the use of such large-diameter timbers in the 5th millennium BCE may reflect differences in construction techniques, as comparable piles of that size were no longer employed in later periods.

Regional comparisons are still limited, yet emerging datasets are informative. At Lin 3 dated timber assemblages from the mid-5th millennium BCE reveal a predominance of old pine trees, with fewer oak

and no juniper elements (Yermokhin et al., 2025). At late 6th millennium BCE Dispilio, juniper dominates the vertical wood assemblage (>60%), with pine and oak representing smaller proportions (Maczkowski et al., 2024a,b). Preliminary observations from these sites suggest that successional patterns in oak growth may also be detectable elsewhere upon further analysis. Comparisons of pile diameters with Lin 3 and Dispilio – which are contemporaneous and closer in time, respectively, than the Bronze Age phases of Ploča Mičov Grad – suggest that besides the trees used in 5th millennium BCE Ploča Mičov Grad having wider ontogenetic age range, they are of comparably diverse diameters (Fig. 3). The highest diameter selection is visible at Lin 3's palisade III, likely a result of the highly specialized nature of this dendrochronologically-dated structure, in contrast to a potentially more diverse character of Ploča Mičov Grad's settlement, which also lasts longer. However, the comparison with other sites has significant limitations mainly due to different preservation conditions (preserved or eroded outer part) and different species (only pines in Lin 3).

These dendroarchaeological insights complement the archaeobotanical and palaeoecological findings presented in this study. While the palaeoecological record (and, to a lesser extent, the macrobotanical assemblage) reflect woodland composition and vegetation use at a broader ecological and functional level, the timber analyses offer a more direct window into woodland structure, successional dynamics and human engagement with specific tree taxa for construction. The case of fir illustrates this point well: although fir is present in the pollen and archaeobotanical record, it is absent from the preserved construction wood (Table 1). This discrepancy likely reflects a functional selection, rather than limited availability. Fir with its straight-grained stems is well suited for construction, yet due to its lower weight and especially its tendency to split easily may have been preferentially used for elements such as shingles, planks or beams. This was likely the case in 6th millennium BCE Dispilio where fir samples have a significant share in horizontal and non-post finds (Chatzitoulousis, 2008). This interpretation is supported by similar patterns north of the Alps, where fir on pile-dwelling settlements is underrepresented in vertical piles, but known to have served in roofing (Bleicher and Harb, 2015).

While the dendroarchaeological methods applied are in line with those established on lakeshore settlements in central Europe (Billamboz, 2014), the dynamics of woodland use in the southern Balkans likely followed distinct trajectories. Differences in biodiversity, species selection, regeneration cycles and potential management strategies highlight the need for further regional studies and dendrochronologically anchored datasets. Together, these datasets reinforce the interpretation of a diverse arboreal landscape that was exploited seasonally, with oak, pine and juniper fulfilling distinct roles over time—not only ecologically, but also economically, technologically and likely socially.

Many trees and shrubs, notably those of the Rosaceous family (such as *Rubus*), are disturbance-adapted and light-loving. All of the human activities already discussed, such as the establishment and maintenance of forest trails, the foraging of fruits and nuts and felling of timber for construction, likely encouraged the growth of these disturbance-adapted, light-loving shrubs (Brechbühl et al., 2023). Within the palaeoecological core large charcoal influx peaks occur during the settlement phase. While it is likely that some of this microscopic charcoal comes from fireplaces in the settlement, the coeval appearance of microscopic charcoal and cultivation signals in palaeoecological records across western, central and southern Europe, even from the deep centre of lakes, suggests that some burning of the landscape was likely (Lang et al., 2023; Tinner et al., 2005). Burning would have also caused disturbance that would have encouraged the growth of shrubs and trees.

5.2. Cultivation

Given the highly anthropogenic character of the mid-5th millennium BCE organic layer and large amount of cereal chaff relative to grain, it was hypothesised that remains of herbaceous taxa were arable weeds, entering the assemblage with the cereal chaff. An ideal context for weed analyses would be a storage deposit, for which the weed seeds are directly associated with crops (Stroud et al., 2023). Given the limited arboreal and wetland input in contrast to abundant cereal chaff and edible fruit and nut remains, the deposit has been interpreted as primarily domestic waste. The charred taxa had the strongest connection to the settlement likely becoming charred through human activity. However, the number of charred macroremains was too low for many analyses, and so uncharred macroremains were included if the same taxon was found charred in the assemblage.

Following Jones (1984, 1987), the crop processing analysis classified the archaeological samples as winnowing or fine-sieving by-products. The fine-sieving by-product matches the large quantity of cereal chaff remains, another by-product of this crop-processing stage. A high number of winnowing and fine-sieving by-products was also reported at the *Bandkeramik* site of Vaihingen, Germany (Bogaard, 2011). Winnowing by-products include light, fragile seeds which may not routinely survive charring or deposition on a dryland site. These seeds may be under-represented in the typical charred assemblage due to preservation factors. The tossing of material from fine-sieves is a practice known during emmer processing in highland Ethiopia (D'Andrea and Haile, 2002) and during emmer and spelt processing in Asturias, Spain, where a 'winnowing sieve' was used during coarse or fine-sieving (Halstead, 2014, 153). This could create a weed seed assemblage with a mixture of those typically considered as fine-sieving by-products and winnowing by-products, as was suggested for Vaihingen (Bogaard, 2011).

The majority of the herbaceous species/species-groups were annuals and associated with disturbed areas. Short-term/recently cleared and minimally disturbed plots can be excluded due to the abundance of annuals and the rarity/non-occurrence of woodland taxa (Bogaard, 2002). The number of annuals relative to perennials is similar to experimental permanently cultivated plots from Wackershofen (Rösch et al., 2002; Jacomet et al., 2016) and to Late Neolithic archaeobotanical assemblages from storage contexts and mixed assemblages in the circum-Alpine region, which are associated with permanent, labour-intensive cultivation (Jacomet et al., 2016).

Since the crop processing analysis supported the hypothesis that the potential weed seeds were arable weeds entering the assemblage as part of crop-processing by-products, the functional ecological traits of these species were analysed to model crop growing conditions and arable land management. While the samples showed a range of discriminant scores, almost all were classified as high-input (30 out of 34 samples). High-input systems are characterised by elevated soil fertility and disturbance due to labour-intensive activities such as thorough tillage, weeding, and manuring of small garden-like plots (Bogaard et al., 2016, 2018a; Stroud et al., 2023). Previous preliminary analysis of a small number of samples from Ploča Mičov Grad similarly suggested that the agrosystem was small-scale and labour-intensive (Holguin et al., 2025). Functional ecological analysis of archaeological assemblages often produces a range of discriminant scores (as observed here) likely reflecting the variability of 'real' agrosystems (Bogaard et al., 2016). Few Neolithic sites in south-eastern Europe have sufficient weed assemblages for such analysis and so at present we can make limited comparisons with contemporary sites in the region. However, this result compares well to other models of Neolithic agrosystems based on functional weed ecology across Europe and south-west Asia which favour (to varying degrees) a small-scale, intensive arable system (e.g. *Linearbandkeramik* sites in central Europe, Bogaard et al., 2016, the Körös site of Ecsegfalva, Hungary, Bogaard et al., 2016, 2007 and Neolithic Çatalhöyük, Türkiye, Green et al., 2018; Bogaard, in press). Furthermore, analyses using stable isotope analysis support the suggestion that small-scale intensive cultivation was commonplace in south-east Europe (Bogaard et al., 2013; Vaiglova et al., 2014, 2020, 2023). This indicates that wetland, upland arable agricultural systems at Lake Ohrid during the mid-5th millennium BCE were similar to those of

contemporary dryland, lowland sites in this region.

The wheat and disturbance-associated taxa pollen percentages were very high in the palaeoecological record. As the cores were extracted near to the settlement, it is probable that on-site crop processing contributed a large amount of pollen to the record. However, it is also possible that some pollen came directly from arable cultivation plots. If this is the case, given the limited dispersal of wheat pollen, these small-scale intensive plots would have been positioned within 200-300 m of the coring site (Brechbühl et al., 2023; Behre and Kučan, 1986; Fig. 8). As small cultivation plots would have needed regular tending and protection (seasonally and to some extent, year around) it is plausible that this would have occurred near to the site (Jones et al., 1999). This inference is supported by the local topography: the site is positioned within limited terrain at the foot of a steep mountain range, restricting the placement of the arable plots (Fig. 1). This result also broadly resonates with observations regarding the plausible location of long-term cultivated plots near lakeshore sites in the northern Alpine foreland (Baum et al., 2016).

It has been presumed that autumn sowing by early agricultural communities was infeasible in European regions due to winter frosts (Butzer, 1972). The presence of short/early-flowering species germinating in the autumn suggests autumn sowing was practised in this region and that the crops were successfully adapting to the upland regions of the Balkans. While evidently using modern crop varieties and agricultural approaches, it is interesting to note that in living memory, cereal sowing near Lake Kastoria (northwest Greece, less than 100 km from Ploča Mičov Grad) began in late October, when the ground had been softened by rain, and finished before December to avoid the hardened soils in winter (Halstead et al., forthcoming). As has been argued for the circum-Alpine lakeshore settlements, the inferred autumn sowing of cereals demonstrates that the mid-5th millennium agricultural system at Ploča Mičov Grad did not follow a floodplain cultivation regime, which would enforce spring sowing to avoid winter-early spring flooding (Bogaard, 2004; Sherratt, 1980). Indeed, the floodplains near Lake Kastoria were traditionally used primarily for communal pasture, becoming dry enough for cultivation too late in the year for wheat (Halstead et al., forthcoming).

Opportunistic weeds, attracted to the high fertility and high disturbance of the tended plots, would have been thinned out by hand-weeding to reduce competition with the crops for vital resources such as light, water and nutrients and could have offered new seasonal resources since weeds that thrive under fertile and disturbed conditions are more likely to be edible (Bogaard et al., 2018b). Edible weeds might have served as an additional plant food for humans (e.g. use of arable weeds as cooked greens in Morocco; (Bensbih and Ater, 2017) or livestock fodder (Bogaard et al., 2018b)), while others might have had

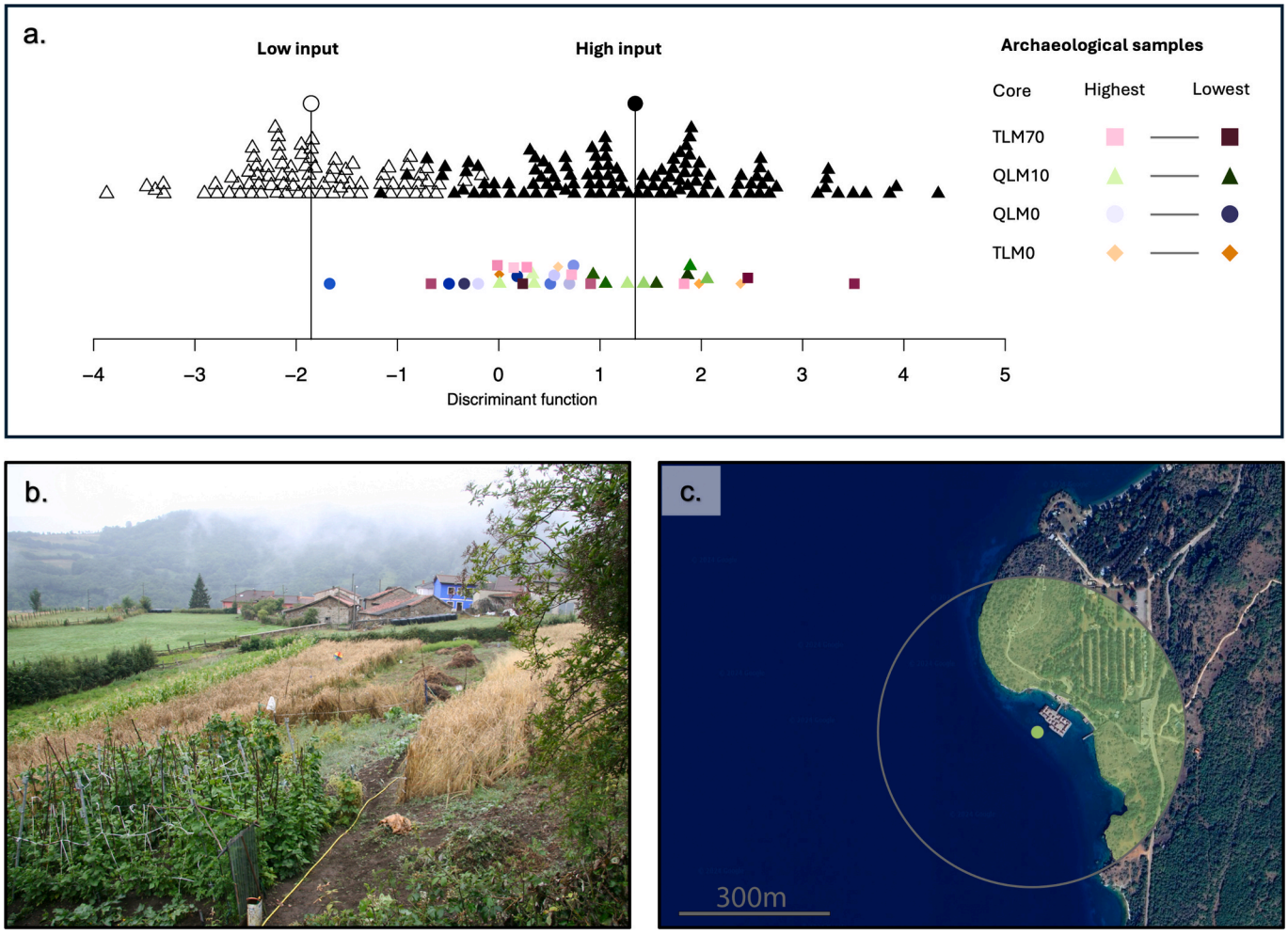


Fig. 8. The agrosystem of Ploča Mičov Grad. A. The results of the functional weed ecological analysis. The modern dataset is shown with samples classed as 'high-input' represented by black triangles and samples classed as 'low-input' represented by white triangles. The modern group centroids are marked by larger points. The majority of the archaeological samples (shown directly below the modern dataset) are classified as 'high-input'. The archaeological samples are coded as in Fig. 5. The shade reflects the depth of the samples with the darkest colours found at the base of the sedimentary sequence. B. Modern traditional high-input agricultural system in Asturias, Spain (Photo: A. Bogaard). C. The pollen of Cerealia type and disturbance associated taxa likely came from within a 300 m radius of the palaeoecological cores (image adapted from GoogleMaps).

medicinal or other values. Many herbaceous plants or shrubs might have been planted within or encouraged to grow near to arable plants to protect cultivated plots – for example, plants such as oregano and bitter vetch were two of many plants used by classical and medieval agronomists to deter pests, while *Rubus* shrubs might have served as fencing (Antolín and Schäfer, 2020; Zadoks, 2013). Many plants likely had multiple values to the prehistoric community; for example, aromatic herbs such as oregano could have been used as a flavouring or in medicine (Singletary, 2010; with antibacterial, antifungal and anti-inflammatory benefits; Giannenas et al., 2018; Mathesius, 2018) while bitter vetch was likely processed as a nutritious crop for human consumption (Holguin et al., 2026) and was also a component of ancient medicines (Flint-Hamilton, 1999).

Wheat was both the most common cereal pollen type (Brechbühl et al., 2023) and cereal macroremain identified. In the archaeobotanical assemblage, einkorn and emmer were the most important wheats. Timopheev's wheat and bread wheat were also recovered. Despite its presence in the earlier settlement phase (c. 5550–5350 cal BCE), barley (*Hordeum* type) pollen grains were scarce during the main mid-5th millennium BCE occupation phase (Brechbühl et al., 2023). On the other hand, barley was identified throughout the archaeobotanical assemblage, although at lower levels than wheat, with naked (two-row and six-row) and hulled (two-row and six-row) varieties present. This suggests that barley was perhaps cultivated further away from the site, threshed outside the settlement (while wheat was threshed inside) and/or in lower amounts than wheat as a minor crop. Further research, such as stable isotope analysis, could explore whether wheat and barley were grown under similar or differing conditions. Other crops represented in the archaeobotanical assemblage included bitter vetch, lentil, pea and flax. All of these crops are poor pollen dispersers and are rarely detected in pollen records (Brechbühl et al., 2023). While the pollen record is correspondingly limited, the archaeobotanical record shows that the plant food system was particularly diverse with a breadth of cultivated cereals, pulses and other crops, complemented by the wide range of collected local fruits and nuts (for a comparison to other contemporary sites see Holguin et al., 2024 Supplementary Materials). Biodiversity analysis of the palaeoecological record (including palynological richness PRI and the probability of interspecific encounter PIE proxies) suggests that biodiversity levels increased during the settlement phase, likely thanks to anthropogenic disturbance, land-clearance or woodland thinning and agricultural practices, including the introduction of adventive and cultural plants (Brechbühl et al., 2023). This suggests that the biodiverse food systems, including small-scale, intensive cultivation and systematic foraging, were part of a sustainable biocultural landscape.

6. Conclusions

The integration of near-site palaeoecological and on-site archaeobotanical and dendroarchaeological records, all preserved thanks to the wetland setting, provides new insights into the many ways in which the mid-5th millennium BCE community of Ploča Mičov Grad interacted with local flora, offering a richer understanding of the biocultural landscape around the bay. The dendroarchaeological results show preferences towards specific tree species and large-diameter timbers for construction, reflecting timber selection practices and woodland structure. Increased human activity was positively correlated with the inferred local abundances of Rose (Rosaceae) family taxa, suggesting that systematic collection of the rosaceous fruits and nuts (notably including almonds) and land-clearance encouraged these local fruit tree/shrub populations to thrive. In addition to the fruit and nut remains, large numbers of chaff and weed seeds in the archaeobotanical assemblage imply that the rich mid-5th millennium BCE organic layer is largely refuse from plant foods, including the by-products of crop processing. Based on the arable weed compositions and ecology, cultivation in this upland, wetland setting was similar to that of contemporary dryland, lowland sites, with small-scale, intensive 'garden-like' management of long-lived arable plots, which were likely positioned near to the settlement. This is the first time that such weed analyses have been applied to a prehistoric waterlogged site in the southern Balkans, anchored in both palynological and archaeobotanical datasets. As biodiversity increased in the palaeoecological record during the settlement phase, we infer that the broad-spectrum cultivated and foraged plant food systems were part of a sustainable biocultural landscape.

CRediT authorship contribution statement

Amy Holguin: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Lieveke van Vugt:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Matthias Bolliger:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Andrej Maczkowski:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Elizabeth Stroud:** Writing – review & editing, Formal analysis. **John Francuz:** Formal analysis, Investigation, Resources, Methodology. **Erika Gobet:** Writing – review & editing, Methodology, Formal analysis. **Michael Charles:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Albert Hafner:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition. **Willy Tinner:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition. **Amy Bogaard:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2026.106028.

Data availability

All data is in paper or citations given to publications with full data

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