Vegetation History and Archaeobotany
https://doi.org/10.1007/s00334-023-00931-3

ORIGINAL ARTICLE

Vegetation dynamics and land-use change at the Neolithic lakeshore settlement site of Ploča Mičov Grad, Lake Ohrid, North Macedonia

Sarah Brechbühl[1] · **Lieveke van Vugt**[1,2] · **Erika Gobet**[1,2] · **César Morales-Molino**[1,2] · **Joseph Volery**[1] · **André F. Lotter**[1,2] · **Ariane Ballmer**[2,3] · **Sandra O. Brugger**[1,2,5] · **Sönke Szidat**[2,4] · **Albert Hafner**[2,3] · **Willy Tinner**[1,2]

Received: 8 November 2022 / Accepted: 19 April 2023

Abstract

Detailed knowledge about the interactions between vegetation, climate and land use during the Mesolithic and Neolithic, at the transition from foraging to farming, is still scarce in the Balkans. Here we present a palaeoecological study combining pollen, spores and charcoal found in sedimentary cores from Lake Ohrid, Ploča Mičov Grad, North Macedonia, with a particular focus on the vegetation dynamics during the Late Glacial-Holocene and the Mesolithic-Neolithic transitions. Our record begins at ca. 13,500 cal BP (11,550 cal BC) when partially open vegetation, consisting mainly of *Pinus*, *Abies* and deciduous *Quercus* tree stands grew on the hilly flanks of the bay of Ploča. From 12,650 cal BP (cal 10,700 BC), herbs dominated the record until the onset of the Holocene (ca. 11,700 cal BP; 9750 cal BC), when increasing temperatures led to the establishment of pine-deciduous oak forests including *Alnus*, *Fraxinus ornus*, *Tilia*, *Ulmus* and *Abies*. These forests persisted until 7,500 cal BP (cal 5550 BC), when deforestation started due to Neolithic land use. This first phase of Neolithic activities in the Ploča Mičov Grad area precedes the earliest archaeological structures so far recorded by almost 1,000 years. Our data suggest two phases of human land use between 7,500 and 6,300 cal BP (5550–4350 cal BC), when high values of Cerealia type pollen and other cultural indicators indicate intense arable and pastoral farming activities. Once human activities decreased, forests were able to re-establish quickly (within 100–250 years), although the composition changed with disturbance-adapted *Ostrya* type (mostly *Ostrya carpinifolia*) and *Fagus* becoming more important. We conclude that forests were resilient to early human disturbance, despite intensive land use and logging activities gradually leading to forest composition changes. Many of these composition changes can still be seen today, suggesting the legacy of Neolithic farmers is still present in today's landscape.

Keywords Pollen · Palaeoecology · Vegetation history · Southern Balkans · Holocene · Land use

Introduction

The introduction of farming during the Neolithic marks the shift to a production economy and is one of the most remarkable transitions in human history (Vierra and Carvalho 2019). It has been shown that during the mid-seventh millennium BC, the Neolithic lifestyle and subsistence economy arrived in the region of the European Aegean, introducing the cultivation of cereals (e.g. wheat and barley), legumes (e.g. beans, peas, lentils), plants for fibre and oil extraction (flax), new practices and technologies (e.g. permanent settlements and housing, stone axes, grinding stones, pottery) as well as animal husbandry with sheep and goat (Weiss and Zohary 2011; Krauß et al. 2018; Vierra and Carvalho 2019). For this first introduction of agriculture in Europe, environmental conditions were crucial, as short summers

Communicated by F. Bittmann.

✉ Lieveke van Vugt
lieveke.vanvugt@unibe.ch

[1] Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland

[2] Oeschger Centre for Climate Change Research, University of Bern, Hochschulstrasse 4, 3012 Bern, Switzerland

[3] Institute of Archaeological Sciences, University of Bern, Mittelstrasse 43, 3012 Bern, Switzerland

[4] Department of Chemistry, Biochemistry and Pharmaceutical Sciences, University of Bern, Freiestrasse 3, 3012 Bern, Switzerland

[5] Department of Environmental Sciences, University of Basel, Klingelbergstrasse 27, 4056 Basel, Switzerland

or late frosts were a serious problem and posed a threat to the newly introduced crops (e.g. Krauß et al. 2018). In this regard, the sub-mediterranean region around Lake Ohrid, which includes today's states Albania and North Macedonia, offered sub-optimal conditions for agriculture featuring harsher environmental conditions with colder summers and winters than at the Mediterranean coast. Thus, the expansion to the North through this "climatic barrier" of cooler temperatures and shorter growing seasons required an adaptation of crops as well as of technologies (Ivanova et al. 2018; Krauß et al. 2018).

The introduction of agriculture and livestock husbandry profoundly altered European ecosystems (Stephens et al. 2019; Gassner et al. 2020). For instance, the use of fire to clear forests to gain arable land had drastic impacts on vegetation structure, composition, and diversity (Gassner et al. 2020). Additionally, climate may have also driven vegetation change, not only directly but also indirectly by influencing early agricultural societies (Panagiotopoulos et al. 2013; Krauß et al. 2018; Gassner et al. 2020). More specifically, changing climatic conditions at about 8,200 years ago (i.e. the "8.2 ka event") may have influenced the establishment and spread of early Neolithic communities into and across the Balkans. Such complex, partially reciprocal interactions and impacts are difficult to disentangle (Tinner et al. 2016), also considering that past climatic changes in the southern Balkans are still poorly understood (Zhang et al. 2014). Studies showing the use of manure by Neolithic people to enhance crop production on small plots (Bogaard 2005; Bogaard et al. 2013, 2019), illustrate the importance of knowledge on the extent, intensity and interdependence of crop plantation and animal husbandry. Hence, the processes and mechanisms related to the interactions between humans, climate and vegetation in the past need to be further investigated, for instance by studying the dynamics at the onset of the Neolithic when humans shifted to production economies (Tinner et al. 2016; Rey et al. 2020). Detailed palaeoecological studies covering this transition from natural to anthropogenic conditions (Whitlock et al. 2018) are, however, scarce from the Balkan region (Gassner et al. 2020) even though understanding the developments of early agriculture in these key regions is essential (Krauß et al. 2018). Additionally, knowledge about the process and development of the spread of the Neolithic way of life, including farming subsistence economy, from the Balkans to the rest of Europe is still fragmentary (Bogaard 2005; Kotsakis 2014).

Lake Ohrid is well suited to address such questions, because its sediment record covers the past 1.36 Ma (Wagner and Wilke 2011); its catchment includes the earliest Neolithic sites in the Southern Balkans (Krauß et al. 2018) and the lake is geographically close to Northern Greece, a region of major importance for the earliest Neolithisation of Europe (Gkouma and Karkanas 2018). Besides its archaeological importance (Naumov et al. 2018), Lake Ohrid has been the object of various palaeoenvironmental and environmental studies (e.g. Wagner et al. 2009, 2019; Vogel et al. 2010a; Lorenschat et al. 2014; Sadori et al. 2016; Sinopoli et al. 2018; Donders et al. 2021).

Several of these studies show the potential of Lake Ohrid for pollen-based vegetation reconstructions (e.g. Wagner et al. 2009; Sadori et al. 2016; Donders et al. 2021). The analysis of pollen, spores and other microfossils including microscopic charcoal is an ideal tool to reconstruct past vegetation dynamics as well as to trace early human impact and its consequences on ecosystems through time (Birks 2019). In this regard, on-site palynological studies (i.e. those based on sediment cores taken inside archaeological settlements) can deliver very detailed insights into the resources used by local populations, but they have limited power to reconstruct the surrounding vegetation and particularly its dynamics before and after settlement phase(s) (Gobet et al. 2017). In contrast, off-site studies (i.e. based on sediment cores well outside archaeological settlements) provide better reconstructions of the extra-local to regional vegetation dynamics before, during, and after settlement phases, but are not particularly informative about the activities inside the settlements (Gobet et al. 2017). In this study, we apply an intermediate approach, using the off-site methodology in very close proximity (10–30 m) to Ploča Mičov Grad, a Neolithic and Bronze Age archaeological site, to gain information on both the activities and impacts of the local Neolithic inhabitants. This approach is one of the first for the Southern Balkans; so far only a few palynological studies from close proximity to prehistoric settlements exist from this area (Marinova et al. 2012). We reconstruct the vegetation and fire dynamics at Lake Ohrid and provide detailed insights into the impact of Neolithic land use on the local and extra-local vegetation.

The specific aims of this study are: (1) to investigate the natural vegetation and fire dynamics as well as the anthropogenically caused changes to the vegetation and (2) to reconstruct the local development of Neolithic land use. Specifically, we want to investigate whether the materially tangible settlement remains of Ploča Mičov Grad represent the first Neolithic settlement at the site and whether the palynological evidence is in agreement with the archaeological record of the latest excavations (Hafner et al. 2021; Bolliger et al. 2023). We put the age of the earliest unambiguous traces of Neolithisation at Ploča Mičov Grad into context with other sites, e.g. Limni Orestiás Kastorias (Kouli and Dermitzakis 2008) and Limni Zazari (Gassner et al. 2020) and address the question of whether early Neolithic land use activities in Western Macedonia, Greece, (onset ca. 6400 cal BC; Chrysostomou et al. 2015) preceded those in the Lake Ohrid region. To be able to assess the impact of Neolithic land use on the vegetation, we also reconstruct the Late-Glacial and Early Holocene vegetation dynamics as they were still undisturbed by anthropogenic impact.

Study site

Lake Ohrid (Fig. 1, 41°00′N, 20°45′E) is a large lake of tectonic origin located between North Macedonia and Albania (Popovska and Bonacci 2007; Panagiotopoulos et al. 2014). It is situated at 693 m a.s.l., has a surface area of 358 km^2, a water volume of 55.5 km^3, a maximum depth of 289 m and a mean depth of 155 m. The catchment area of Lake Ohrid covers about 3,920 km^2 and includes Lake Prespa (849 m a.s.l., water volume of 3.0 km^3) and its catchment (area of 2,520 km^2), as both lakes are connected by karst aquifers (Matzinger et al. 2006; Panagiotopoulos et al. 2014). The bedrock consists mainly of karstified Triassic carbonates and clastics (Wagner et al. 2009). The sheltered location of Lake Ohrid in a relatively deep valley surrounded by high mountain chains, its proximity to the Adriatic Sea and the thermal capacity of the lake itself lead to temperate and rather continental climatic conditions (Watzin 2003; Vogel et al. 2010a). The current average temperature at Ohrid town is 20.9 °C for July and 2.3 °C for January; the average annual precipitation is 662 mm (WMO WWIS 2022). Our coring site is located on the eastern shore of Lake Ohrid, 12 km south of Ohrid town and 1 km south of the village of Peštani, at the foothills of the Galičica mountain chain and in very close proximity

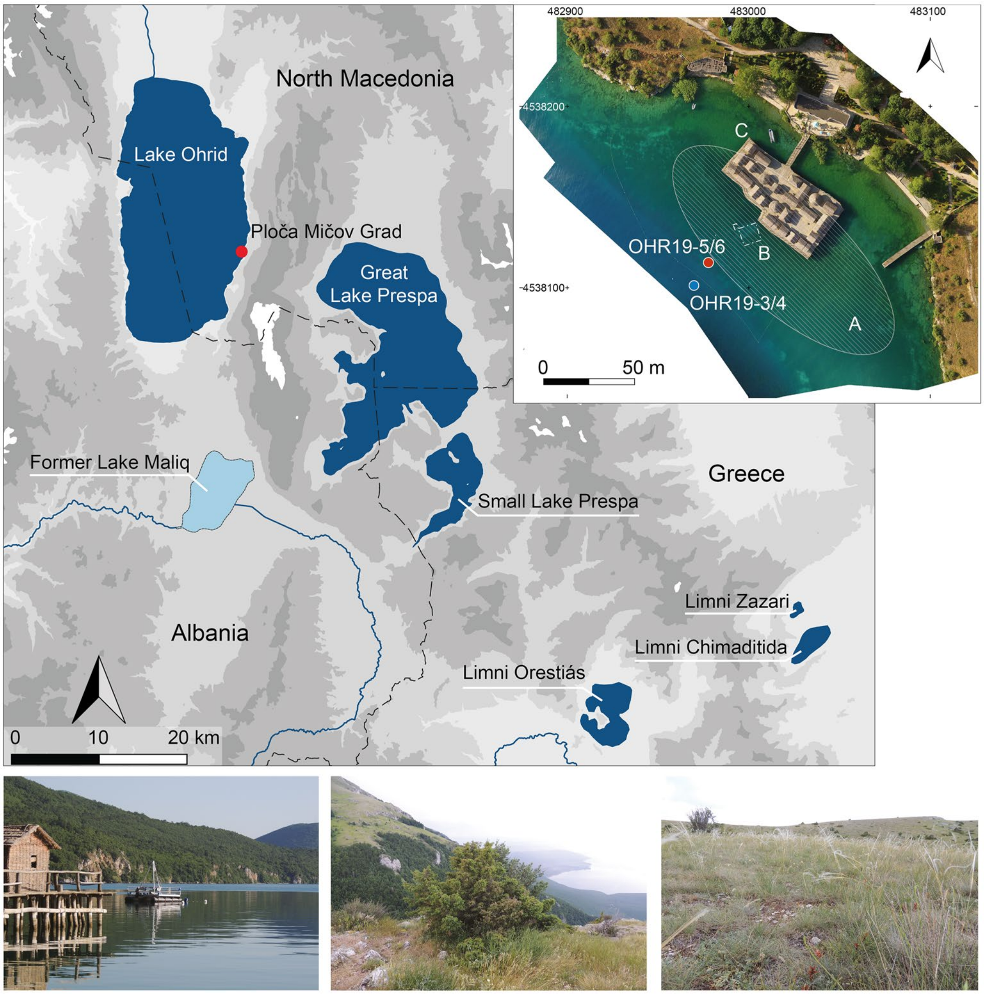


Fig. 1 Overview of Lake Ohrid and its surroundings. Top: Map of the study site with the location of Ploča Mičov Grad (red dot) and other palaeoecological sites mentioned in the text (adapted from Reich et al. 2021). Insert: Orthophoto of the study site at Ploča Mičov Grad with the coring locations of cores Ohrid plateau (OHR19-3/4; blue dot) and Ohrid settlement (OHR19-5/6; red dot), the estimated extent of the settlement **A**, the investigated area of the archaeological diving campaigns 2018–2019 **B** and the open-air 'Museum on Water' **C**; adapted from Reich et al. 2021; Bottom left: Photograph of Lake Ohrid with the open-air museum, the coring platform and part of the Galičica mountain chain (E. Gobet/W. Tinner); Bottom middle and right: Photographs of the surrounding vegetation, taken in the Galičica mountains at ca. 1,650 m a.s.l. (E. Gobet/W. Tinner)

to the Neolithic and Bronze Age 'pile-dwelling' settlement of Ploča Mičov Grad (4600–1200 cal BC; Naumov 2016; Naumov et al. 2019; Hafner et al. 2021).

Based on our survey, today's vegetation in the closer surrounding of Ploča Mičov Grad consists of oak-dominated forests with *Quercus trojana*, *Q. pubescens*, *Fraxinus ornus*, *Acer opalus* subsp. *obtusatum*, *Ostrya carpinifolia*, *Fagus sylvatica*, *Cornus mas*, *Sorbus aria*, *S. aucuparia* and *S. torminalis*. The closed forest reaches down to the lake shore. We found scattered tree stands of *Pinus* around 1,400 m a.s.l. The upper part of the forest, up to the timberline, is dominated by *Fagus sylvatica*. Locally, higher elevations (up to 1,650 m a.s.l.) are dominated by grasslands and shrublands with *Juniperus communis* subsp. *communis* and *J. communis* subsp. *alpina* (Fig. 1). In the region, *Quercus frainetto*, *Q. cerris*, *Fraxinus ornus* and *Ostrya carpinifolia* can dominate in the warmest sub-mediterranean vegetation stands (Matevski et al. 2011), in which *Carpinus orientalis* and *Juniperus excelsa* may co-occur. Above this belt, fragmented *Quercus petraea* dominated forests occur, followed by cool-temperate montane fir-beech forests dominated by *F. sylvatica* and *Abies borisii-regis* (Matevski et al. 2011). In this forest belt, *Corylus colurna* and *O. carpinifolia* stands can be found in the ravines as well as *Acer opalus* subsp. *obtusatum* on steep slopes, and at the highest forested altitudes, oro-mediterranean beech forest dominates (Matevski et al. 2011). Regionally, the timberline is located at 1,900 m a.s.l., whereas grazed karstic plateaus on altitudes around 1,600 m a.s.l. are dominated by *Juniperus communis* communities (Matevski et al. 2011). At Lake Prespa, pines are found in a subalpine conifer forest belt between 1,800 and 2,200 m a.s.l. consisting of *A. borisii-regis*, *Pinus peuce*, *P. sylvestris*, *P. nigra* and *P. heldreichii* (Panagiotopoulos et al. 2013).

Methods

Fieldwork

During June and July 2019, we took four sediment cores (OHR19-3, OHR19-4, OHR19-5, OHR19-6) from Lake Ohrid. The coring was executed on a shoreline plateau, in the direct vicinity of the submerged archaeological site of Ploča Mičov Grad (Fig. 1). We retrieved the cores in 3 m long segments by using a UWITEC piston corer (5.9 cm diameter) and cut them into 1 m segments for further processing.

Two parallel cores OHR19-3 and OHR19-4 (composite core OHR19-3/4; 40°59′38.3″N, 20°47′51.3″E) were taken from the edge of the shoreline plateau, at ca. 90 m from the shore and at a water depth of 8.6 and 9.1 m respectively. In addition, we took two more parallel cores OHR19-5 and OHR19-6 (composite core OHR19-5/6; 40°59′38.8″N, 20°47′51.7″E) on the edge of the prehistoric settlement perimeter at a water depth of 4.7 m and at ca. 75 m from today's lake shore. The cores were opened and correlated visually with lithological marker horizons (Tables 1, 2) in the laboratory at the Institute of Plant Sciences (IPS) of the University of Bern. For simplicity we named the composite core OHR19-3/4, which has a length of 698 cm, "Ohrid plateau". The composite core OHR19-5/6 was named "Ohrid settlement" and has a length of 750 cm.

Chronology

For the age-depth model, we analysed a total of 76 macrofossil samples, from which we selected 22 subsamples of terrestrial plant macrofossils for radiocarbon dating (Table 3). We sieved the samples with a 200 µm mesh size and analysed them with a stereo microscope at 6–50× magnification. We identified the macrofossils by means of standard plant morphology keys (e.g. Cappers et al. 2006) and the reference collection at the IPS. The samples were dated by using accelerator mass spectrometry (AMS) in the Laboratory for the Analysis of Radiocarbon with AMS (LARA) at the University of Bern in Switzerland (Szidat et al. 2014). We used the package 'clam' (Blaauw 2010, version 2.4.0)

Table 1 Detailed description of the lithology from the Lake Ohrid plateau record (core OHR19-3/4)

Depth (cm)	Top to bottom age (cal BP)	Description
0–7	-69	Calcareous gyttja and lake marl
7–15	–	Detritus gyttja
		Assumed hiatus
15–140	5,150–5,826	Lake marl
140–167	5,826–5,990	Calcareous gyttja and lake marl
167–172	5,990–6,032	Coarse detritus gyttja
172–179	6,032–6,091	Silty mollusc layer
179–222	6,091–6,379	Coarse detritus gyttja
		Hiatus
222–251	10,273–10,765	Lake marl
251–331	10,765–11,802	Calcareous gyttja and lake marl
331–465	11,802–12,658	Calcareous gyttja with increasing lake marl layers
465–518	12,658–12,866	Calcareous gyttja and lake marl
518–668	12,866–13,452	Silty-clayey calcareous gyttja
668–688	13,452–13,531	Silty fine sand in layers
688–698	13,531–13,570	Sand

A second hiatus likely occurs within the top 50 cm; its exact location is unclear. Assigned ages are based on the modelled ages from the age-depth model (Fig. 2)

Table 2 Detailed description of the lithology from the Lake Ohrid settlement record (core OHR19-5/6)

Depth (cm)	Top to bottom age (cal BP)	Description
0–20	6,276–6,302	Cultural layer with ceramics
20–44	6,302–6,335	Coarse detritus gyttja
44–61	6,335–6,359	Silty fine detritus gyttja
61–74	6,359–6,376	Coarse detritus gyttja
74–102	6,376–6,564	Coarse detritus gyttja with indications of cultural layer
102–114	6,564–6,725	Sandy lake marl with coarse detritus gyttja
114–131	6,725–7,018	Coarse detritus gyttja
131–148	7,018–7,431	Calcareous gyttja
148–196	7,431–8,603	Lake marl
196–200	8,603–8,676	Lake marl with molluscs
200–241	8,676–9,422	Lake marl
241–251	9,422–9,580	Lake marl with molluscs
251–303	9,580–9,909	Lake marl
303–323	9,909–10,036	Lake marl with laminations
323–377	10,036–10,378	Lake marl
377–604	10,378–11,757	Lake marl with laminations
604–625	11,757–11,894	Lake marl with sandy layers
625–627	11,894–11,907	Sand layer with organic debris
627–648	11,907–12,039	Lake marl with thin sandy layers
648–654	12,039–12,076	Sandy lake marl
654–676	12,076–12,212	Lake marl with thin sandy layers
676–678	12,212–12,224	Sand layer
678–684	12,224–12,261	Lake marl
684–720	12,261–12,483	Lake marl with sparse organic debris (mostly terrestrial origin)
720–732	12,483–12,557	Lake marl with abundant coarse organic debris
732–770	12,557–12,792	Lake marl with thin sandy layers
770–773	12,792–12,810	Sand layer
773–782	12,810–12,866	Lake marl
782–783	12,866–12,872	Sand layer
783–793	12,872–12,935	Lake marl

Assigned ages are based on the modelled ages from the age-depth model (Fig. 2)

in R (R Core Team 2021, version 4.1.1), with the IntCal20 calibration curve (Reimer et al. 2020) to calibrate the radiocarbon dates (cal BP and cal BC) and to construct the age-depth models (Fig. 2). Both age-depth models are based on linear interpolation and use extrapolation to determine the age for the bottom samples of the two cores. We also added the 95% confidence interval from the generalised additive model (GAM; Heegaard et al. 2005), which takes both depth and age uncertainties into consideration.

Pollen and charcoal analysis

We analysed a total of 70 pollen samples of 1 cm^3, 34 from the Ohrid plateau (OHR19-3/4) and 36 from the Ohrid settlement (OHR19-5/6) record. For the Ohrid plateau record, we generally sampled every 18 cm, except between 260 and 0 cm where we increased the sampling resolution. In the Ohrid settlement record we started sampling from 384 cm upwards at every 16 cm. In the upper part of the core (240–0 cm) the sampling resolution varies from 10 to 4 cm. To prepare the samples for pollen and charcoal analysis, we followed the standard procedure of Moore et al. (1991) with chemical treatment (HCl, KOH, HF and acetolysis), sieving (0.5 mm mesh size), and decanting. Afterwards, the samples were stored in glycerine. We added *Lycopodium* spore tablets before chemical treatment to estimate microfossil concentrations and influx (Stockmarr 1971). Terrestrial pollen counts of all samples were > 500 (except for one sample from core Ohrid plateau at 200 cm depth). We analysed microscopic charcoal (> 10 µm) according to Tinner and Hu (2003) and Finsinger and Tinner (2005) and estimated the concentrations (particles cm^{-3}) as well as influx (particles cm^{-2} yr^{-1}). Microscopic charcoal can be transported over long distances (20–100 km) and is used as a proxy for regional fire activity (Conedera et al. 2009; Adolf et al. 2018). For the analysis of pollen, spores, non-pollen palynomorphs (NPP) and

Table 3 Radiocarbon measurements (^{14}C ages, with 1σ uncertainties) and corresponding calibrated calendar ages from Lake Ohrid

Lab code	Core	Depth (cm)	Dry weight (mg)	Plant material dated	^{14}C age (BP)	Cal age, 2 σ-range (BC)	Cal age, 2 σ-range (cal BP)	Median (cal BP)	Modelled in diagrams (cal BP)
Lake Ohrid plateau record (core OHR19-3/4)									
BE-15420.1.1	3	48–50	0.9	Twig fragment	4,605 ± 45	3519–3108	5,468–5,057	5,332	5,328
BE-15419.1.1*	3	78–80	0.6	Leaf, periderm, bark, twig, bud scale	6,240 ± 100	5470–4945	7,419–6,894	7,133	rejected
BE-14810.1.1	3	119–121	3.2	Bark	4,985 ± 30	3935–3653	5,884–5,602	5,702	5,712
BE-14278.1.1	3	162–164	0.8	Bud with base, periderm, wood/twig, bark	5,190 ± 35	4055–3947	6,005–5,897	5,950	5,956
BE-14809.1.1	3	208–210	7.6	Bud complete (deciduous)	5,610 ± 30	4531–4356	6,480–6,305	6,369	6,339
BE-14808.1.1	3	221–223	4.1	*Pinus* needle base, *Rubus* seed	5,590 ± 30	4489–4353	6,438–6,302	6,356	6,376
BE-14279.1.1	3	230–232	2.9	Leaf (deciduous)	9,240 ± 40	8562–8306	10,512–10,256	10,404	10,401
BE-15418.1.1	4	260–262	4.3	Leaf	9,600 ± 35	9213–8821	11,162–10,770	10,934	10,947
BE-14280.1.1	4	342–344	2.5	*Juniperus* twigs, leaf fragment, bud scale	10,245 ± 40	10,153–9861	12,103–11,811	11,930	11,924
BE-14281.1.1	4	461–463	10.2	*Pinus* needle fragments	10,615 ± 25	10,763–10,665	12,713–12,615	12,658	12,641
BE-14282.1.1	4	546–548	4.4	*Juniperus communis* twig, *Pinus* needle, leaf, *Pinus* periderm, bud scale	11,040 ± 25	11,131–10,943	13,081–12,893	12,979	12,979
BE-1483.1.1	3	684–686	0.7	Woody plant material, periderm	10,475 ± 60	10,678–10,475	12,628–12,425	12,470	Rejected
Lake Ohrid settlement record (core OHR19-5/6)									
BE-15417.1.1	5	40–42	1.4	Twig, bark, bud scale, *Pinus* needle	5,585 ± 45	4531–4344	6,480–6,293	6,362	6,331
BE-15416.1.1	5	78–80	3.7	Twig fragment, bark, leaf midrib	5,585 ± 40	4495–4346	6,444–6,295	6,358	6,383
BE-15415.1.1	5	106–108	1	Bark, leaf, *Rubus* seed	5,805 ± 50	4786–4542	6,735–6,491	6,604	6,603
BE-14806.1.1	5	136–138	4.4	Leaf, *Rubus* seeds, twig/periderm	6,220 ± 30	5301–5056	7,250–7,005	7,100	7,122
BE-14807.1.1	6	177–179	1.4	Leaf, periderm	7,470 ± 50	6427–6236	8,376–8,185	8,281	8,275
BE-14805.1.1	6	248–250	25.3	*Alnus glutinosa* twigs	8,605 ± 30	7729–7579	9,678–9,528	9,548	9,568
BE-15414.1.1*	5	398–400	1.3	Leaf, periderm	9,305 ± 120	9117–8279	11,066–10,228	10,508	10,517
BE-15413.1.1	5	498–500	7.3	Leaf (cf. *Quercus*)	9,675 ± 35	9253–8861	11,202–10,810	11,116	11,072
BE-14804.1.1	6	635–637	4.4	*Juniperus* and *Pinus* needles	10,260 ± 35	10,478–9871	12,427–11,820	11,954	11,965
BE-15412.1.1	6	786–788	9.9	*Juniperus* and *Pinus* needles, *Alnus* fruit, *Rubus* seed	10,985 ± 35	11,113–10,819	13,062–12,768	12,889	12,897

Samples marked with * showed a low carbon mass and were analysed by gas measurement

The depth refers to the position of the sample in the master core for each record

microscopic charcoal we used a light microscope at 200× to 1,000× magnification. Besides palynological keys (e.g. Punt 1976; Moore et al. 1991; Beug 2004; van Geel and Aptroot 2006) and photo atlases (Reille 1992), we used the reference collection at the IPS for pollen and spore identification. We distinguished three different types of *Quercus* pollen: *Quercus frainetto* type, which includes *Quercus frainetto*, *Q. petraea* and *Q. pubescens* in the study area; *Q. cerris* type,

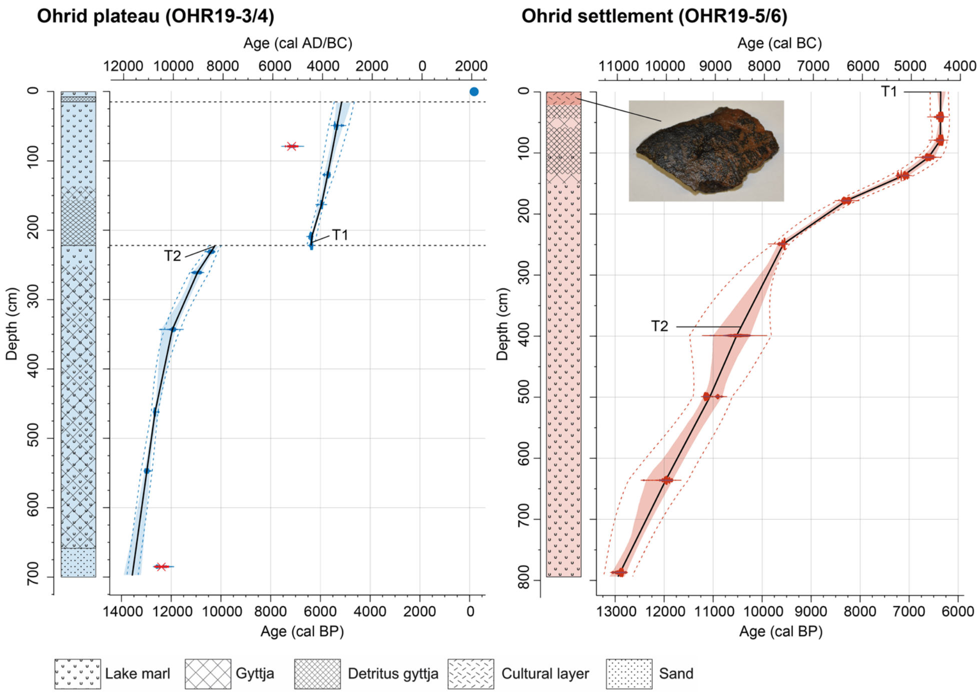


Fig. 2 Age-depth models and lithologies for the Lake Ohrid cores from Ploča Mičov Grad with core Ohrid plateau (OHR19-3/4; left) in blue and core Ohrid settlement (OHR19-5/6; right) in red. The blue and red horizontal integrals show the probability density functions of the individual radiocarbon dates (IntCal20; Reimer et al. 2020); the black lines represent the modelled chronologies using linear interpolation, ('clam' version 2.3.7; Blaauw 2010). The blue and red envelopes show the 95% confidence intervals of the clam models and the dashed lines show the 95% confidence intervals from the generalised additive models (GAM; Heegaard et al. 2005). The horizontal dashed lines in the Ohrid plateau age-depth model indicate hiatuses and the blue dot indicates the surface sample. Two dates in the Ohrid plateau model were rejected (red crosses). The photo in the Ohrid settlement model is an example of the ceramics found in the cultural layer. The tie points used to combine the two cores into one record are marked as T1 and T2

which includes *Q. cerris* and *Q. trojana*; and *Q. ilex* type, which includes *Q. ilex* and *Q. coccifera* (Beug 2004; Senn et al. 2022). *Ostrya* type pollen includes *O. carpinifolia* and *Carpinus orientalis*; based on today's vegetation (Matevski et al. 2011) we assume that a larger proportion of this type derives from *Ostrya carpinifolia* and a smaller proportion from *Carpinus orientalis*. Despite the large size of the lake and due to the location of our site in a bay very close to the shore, we expect most of the pollen to come from a 3–5 km radius around the coring site, mainly representing the lower vegetation belts (Matevski et al. 2011).

We combined the pollen and microscopic charcoal data from both Ohrid plateau and Ohrid settlement composite cores into one dataset, based on their respective overlapping radiocarbon chronologies and matching biostratigraphies (Fig. 2, ESM). The combined dataset of Lake Ohrid (OHR) spans a period from ~ 5,200–13,500 cal BP (3250–11550 cal BC). Finally, we subdivided the pollen diagram into local pollen assemblage zones (LPAZ), by using the zonation method of optimal partitioning with sum-of-squares (Birks and Gordon 1985) identifying the statistically significant zones with the broken-stick method (Bennett 1996).

Numerical analysis

To identify environmental gradients in the data, we used an ordination analysis done with Canoco5 (ter Braak and Šmilauer 2012). Because the length of the DCA axis 1 was 1.9 standard deviation (SD) units, we decided to use a principal component analysis (PCA). Before the analysis we log-transformed the data to reduce the effects of dominant taxa. Due to the large hiatus between the surface sample and the rest of the record, we excluded this sample from the analysis and added it as a supplementary case. Microscopic charcoal influx (as a proxy for fire) was added passively to the analysis as a supplementary variable. To investigate and quantify the impact of human land use we calculated the Land Use Probability (LUP) index (Deza-Araujo et al. 2022). Based on different cultural indicator pollen types, this index provides a probability measure for past land use activities (Deza-Araujo et al. 2022). The LUP is a simple way to weight and summarise the most important cultural indicator pollen types at a site. It can be adjusted to different regions, aiding comparisons between sites (Deza-Araujo et al. 2022). We used the Anthropogenic Indicator Values (AIV) for the taxa of the sub-mediterranean vegetation belt as proposed by Deza-Araujo et al. (2022).

Biodiversity analysis

To investigate past plant diversity trends, we calculated the palynological richness (PRI; Birks and Line 1992) as well as the probability of interspecific encounter (PIE; Hurlbert 1971). One sample was excluded from the biodiversity analysis, as it only had a terrestrial pollen sum of 256 (sample at 6,268 cal BP). PRI is a proxy to estimate diversity by the number of taxa in a sample based on the smallest terrestrial pollen sum (i.e. 502). It was calculated by means of rarefaction analysis (Birks and Line 1992) with the package 'vegan' (version 2.5.7; Oksanen et al. 2020) running in R (R Core Team 2021). PIE is here used as a proxy for palynological evenness, to investigate whether the samples are dominated by certain taxa or whether it is likely to find all taxa equally represented (e.g. Lepori et al. 2005; Lestienne et al. 2020). We also calculated the evenness detrended palynological richness (DE-PRI) to reduce the potential effect of evenness on palynological richness, as e.g. resulting from strong pollen producers such as pines (Colombaroli and Tinner 2013; Senn et al. 2022).

Results and interpretation

Lithology and chronology

Ohrid plateau record (OHR19-3/4)

The sediments of Ohrid plateau mostly consist of calcareous gyttja and lake marl (668–222, 167–15, 7–0 cm), with sand and silty fine sand at the bottom (698–668 cm) and with two distinct layers of coarse detritus gyttja towards the top (222–179 and 172–167 cm) divided by a thin layer of silt with molluscs (179–172 cm; details in Table 1 and Fig. 2). The age-depth model (Fig. 2) shows a likely age of 13,600 cal BP (11650 cal BC) for the oldest sediments. However, this date has large uncertainties as it was extrapolated from the lowermost radiocarbon date at 546–548 cm. Two dates (Table 3) were considered as outliers; they had a dry weight of less than 1 mg and the carbon content was low. The lithology and the chronology indicate a hiatus at the start of the coarse organic detritus layer (ca. 222 cm) that would span from ca. 10,000 to 6,500 cal BP (8050–4550 BC; Fig. 2). A second hiatus occurs in the top 50 cm; its precise depth is unknown. The hiatuses could be the result of mass wasting events in the lake. These events occur regularly along the steep basin slopes of Lake Ohrid (Wagner et al. 2008) and are often triggered by seismic shaking (Vogel et al. 2010b). For the age-depth model we assumed a hiatus at 15 cm when the sediments show a change from lake marl to detritus gyttja. The ages of the top 15 cm were not modelled. Overall, the age-depth model shows high and fairly constant sedimentation rates. The rates decrease slightly between 352 and 224 cm (12,000–10,000 cal BP, 10050–8050 cal BC).

Ohrid settlement record (OHR19-5/6)

Most of the Ohrid settlement sediment sequence (783–148 cm; Table 2, Fig. 2) consists of lake marl with thin sandy layers. Following a transitional section of calcareous gyttja (148–131 cm), the uppermost sediment is mostly coarse detritus gyttja, only interrupted by a layer of sandy lake marl (114–102 cm). Some of the coarse detritus gyttja layers contained archaeological artefacts and are thus named as cultural layers (Table 2). The oldest date of this core is ca. 12,900 cal BP (10950 cal BC; Table 3, Fig. 2) and corresponds to the final phase of the Bølling-Allerød interstadial (ending at ca. 12,800 cal BP; 10850 cal BC; Reinig et al. 2021). The youngest date at 40–42 cm has an age of ca. 6,300 cal BP (4350 cal BC; Table 3). As the core ends with detritus gyttja and a cultural layer with artefacts from the Neolithic and Bronze Age, we expect a hiatus at 0 cm. This hiatus is most likely caused by erosion from wind-driven surface currents (Vogel et al. 2010b; Hafner et al. 2021); a mass wasting event is less likely as the Ohrid settlement cores are on a shelf, away from the steep basin slope (Fig. 1). The age-depth model of Ohrid settlement shows two changes in the sedimentation rates (Fig. 2). Most of the core (793–249 cm; 12,900–9,600 cal BP, 10950–7650 cal BC) is characterised by stable sedimentation rates. From 248 to 136 cm (9,600–7,100 cal BP, 7650–5150 cal BC) the accumulation rate decreases and after 136 cm increases again to very high sedimentation rates.

Pollen and charcoal analysis

We subdivided the combined Ohrid settlement and plateau pollen diagram (OHR; Fig. 3) into six statistically significant local pollen assemblage zones (LPAZ OHR-1 to OHR-6). OHR-4 was subdivided into two non-significant subzones (OHR-4a/b), to highlight important vegetation changes such as the forest decline and the first appearance of cultural indicators.

OHR-1 (13,500–12,800 cal BP, 11550–10850 cal BC): Arboreal pollen (AP) fluctuates in this zone between 55 and 70%, with *Pinus* (ca. 40%), *Q. frainetto* type (10–20%), *Betula* (ca. 5%), *Abies* (up to 5%), and *Quercus cerris* type (up to 5%) dominating (Fig. 3). The presence of pollen from *Fagus*, *Tilia*, *Acer*, *Ostrya* type as well as *Phillyrea* and *Quercus ilex* type suggests that these species were growing in the region during this period (absolute pollen limit reached). *Fagus* is continuously present, i.e. reached the empirical pollen limit, suggesting that it was growing in the catchment. Non arboreal pollen (NAP) is mostly represented by Poaceae and *Artemisia* (both between 10 and 20%), suggesting a high relevance of grassland and/or steppic vegetation. Taken together the pollen data indicate a partially open vegetation, consisting mainly of pine, fir and oak tree stands interspersed with steppe habitats. Two high peaks in microscopic charcoal influx (up to 50,000 particles cm^{-2} yr^{-1}) and concentrations (around 200,000 particles cm^{-3}) suggest an increase of fire activity at ca. 13,300 and 13,000 cal BP (11350 and 11050 cal BC).

OHR-2 (12,800–11,100 cal BP, 10850–9150 cal BC): AP drops below 50% in OHR-2, indicating a decline of tree and shrub stands. *Pinus* pollen percentages show the largest decrease (from 40 to 20%), but other tree taxa like *Abies*, *Tilia* and *Ulmus* also show a reduction in pollen percentages. *Fagus* was reduced in the pollen catchment as its pollen is missing shortly after the onset of this zone. Pollen percentages of *Q. frainetto* type decline at the onset of the zone to recover later, while other temperate trees such as *Abies*, *Tilia*, *Ulmus*, *Q. cerris* type and *Ostrya* type did not recover throughout the zone, suggesting long-lasting reductions of temperate habitats. *Artemisia* (up to 40%) and Chenopodiaceae (5–10%) show their highest pollen percentages in the record around 12,500 cal BP (10550 cal BC), suggesting the expansion of cold and drought adapted steppes. *Galium* type, *Rumex acetosella* type, *Paronychia*, *Achillea* type, Apiaceae and Asteroideae pollen percentages contribute to maximum values of 60% of NAP. *Ephedra* species also expanded into the steppes. Towards the end of this zone, AP starts to rise, suggesting an expansion of forested conditions. Microscopic charcoal influx suggests a general decrease in regional fire activity, which may reflect cool climatic conditions and/or low biomass and thus fuel availability. Peak values around 12,600 cal BP (10650 cal BC) reach ca. 30,000 particles cm^{-2} yr^{-1}, and more than 100,000 particles cm^{-3}.

OHR-3 (11,100–8,200 cal BP, 9150–6250 cal BC): At the onset of this zone, AP rises quickly over 80% indicating the establishment of relatively closed forests and then gradually increases throughout the zone to reach a first maximum of 90% at ca. 8,500 cal BP (6550 cal BC). The AP assemblage is dominated by *Pinus* (40%) and *Q. frainetto* type (30%), together with *Alnus glutinosa* type, *Tilia*, *Ulmus* and *Fraxinus ornus*, showing that a diverse temperate forest grew around Lake Ohrid. The slight increase in *Abies* pollen at the start of the zone indicates that its population recovered from the decline in the previous zone. Single finds of *Fagus* pollen grains suggest it was present in the region but could not spread locally. Oaks played an important role in the vegetation, especially deciduous oak species such as *Q. frainetto*, *Q. pubescens* and *Q. petraea*. Semi-evergreen (*Q. trojana*) to evergreen oaks (*Q. coccifera*, *Q. ilex*) were only a marginal component of the vegetation, as their low percentages (ca. 1–2%) indicate. Pollen from *Vitis vinifera*, *Phillyrea* and *Pistacia* start to appear regularly from ca. 10,500 cal BP (8550 cal BC) onwards, indicating the presence of these Mediterranean woody taxa in the catchment. From ca. 8,900 cal BP (6950 cal BC) some small changes in the pollen assemblage are visible, with first an increase of *Abies* pollen from 3 to 7%. Then, at ca. 8,200 cal BP (6250 cal BC), *Quercus frainetto* type pollen percentages decrease, whereas *Pinus*, *Abies* and *Ulmus* show a small increase. The first cereal pollen (*Triticum* type) appears around 8,500 cal BP (GAM range 8,770–8,385 cal BP; 6820–6435 cal BC) together with minor increases in *Galium* type and Chenopodiaceae, during a phase with rather dense forests. Although the Land Use Probability index (LUP) remains low this finding might suggest first small-scale agricultural activities close to the lakeshore. Low to very low microscopic charcoal influx (ca. 10,000 particles cm^{-2} yr^{-1}) suggest reduced fire activity.

OHR-4a (8,200–7,500 cal BP, 6250–5550 cal BC): High AP (80–90%) suggests the presence of relatively closed forests. *Quercus frainetto* type pollen continues to decline to ca. 20%, while *Pinus* pollen percentages increase to over 50% at ca. 7,600 cal BP (5650 cal BC). Increasing or elevated *Abies*, *Tilia*, *Carpinus betulus*, *Corylus* and *Ostrya* type values indicate a slight change in the forest composition. Poaceae percentages are at their lowest level, suggesting that grasslands were rare. Charcoal concentrations and influx values are very low (ca. 3,000 particles cm^{-2} yr^{-1}) indicating that fire activity continued to be low during this period.

OHR-4b (7,500–7,300 cal BP, 5550–5350 cal BC): Pollen percentages of *Pinus* decrease, whereas most other tree taxa remain stable, suggesting a reduction of pine stands. *Fagus* is now continuously represented in the pollen spectrum (empirical limit reached at ca. 7,500 cal BP, 5550 cal BC; Ammann et al. 2013), indicating that the tree established first stands in proximity to the site. *Abies*, *Ulmus* and *Tilia* pollen percentages show a minor decrease in this subzone. This period is characterised by the onset of a steady increase of herb pollen (from 10 to 30%), indicating a marked opening of the forest. In the new open lands, herbs such as *Artemisia* and Cichorioideae were important. The occurrence of cereal pollen (particularly of *Triticum* type) and *Polygonum aviculare* type pollen (a ruderal plant) as well as a clear increase in LUP (Fig. 5) suggest agricultural activities in the area, a finding which is underscored by the occurrence of *Plantago lanceolata* type and a pollen grain of *Linum usitatissimum* type. Microscopic charcoal concentrations and influx values show a peak around 7,300 cal BP (5350 cal BC), indicating slightly increased fire activity. The decline in fire-sensitive trees (*Abies*, *Ulmus* and later *Tilia*) may indicate a response to increased fire disturbance.

OHR-5 (7,300–6,100 cal BP, 5350–4150 cal BC): This zone is characterised by remarkable strong fluctuations of

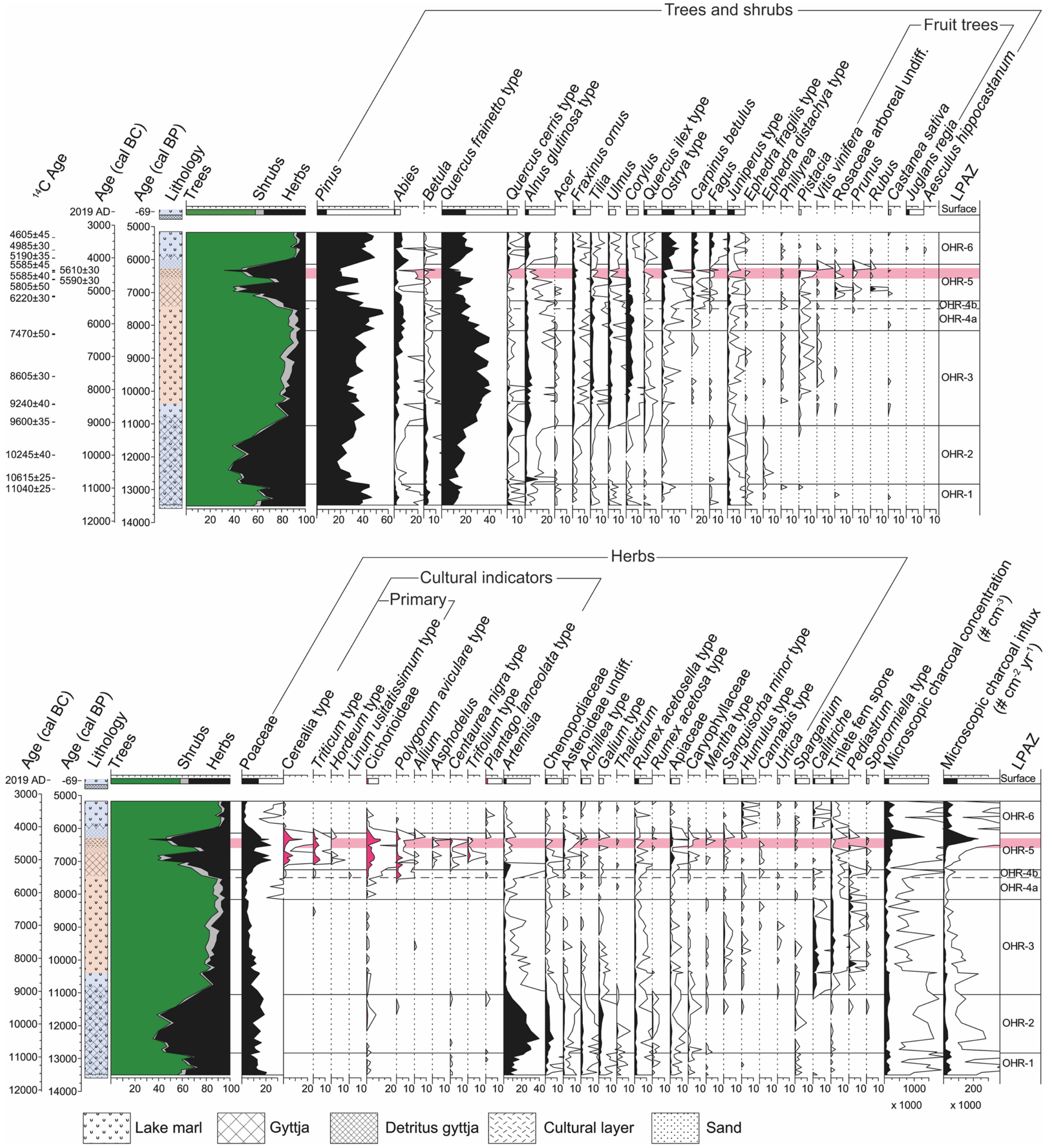


Fig. 3 Selected pollen and spore percentages of the Lake Ohrid record based on the terrestrial pollen sum, together with the radiocarbon dates, lithology (blue sediments correspond to the Ohrid plateau core, red sediments to the Ohrid settlement core), microscopic charcoal influx and concentration values. Empty curves show 10×exaggeration. LPAZ correspond with statistically significant pollen zones. The pink horizontal shading corresponds to the excavated Neolithic settlement (Hafner et al. 2021). Cultural indicators are based on Behre (1981) and Deza-Araujo et al. (2020)

AP values ranging from 40 to 70%, indicating two distinct forest openings. At the onset of the zone, AP values decline rapidly to 50%, mainly driven by those of *Pinus*¸ *Q. frainetto* type, *Abies*, *Tilia* and *Ulmus*, indicating a forest disruption and a reduction of these forest taxa. After ca. 500 years at 6,800 cal BP (4850 cal BC), tree pollen percentages increase

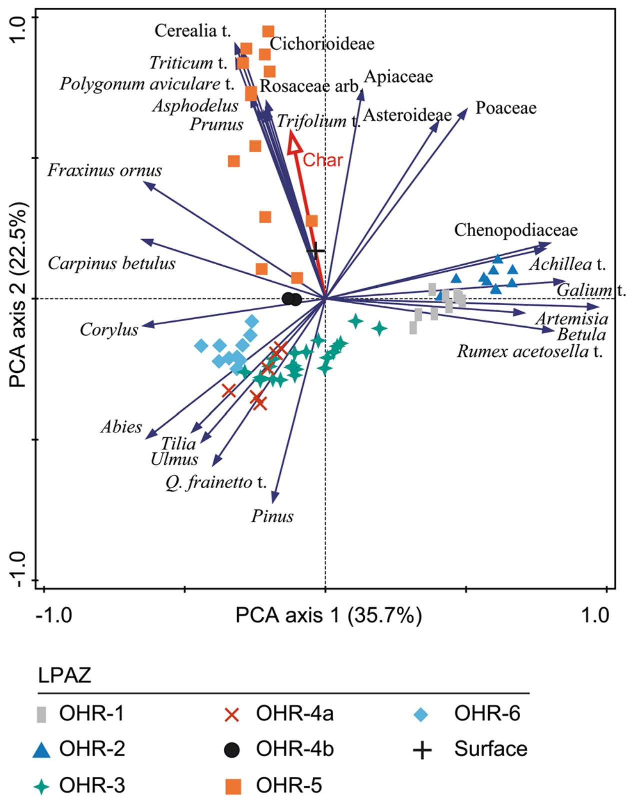


Fig. 4 Principal component analysis (PCA) triplot with species (blue arrows) and samples scores (symbols, classified according to LPAZ) of the Lake Ohrid record. Charcoal influx is a supplementary explanatory variable and was projected onto the ordination (red arrow). The surface sample was added as a supplementary case. The first axis explains 35.7% of the variance in the pollen composition, and the second axis 22.5%

again quickly from < 50% to ca. 70% and the forest partly recovered for about 200 years. The pollen data suggest that late-successional *Abies*, *Tilia* and *Ulmus* were able to recover during this time. The second forest opening phase started at ca. 6,600 cal BP (4650 cal BC) as indicated by rapidly declining AP values (40–50%) and the same forest taxa as during the first opening phase were affected. This phase lasted ca. 400 years and finished when towards the end of this zone at ca. 6,200 cal BP (4250 cal BC) AP values start to increase again.

The increases in NAP during the two opening phases are mainly driven by Poaceae pollen and cultural indicators like Cerealia type (*Triticum* type and *Hordeum* type), indicating agricultural activities at this time. This is supported by the LUP index, which reaches very high values (Fig. 5). During the first open phase, Cerealia type pollen reaches 10% and during the second open phase even 15%. *Hordeum* type pollen appear less frequent than *Triticum* type and mainly in the first half of this zone, suggesting that wheat was more extensively cultivated than barley. Interestingly, a peak in *Rubus* pollen percentages alongside *Rubus* seed findings (Fig. 5) suggests that people could have favoured the expansion of raspberries or brambles. From 6,800 to 6,600 cal BP (4850–4650 cal BC) Poaceae pollen and cultural indicators declined substantially, suggesting a short period of reduced local land-use activities.

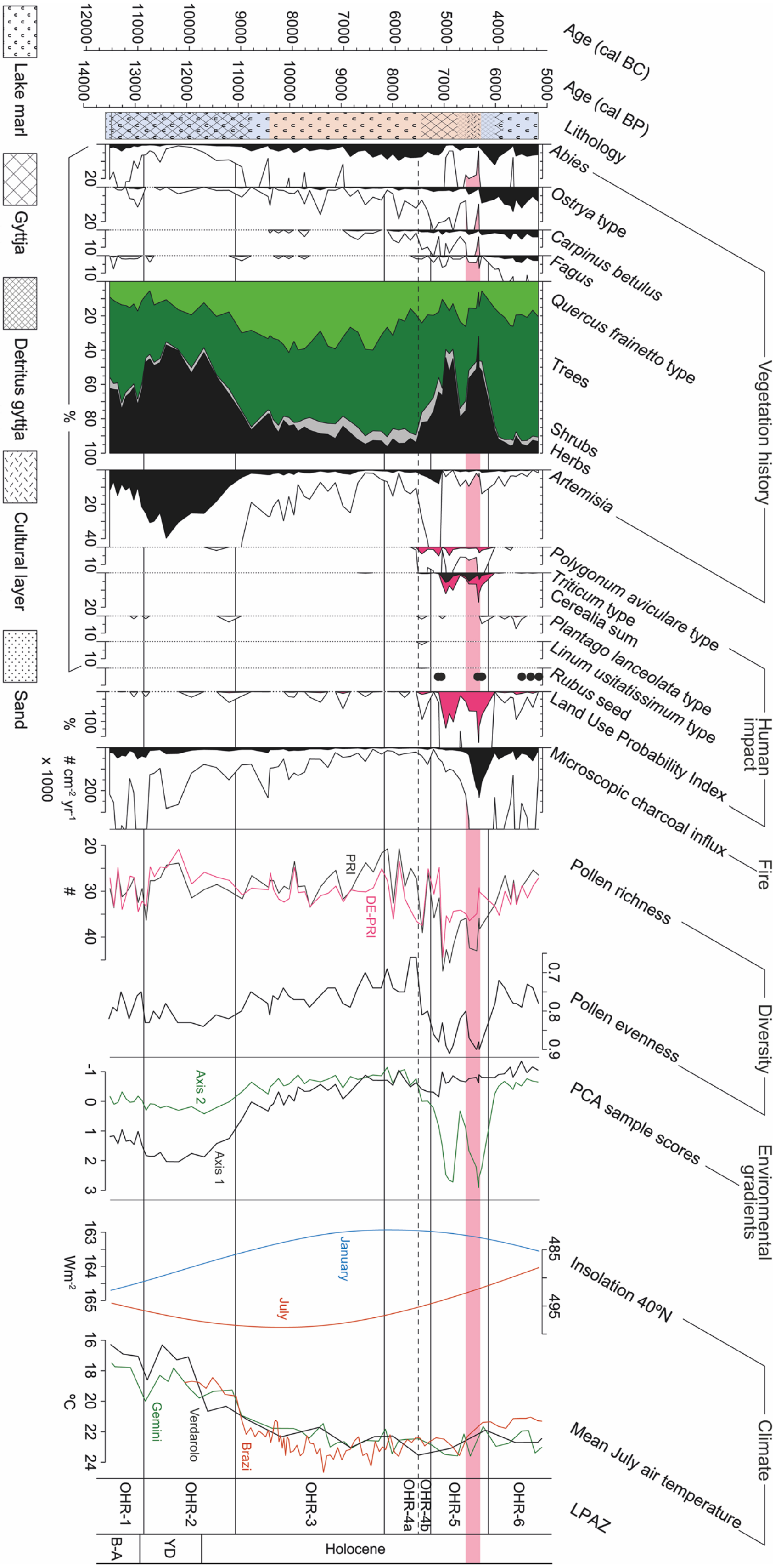
Charcoal concentration values rise to high levels (ca. 250,000–320,000 particles cm^{-3}) after 7,000 cal BP (5050 cal BC) and during the second opening phase, charcoal influx values increase enormously (ca. 180,000–230,000 particles cm^{-2} yr^{-1}), suggesting a strong increase of fire activity. As these samples were taken from the cultural layer (Figs. 2, 3), however, it is likely that charcoal from the settlement is overrepresented in the sediments.

OHR-6 (6,100–5,200 cal BP, 4150–3250 cal BC): At the start of the zone, AP values are rapidly increasing to 80–90%, suggesting a return to dense forest conditions. Pollen percentages of *Pinus* reach over 40% and *Abies* pollen is at its highest level (ca. 5–10%), except for a short phase of lower percentages around 5,700 cal BP (3750 cal BC). The percentages of *Q. frainetto* type pollen decline slightly but stay well represented in the pollen samples. The tree pollen percentages show a strong increase in deciduous broadleaved *Ostrya* type and *Carpinus betulus* suggesting that these taxa spread in the forests together with *Fagus* (1–5%). Altogether, the dominant forest trees were *Abies*, *Quercus*, *Ostrya* (inc. *Carpinus orientalis*) and *Pinus*. Around 5,700 cal BP (3750 cal BC), we found single grains of *Aesculus hippocastanum* pollen in two consecutive samples. Furthermore, the regular presence of cultural indicator pollen like Cerealia type, *Urtica* and *Plantago lanceolata* type indicate farming activities in the area. Maxima in charcoal influx and concentrations suggest high regional fire activity. Interestingly, these fire events are accompanied by small Cerealia type peaks and declines of AP, suggesting a link between agriculture, deforestation and fire incidence.

Surface sample

The surface sample likely reflects present day conditions (Fig. 3). It contains ca. 65% AP, with pollen of *Quercus frainetto* type (20%), *Ostrya* type (10%), *Fagus* (5%), *Alnus glutinosa* type (3%) and *Juglans* (3%). *Pinus* is less abundant when compared to the rest of the Holocene (ca. 8%), as is *Ulmus* (1%) and particularly *Abies* (< 1%), while *Q. ilex* type and *F. ornus* values are slightly higher (2–5%, 2% respectively). Overall, the data suggest a diverse tree composition reflecting modern forest vegetation. Pollen percentage values of shrubs and herbs such as *Juniperus* type (ca. 6%), Poaceae (14%), *Rumex acetosella* type (3.5%) and *Artemisia* (3%) suggest that these taxa dominate in the more open parts of the vegetation.

Fig. 5 Comparison diagram of the vegetation and fire history of Lake Ohrid with different climatic proxies and the lithology (blue sediments correspond to core Ohrid plateau, red sediments to Ohrid settlement). Vegetation history: pollen percentages of selected taxa (10 × exaggeration); Human impact: pollen percentages of selected taxa (10 × exaggeration), presence of *Rubus* seeds, Land Use Probability Index (10 × exaggeration); Fire: microscopic charcoal influx; Diversity: pollen richness index (PRI), detrended palynological richness (DE-PRI) and pollen evenness (PIE) as proxies for species richness and diversity; Environmental gradients: sample scores of PCA axis 1 and axis 2; Climate: July and January insolation at 40°N (Laskar et al. 2004) and chironomid-based July air temperature reconstructions from Lago Gemini, Lago Verdarolo (Samartin et al. 2017) and Lake Brazi (Tóth et al. 2015), the temperatures were transformed to sea level (0.6 °C/100 m); LPAZ: local pollen assemblage zones. The pink horizontal shading corresponds to the excavated Neolithic settlement (Hafner et al. 2021). To the right of the diagram different climatic periods are indicated: the Bølling–Allerød interstadial (B-A), the Younger Dryas cold period (YD) and the Holocene



Numerical analyses

Ordination analyses

The biplot of the PCA (Fig. 4) shows the samples grouped by their LPAZs. Axis 1 explains 35.7% of the variance and shows a gradient from cold and/or drought adapted taxa (e.g. Chenopodiaceae, *Achillea* type) to more temperate and mesophilous taxa (e.g. *Abies*, *Fraxinus ornus* and *Ulmus*). The sample scores of axis 1 plotted against time (Fig. 5) closely follow the NAP and AP curves until the start of zone OHR-4b, when human activity started. The sample scores of axis 1 also show trends similar to the chironomid-inferred summer temperature reconstructions for northern-central Italy and the Carpathians (Fig. 5), suggesting that climate was an important driver of vegetation in the Lake Ohrid record. Axis 2 explains 22.5% of the variance and shows a gradient from forested vegetation to open herbaceous vegetation. The PCA biplot (Fig. 4) shows that cultural indicators are a major driver behind this gradient. The sample scores of axis 2 plotted against time (Fig. 5) closely follow the human-induced forest opening during zone OHR-5 and the increase in cultural indicators, also suggesting human impact as the second main driver of change.

Diversity proxies

Pollen richness (PRI; Fig. 5) is high at the start of our record from 13,500 to 12,800 cal BP (11550–10850 cal BC) with an average of ca. 30–32 taxa. Interestingly, PRI peaks around 12,800–12,600 cal BP (10850–10650 cal BC), at the Bølling/Younger Dryas (YD) transition. During the YD cooling, around 12,400 cal BP (10450 cal BC), PRI reaches low values (25) suggesting major plant diversity declines in response to cold and dry conditions. After 12,000 cal BP (10050 cal BC), richness increases again (ca. 30), while the vegetation was still quite open, suggesting the persistence of a diverse steppe vegetation. PRI does not significantly increase at the onset of the Holocene but stays constant until 6,400 cal BP (4450 cal BP). After this time, PRI starts to increase with strong fluctuations that generally correspond well to the increasingly human-caused openness of the vegetation.

In agreement, two peaks in PRI, at 7,000 cal BP (5050 cal BC) and 6,600 cal BP (4650 cal BC) coincide with increasing percentages of herb pollen and are likely caused by increasing agricultural activities and deforestation. After 6,000 cal BP (4050 cal BC), PRI values generally decline, when forest cover is high.

Pollen evenness (PIE, Fig. 5) shows strong fluctuations during the Late Glacial, reflecting the dynamics in AP. PIE then peaks at the end of the YD open phase and decreases again when the forest closes, suggesting rather uneven conditions during the early Holocene. PIE (0.7–0.8) points to even conditions during the forested period, however it reaches a minimum at 7,500 cal BP (5550 cal BC), when *Pinus* pollen dominates the assemblage (Fig. 3). Subsequently, pollen evenness generally increases (> 0.8) in relation to the decline of *Pinus* and the opening of vegetation in response to anthropogenic disturbance.

PRI and DE-PRI curves are similar for the first half of the record until about 7,700 cal BP (5750 cal BC), indicating that palynological richness was not strongly influenced by palynological unevenness (Colombaroli and Tinner 2013). From 7,700 to 7,500 cal BP (5750–5550 cal BC) the two curves diverge, when *Pinus* dominates the record, confirming that rather uneven pollen assemblages may have lowered PRI estimations of plant diversity (Colombaroli and Tinner 2013; Senn et al. 2022). Conversely, PRI seems to accurately reflect plant diversity after 7,400 cal BP (5450 cal BC), likely due to the even conditions during this time. The observed differences between PRI and DE-PRI suggest that pollen evenness had a substantial effect on species diversity estimations between ca. 7,700–6,200 cal BP (5750–4250 cal BC), when agricultural activities became increasingly important.

Discussion

Climate-driven vegetation changes

Climate is generally regarded as an important driver of vegetation change (Ammann et al. 2000; Tinner and Lotter 2001). At the start of our record, between 13,500 and 12,800 cal BP (11550–10850 cal BC, Fig. 5), open forest vegetation thrived around Lake Ohrid, however these ages must be taken with caution as they are based on extrapolation. This period would correspond to the Bølling-Allerød interstadial (~ 14,700–12,800 cal BP, 12750–10850 cal BC; Fig. 5), a period when summer temperatures were only about 4 °C colder in northern-central Italy than today (Samartin et al. 2017). However, winters were still rather cold (Vogel et al. 2010a), which may have impeded further forest development. The availability of woody biomass (Lawson et al. 2013) and dry climatic conditions (Zhang et al. 2014) may explain the relatively high fire dynamics around 13,300 and 12,600 cal BP (11350 and 10650 cal BC; Figs. 3, 5).

During the subsequent Younger Dryas cold period (YD; 12,800–11,700 cal BP, 10850–9750 cal BC), cool and dry conditions prevailed in the north-eastern Mediterranean region (e.g. Bar-Matthews et al. 1999; Aufgebauer et al. 2012; Zhang et al. 2014). Sea surface temperature reconstructions from the Adriatic sea (Sicre et al. 2013) and chironomid-based summer temperature reconstructions from central/northern Italy (Samartin et al. 2017) show a decrease in temperatures during the period. Although summer temperatures in the southern Carpathians were almost as low as in Italy (ca. −3 °C as compared to the Holocene) no significant decrease occurred during the YD in comparison to the Bølling–Allerød interstadial (Tóth et al. 2012). Interestingly, steppe vegetation expanded, but the treeline ecotone did not lower (Magyari et al. 2012), suggesting moisture availability played an important role. In agreement, a diatom record from Lake Prespa (Fig. 1) indicates lower lake levels during the YD (Cvetkoska et al. 2014). These climatic conditions likely led to the retreat of trees and enabled the spread of herbs such as *Artemisia* and Chenopodiaceae around Lake Ohrid (Figs. 3, 5). However, climatic conditions at Lake Ohrid are quite complicated during this period and are not always in accordance with other palaeoclimatic records (Vogel et al. 2010a). The basin's north–south orientation exposes the area to cold polar air masses, which could lead to cooler regional winters (Vogel et al. 2010a), whereas the lake's water mass could buffer large temperature changes (Popovska and Bonacci 2007).

The observed vegetation opening at Lake Ohrid is a general pattern for the region and is comparable to sites in northern Greece (Glais et al. 2016; Gassner et al. 2020). For example, former Lake Maliq (Fig. 1; Denèfle et al. 2000) shows a coeval YD opening at about 12,700 cal BP (10750 cal BC), whereas at Lake Prespa (Fig. 1) the vegetation may have opened already before 13,000 cal BP (11050 cal BC; Panagiotopoulos et al. 2013). However, the chronology of Lake Prespa relies mostly on radiocarbon dates of bulk organic sediment, which are likely to result in dates that are too old in such a hard water environment (Last and Smol 2002; Panagiotopoulos et al. 2013). Interestingly, the former Lake Maliq record suggests a short-lived warming event within the YD cooling between 12,200 and 11,900 cal BP (10250–9950 cal BC), when tree stands increased (Denèfle et al. 2000; Bordon et al. 2009). This short-lived increase in tree stands can also be observed at Lakes Ohrid and Prespa (Panagiotopoulos et al. 2013), and the transient warming at ca. 12,000 cal BP (10050 cal BC) can also be found in the Lake Ohrid climate reconstruction of Lacey et al. (2015).

The shift from the open boreal and steppic vegetation characteristic of the YD towards the temperate forests of the Holocene (Fig. 5) was the result of increasing temperatures (Tóth et al. 2012; Sicre et al. 2013; Samartin et al. 2017). Other palaeoecological records from the area show similar vegetation changes to Lake Ohrid at the start of the Holocene. For example, at Lake Prespa the establishment of closed *Quercus* forests with *Tilia*, *Fraxinus*, *Ulmus* and *Fagus* followed the initial spread of the pioneer *Betula* (Panagiotopoulos et al. 2013). The vegetation reconstruction from former Lake Maliq also shows a succession with *Betula*, *Pinus* and deciduous *Quercus* (Denèfle et al. 2000; Bordon et al. 2009). However, differences in Holocene afforestation are present between Lake Ohrid and Limni Zazari in northern Greece (Fig. 1; Gassner et al. 2020). While forests at both sites started to close around the same time (ca. 11,500 cal BP, 9550 cal BC), this process lasted ca. 1,000 years longer at Limni Zazari (Gassner et al. 2020). Dense forests (AP > 80%) occurred after 10,800 cal BP (8850 cal BC) at Lake Ohrid, but only after 9,700 cal BP (7750 cal BC) at Limni Zazari. Delayed forest expansion, as in the case of Limni Zazari, might be the result of very dry early Holocene conditions (Kotthoff et al. 2008; Tinner et al. 2009), which could imply that compared to other regions the geographic and hydrological properties of Lake Ohrid enhanced regional moisture availability. This assumption is supported by various studies suggesting a wetter early Holocene at Lake Ohrid (Vogel et al. 2010a; Lacey et al. 2015). The large water body may have led to increased evaporation, while the mountain ranges may have augmented orographic precipitation.

After 10,500 cal BP (8550 cal BC), forests remained closed, but their composition varied (Fig. 3). Most likely, the generally warm and dry conditions during the early Holocene (Wagner et al. 2009; Lacey et al. 2015) caused the dominance of pine and oak forests (Lawson et al. 2005) together with other temperate trees like *Tilia* and *Abies*. Fir became more important in the vegetation after 9,000 cal BP (7050 cal BC), which might have been the result of higher moisture availability (Tinner and Lotter 2006; Panagiotopoulos et al. 2013). Pollen data from Lake Ohrid and other sites such as Lake Prespa or further to the east Lake Trilistnika (Rila mountains, Bulgaria) suggest that *Fagus* expanded rather late in the region, after the onset of the mid Holocene ca. 8,200 years ago (Tonkov et al. 2008; Panagiotopoulos et al. 2013). Today, *Fagus sylvatica* grows in the cool-temperate montane elevation belt of the Galičica Mountains (Matevski et al. 2011) and is represented in the surface sample by high percentages (5%). Taking the dispersal limitations and the current location of beech forests in the Lake Ohrid region into account, it is possible that beech stands were present in the wider region during the early Holocene, but not recorded in the pollen record. The absence of pollen evidence for *Fagus* is confined to the period between ca. 9,600–7,600 cal BP (7650–5650 cal BC) and a similar pattern occurs in the pollen record of Limni Zazari (Gassner et al. 2020), where *F. sylvatica* is absent from ca. 10,700–6,000 cal BP (8750–4050 cal BC) i.e. during the Holocene Thermal Maximum. During this period the species may have suffered from late frost and/or summer drought; in addition land use may have facilitated its late Holocene expansion (Gassner et al. 2020).

Human-induced vegetation changes at the onset of the Neolithic

Indications for the first agricultural activities in the Lake Prespa and Lake Ohrid region have been postulated for the middle of the ninth millennium cal BP (ca. 6400 cal BC), based on (unfortunately preliminarily and incompletely published) radiocarbon dated charcoal fragments from the archaeological site of Vastëmi near former Lake Maliq (Allen and Gjipali 2014). However, a single wooden construction element found at the lakeshore site of Penelopa, Ohridati (ca. 13 km north of Ploča Mičov Grad) confirms that Neolithic settlements were present on the shores of Lake Ohrid at the latest around 7,570–7,330 cal BP (5620–5380 cal BC; Westphal et al. 2010). The archaeological remains from the Neolithic occupation of Ploča Mičov Grad can be attributed to ca. 6,550–6,250 cal BP (4600–4300 cal BC), based on dendrochronology and radiocarbon dating (Hafner et al. 2021; Bolliger et al. 2023). The earliest Neolithic settlements further south, in northern Greece, are dated to ca. 8,450 cal BP (6500 cal BC; Lespez et al. 2013; Chrysostomou et al. 2015). Also pollen data suggest early Neolithic land use in this region, with the first indications for agricultural activities at Tenaghi-Phillipon starting ca. 8,450 cal BP (6500 cal BC; Glais et al. 2016) and at Limni Zazari ca. 8,200 cal BP (6250 cal BC; Gassner et al. 2020). Towards the east in the Struma Valley, an early Neolithic settlement has been dated to ca. 8,200 cal BP (6250 cal BC; Higham et al. 2011; Grębska-Kulow and Zidarov 2021) and in the region of Bulgarian Thrace, at approximately the same latitude as Lake Ohrid, an age of 8,000 cal BP (6050 cal BC) has been proposed for the first Neolithic settlements (Boyadzhiev 2009).

The appearance of the first Cerealia type pollen around ca. 8,500 cal BP (6550 cal BC) may indicate early cereal cultivation at Ploča Mičov Grad, but due to the absence of other unequivocal cultural indicators (Fig. 3) this interpretation remains ambiguous. Unambiguous palaeoecological evidence of agricultural activities at Ploča Mičov Grad dates to 7,500 cal BP (5550 cal BC; Figs. 3, 5), falling within the time range for the onset of agricultural activities in the closer Ohrid area. Interestingly, our results indicate clear farming activities nearly 1,000 years prior to the up to now proven archaeologically-inferred local settlement phase at Ploča Mičov Grad (Naumov et al. 2018; Hafner et al. 2021; Bolliger et al. 2023). The pollen signal is unambiguous, with abundant pollen of cereals (including *Triticum* type), the disturbance indicator *Polygonum aviculare* type (Strid 1980; Behre 1981), *Rubus* fruit bushes and high LUP values (Fig. 5). Cerealia type pollen does not disperse far and is a primary indicator for local agriculture, specifically if taxonomically resolved to subtypes such as *Triticum* type (Behre 1981; Behre and Kucan 1986; Vescovi et al. 2018). We can only speculate about the location of these early agricultural activities, however, given the very strong pollen signal, they must have been close (within ca. 200–300 m) to the coring site. Indeed, the archaeological investigations to date only consist of a small trench in the centre of the large-scale settlement area (Fig. 1). Therefore it cannot be excluded that older settlement phases may still be discovered.

Significant Neolithic forest declines as observed at Ploča Mičov Grad are generally missing from sites in Northern Greece. At Lake Prespa (Panagiotopoulos et al. 2013), forests started to decline only after 2,000 cal BP (50 cal BC) and at Limni Zazari around 3,000 cal BP (1050 BC; Gassner et al. 2020). Also the Lake Ohrid off-site record by Wagner et al. (2009), situated ca. 6 km further south from our site, does not register the Neolithic phase at Ploča Mičov Grad and only shows a first forest disruption after 2,500 cal BP (550 cal BC), ca. 3,000 years later than at our site. The difference between the two Lake Ohrid records, underscores that the human impact at Ploča Mičov Grad was local. Neolithic arable fields were likely relatively small-scale (Bogaard et al. 2013; Marinova and Ntinou 2018) and are difficult to detect in palynological off-site records. However, as our record is very close to the settlement and the temporal resolution is much higher than in standard palynological records, we were able to detect the Neolithic land use signal. This finding highlights the importance of site selection, pollen-source area and temporal resolution when designing studies for pollen-based human impact reconstructions with the aim of disentangling local and regional effects on vegetation.

The gradual forest decline in response to anthropogenic disturbance that starts at Ploča Mičov Grad at about 7,500 cal BP (5550 BC; Fig. 3) can also be found at Lake Orestiás (Fig. 1; Kouli and Dermitzakis 2008), although in contrast to Lake Orestiás (Kouli and Dermitzakis 2008), the deforestation at Ploča Mičov Grad starts with *Pinus* and *Ulmus*, while other established taxa remain relatively stable. Interestingly, at our site *Carpinus* increased with the forest opening, most likely due to increased forest disturbance and light availability (Gobet et al. 2000). While *Tilia* and *Ulmus* had already declined at ca. 7,100 cal BP (5150 BC), *Abies* only followed another 100–300 years later. Given that declines of disturbance-sensitive trees such as *Tilia*, *Ulmus* and *Abies* in response to land use are common in the area and elsewhere in Europe (e.g. Kouli and Dermitzakis 2008; Panagiotopoulos et al. 2013; Tinner et al. 2013; Gassner et al. 2020; Morales-Molino et al. 2021), we assume that the impacts of the settlement (fire, browsing and logging) before ca. 7,000–6,800 cal BP (5050–4850 cal BC) were local and extended to the areas where these species were growing. We therefore assume that at that time *Abies* was not restricted to higher altitudes.

After 6,800 cal BP (GAM range 7,030–6,530 cal BP; 5080–4580 cal BC), forests recovered and agricultural activities were strongly reduced, coinciding with a change in lake sediments (Fig. 3), which was likely due to a shift of the settlement and local land abandonment. In response to this land abandonment phase at Ploča Mičov Grad, pine, oak, fir, linden and elm stands were able to recover (Fig. 3). For about two centuries the vegetation was again comparable to that of the mid Holocene prior to 7,500 cal BP (5550 cal BC) with no or insignificant farming. Similar Neolithic vegetation dynamics occurred at Lake Orestiás, where forests recovered quickly after land abandonment (Kouli and Dermitzakis 2008). In addition to the forest recovery at Ploča Mičov Grad, woody taxa that had probably been favoured by humans, like *Ostrya* type, *Prunus* and *Rubus* were again outcompeted and disappeared (Fig. 3). However, during the transient land abandonment phase at Ploča Mičov Grad, the cultural indicators did not disappear entirely, emphasising that land abandonment involved only a partial shift of the fields and settlement. In agreement, Lake Orestiás also shows several phases of intensified and slightly changing human activities, as well as land abandonment with forest recovery and continuing cultural indicators, suggesting that humans stayed in the area (Kouli and Dermitzakis 2008). Habitation continuity between settlement phases during which forests recovered but agricultural fields remained in the pollen catchment is not uncommon during the Neolithic (Gobet et al. 2017).

Around 6,500 cal BP (GAM range 6,290–6,730 cal BP; 4340–4780 cal BC), a second phase of even more intensive land use began. This phase coincided with an intensification of local farming activities as evidenced by the cultural layer found in the sediments, consisting of shards of pottery, wooden architectural remains, animal bones and charcoal pieces (Fig. 2), as well as high amounts of Cerealia type pollen (up to ca. 15%; Fig. 5). The presence of a cultural layer shows that the land use signal directly originated from the settlement. Nevertheless, the general vegetation dynamics related to land use were very similar to those observed in the earlier settlement phase at ca. 7,500–6,800 cal BP (5550–4850 cal BC). This phase lasted about 400 years, after which forest conditions rapidly returned. However, the forest composition had changed (Fig. 3). We attribute the mass expansion of disturbance-adapted *Ostrya* type (likely *O. carpinifolia* with some *Carpinus orientalis*) primarily to human impact. Both species are very efficient light-loving re-sprouters and may have benefitted from fire, browsing and cutting disturbance (Horvat et al. 1974; Pasta et al. 2016; Sikkema and Caudullo 2016). Similarly, disturbance-tolerant *Fagus* and *Carpinus betulus* may have benefitted from the long-lasting human disturbance.

With the first intense local land use phase starting at ca. 7,500 cal BP (5550 cal BC), taxa such as *Triticum* type (wheat), *Hordeum* type (barley), *Polygonum aviculare* type, *Centaurea nigra* type and later *Trifolium* type (Figs. 3, 5) started to increase, which is characteristic of arable farming (Behre 1981). A strong preference for wheat over barley is a common pattern present in southern Bulgaria for the first half of the early Neolithic, where 3–6 times more *Triticum* grains than *Hordeum* were found in several Neolithic settlements (Marinova 2006). Barley became more important during the second half of the early Neolithic (7,600–5,600 cal BP; 5650–3650 cal BC) and there are indications that its presence is connected to the influence of other cultures from the western Balkans (Marinova 2006). In Thessaly and north-eastern Bulgaria barley was already an important crop during the early Neolithic, as the frequent finds of *Hordeum* grains show (Marinova and Krauß 2014; Kreuz and Marinova 2017). In our record, barley (*Hordeum*) fields were already established during the first land opening phase at Ploča Mičov Grad and were apparently mostly abandoned during the later phase.

At Limni Zazari in Northern Greece, Neolithic farmers used fire to create open land for agricultural activities (Gassner et al. 2020). Fire activity at Ploča Mičov Grad increased to reach moderate levels during the first settlement phase at ca. 7,500–6,800 cal BP (5550–4850 cal BC; Fig. 5), suggesting that slash-and-burn activities played a certain role during the first land use phase. Likely, fires were used to create small permanent plots for crop cultivation and to promote the growth of edible shrubs (e.g. *Prunus*, *Rubus*; Bogaard et al. 2013; Baum et al. 2020). We assume that during the second opening phase at ca. 6,500–6,300 cal BP (4550–4350 cal BC) local fires (as evidenced by high amounts of macroscopic charcoal, data not shown) led to an overrepresentation of microscopic charcoal and may not necessarily represent regional fire activity. Quite possibly logging of *Pinus* was more important during the first settlement phase, as only *Pinus* pollen percentages significantly decrease during the first opening. However, so far, the construction timbers excavated from Ploča Mičov Grad date only to the second settlement phase and mainly consist of *Quercus* and *Pinus* (most likely *P. nigra*) with a small number of *Juniperus* (Naumov et al. 2018, 2019; Hafner et al. 2021; Bolliger et al. 2023). Furthermore, in the Balkan region wood of *Quercus* was primarily used during the Neolithic, likely reflecting its relevance in the vegetation around the settlements (Moskal-del Hoyo 2013; Marinova and Ntinou 2018).

The creation of open lands provided opportunities for uncultivated herbs and weeds (i.e. adventives and apophytes), such as Cichorioideae, Caryophyllaceae and *Artemisia*, to expand in the pastures and on disturbed ground. *Rubus* shrubs might have been favoured by humans, as *Rubus* greatly benefits from disturbance. Indeed its presence (pollen and seeds, Figs. 3, 5) occurred quite suddenly and relatively prominently in our record; the berries were a popular food source as observed in other on-site studies (e.g. Valamoti 2015). The occurrence of the *Linum usitatissimum* type pollen is particularly interesting. The plant does not belong to high pollen producers, is a poor disperser (Behre 1981) and already single grains might indicate the cultivation of flax (Gobet et al. 2017). However, even if unlikely in this context, it is possible that other plants such as *Linum bienne* producing the same pollen type were native to the Lake Ohrid area, as wild flax had a wide native distribution range, including the Mediterranean Basin (Weiss and Zohary 2011). Whether cultivated or gathered, flax was a known source of fibre and oil (Marinova 2006; Weiss and Zohary 2011).

Diversity and resilience of forests

More open vegetation may cause a more even distribution of different pollen types (Giesecke et al. 2014) and thus more diverse conditions. While this assumption is consistent with the human induced openings it is contradicted by the decreasing diversity trends in the Younger Dryas (YD) period, when pollen richness (PRI, Fig. 5) declined despite the high evenness (PIE, Fig. 5). A plausible explanation for this discrepancy is the introduction of adventive and cultural plants during the Neolithic. Furthermore, increasing slash-and-burn activities may have promoted plant diversity, as the PRI and the PCA together (Figs. 4, 5) suggest that anthropogenic fires and agriculture led to increased biodiversity. Because increased fire disturbance creates a patchwork of many different vegetation communities, it can augment biodiversity, at least up to a certain level and depending on the vegetation type (Colombaroli and Tinner 2013; Pausas and Ribeiro 2017).

Forest structure and composition recovered within ca. 100–200 years after the land abandonment phase around 6,800 cal BP (4850 cal BC), although some herbs previously not present in the record (e.g. *Trifolium, Asphodelus*) remained. The quick recovery of these forests shows how resilient they were to disturbance; it has been shown at other sites that diverse Mediterranean forests are rather resilient to early human impact, fire and browsing (Colombaroli and Tinner 2013; Tinner et al. 2013, 2016). As the composition of the re-established forest was very similar to the pre-settlement forest we do assume that climate and biotic interactions remained an underlying and very important driver of vegetation dynamics (Tinner et al. 2016). Interestingly, after the second land-use phase, the forest recovered again very quickly within ca. 250 years, but now *Pinus*, *Abies*, *Ostrya* type, *Quercus* and *Fagus* became co-dominant, whereas *Tilia* and *Ulmus* were not able to fully recover. Despite these compositional changes the PCA sample scores were still similar to the early Holocene sample scores (Figs. 4, 5) and biodiversity remained comparable, as shown by similar PRI, DE-PRI and PIE values (Fig. 5).

Conclusions

Our record is the first vegetation and fire reconstruction made along an archaeological on-site/off-site gradient at Lake Ohrid. The data provide new insights into the Late Glacial and Holocene vegetation dynamics with an emphasis on human impact during the Neolithisation of Southeastern Europe. Our data show that about 7,500 years ago, arable and pastoral farming intensified in the Ploča Mičov Grad area, a millennium before the earliest dendrochronological and radiocarbon dates from the site Ploča Mičov Grad. There are indications for earlier farming, but this evidence remains ambiguous. It is crucial, however, to keep in mind that only a small section of the settlement has been studied so far and it may not represent the entire settlement period on site. Nevertheless, this finding highlights the importance of palaeoecological studies and the value of palynological studies for archaeological purposes and human impact reconstructions. Specifically, palaeoecology can shed more light on cultivation preferences and the environmental conditions at the beginning of agriculture in Europe. Hence, palaeoecological studies complement archaeology in terms of recognising the continuity and nature of past human activities. The combination of archaeological and palaeoecological methods is currently the most promising approach for clarifying settlement and environmental history over long periods of time, spanning centuries or millennia. Furthermore, our results show that early anthropogenic activities did not significantly alter the forest composition immediately, but rather that forests were very resilient to disturbance. Forest vegetation composition only started to change more than a millennium after the first deforestation activities. Further high-resolution multiproxy studies could contribute significantly to our understanding of these processes, especially to better disentangling the impacts of human activities and climate. Divergent dynamics of species such as the declines of *Tilia*, *Ulmus* and *Abies* and the expansion of *Fagus* and *Ostrya* suggest that first human impact created legacies that are still important for today's vegetation (Matevski et al. 2011). Further palaeoecological research at Ploča Mičov Grad into the Neolithic and Bronze Age settlement phases (Hafner et al. 2021; Bolliger et al. 2023), but also at other archaeological sites on the shores of Lake Ohrid, could provide more insights into these legacies.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00334-023-00931-3.

Acknowledgements We thank Peter Ruprecht for his great help during the coring campaign, his technical knowledge and practical experience were invaluable. Furthermore, we thank Valentina Todoroska (Struga), Goce Naumov, Center for Prehistoric Research (Skopje) and Bojan Taneski, Institute for Protection of Monuments and Museum Ohrid (Ohrid), all in North Macedonia, for their support on site. Many thanks for the underwater assistance during the coring go to Johannes Reich and Marco Hostettler, Institute of Archaeological Sciences, University of Bern, as well as to the Diving Center Amfora, Ohrid. We are grateful to Edith Vogel, Department of Chemistry, Biochemistry and Pharmaceutical Sciences, University of Bern, for the preparation of the samples for ^{14}C dating. We are thankful to Amy Bogaard, Kostas Kotsakis and the whole ERC EXPLO-team for their archaeobotanical and archaeological insights. Discussions with Giorgia Beffa, Carolina Senn and Christoph Schwörer are gratefully acknowledged.

Author contributions SB: conceptualization, investigation, visualization, writing—original draft; LV: advising, visualization, writing—review and editing, EG: advising, project administration, conceptualization, writing—review and editing, CMM: advising, project administration, conceptualization, writing—review and editing, JV: investigation, writing review and editing, AL: project administration, conceptualization, writing—review and editing, AB: funding acquisition, project administration, conceptualization, writing—review and editing, SOB: project administration, conceptualization, writing—review and editing. SS: radiocarbon dating, writing—review and editing, AH: funding acquisition, project administration, conceptualization, writing—review and editing, WT: supervision, funding acquisition, project administration, conceptualization, writing—review and editing.

Funding Open access funding provided by the University of Bern. Research in 2019 at Ploča Mičov Grad was conducted in the framework of the project 'Exploring the dynamics and causes of prehistoric land use change in the cradle of European farming' (EXPLO). This project was financially supported by the European Union's Horizon 2020 research and innovation programme under the grant agreement No 810586 (project EXPLO).

Declarations

Conflict of interests The Authors declare that there is no conflict of interest.

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