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Pollen-based paleoenvironmental and paleoclimatic change at Lake Ohrid (SE Europe) during the past 500 ka

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Abstract

Lake Ohrid is located at the border between FYROM and Albania and formed during the latest phases of Alpine orogenesis. It is the deepest, the largest and the oldest tectonic lake in Europe. To better understand the paleoclimatic and paleoenvironmental evolution of Lake Ohrid a deep drilling was carried out in 2013 within the framework of the Scientific Collaboration on Past Speciation Conditions (SCOPSCO) project that was funded by the International Continental Drilling Program (ICDP). Preliminary results indicate that lacustrine sedimentation of Lake Ohrid started between 1.2 and 1.9 Ma ago. Here we present new pollen data (selected percentage and concentration taxa/groups) of the uppermost ~ 200 m of the 569 m-long DEEP core drilled in the depocenter of Lake Ohrid. The study is the fruit of a cooperative work carried out in several European palynological laboratories. The age model is based on nine tephra layers and on tuning of biogeochemical proxy data to orbital parameters and to the global benthic isotope stack LR04.

According to the age model the studied sequence covers the last ~ 500 000 years at a millennial-scale resolution (~ 1.6 ka) and record the major vegetation and climate changes that occurred during the last 12 (13 only pro parte) marine isotope stages (MIS). Our results indicate that there is a general good correspondence between forested/non-forested periods and glacial/interglacial cycles of marine isotope stratigraphy. Our record shows a progressive change from cooler and wetter to warmer and dryer interglacial conditions. This shift is visible also in glacial vegetation.

The interglacial phase corresponding to MIS11 (pollen assemblage zone, PAZ OD-12, 488–455 ka BP and OD-19, 367–328 ka BP) is dominated by montane trees such as conifers. The two younger interglacial periods, MIS5 (PAZ OD-3, 126–70 ka BP) and MIS1 (PAZ OD-1, 12 ka BP to present) are marked by dominance of mesophilous elements such as deciduous and semi-deciduous oaks. Moreover, MIS7 (PAZ OD-6, 245–189 ka) shows a very high interglacial variability, with alternating expansions of montane and mesophilous arboreal taxa. Grasslands (open vegetation formations requiring

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relatively humid conditions) characterize the first glacial phases of MIS12 (PAZ OD-12, 488–455 ka), MIS10 (corresponding to PAZ OD-10, 421–367 ka) and MIS8 (PAZ OD-7, 285–245 ka). Steppes (open vegetation formations typical of dry environments) prevail during MIS6 (OD-5 and OD-4, 189–126 ka) and during MIS4–2 (PAZ OD-2, 70–12 ka).

Our palynological results support the notion that Lake Ohrid has been a refugium area for both temperate and montane trees during glacials. Close comparisons with other long southern European and Near Eastern pollen records will be achieved through ongoing high-resolution studies.

1 Introduction

The study of past climate change is pivotal to better understand current climate change (Tzedakis et al., 2009) and its impact on terrestrial ecosystems, particularly in the mid-latitudes, where human activities are concentrated. It is well established that the study of fossil pollen contained in sediments fundamentally contributes to the reconstruction of terrestrial palaeoenvironmental changes that occurred during the Quaternary, and constitutes the only quantitative proxy that can provide continuous and accurate representations of vegetation changes. This fact was already clear at the end of the ’60ies when the pioneer pollen study of Wijmstra (1969) at Tenaghi Philippon (Greece) was published. The study of long lacustrine pollen records from southern Europe are particularly important, as at such latitudes, glaciations have not caused stratigraphic gaps in lacustrine systems unlike northern European sequences (e.g. Zagwijn, 1992). The relationship of terrestrial vegetation with terrestrial, marine and ice core records is a further step in the comprehension of global climate dynamics and lead–lag relations. A broader correspondence between the climate signals provided by terrestrial pollen records and marine oxygen isotope records has been observed (e.g. Tzedakis et al., 1997, 2001). Subsequent studies of both terrestrial (pollen) and marine (planktonic and benthic oxygen isotopes) proxies in marine cores from the Iberian margin confirmed the mostly in phase relation of Mediterranean and North Atlantic climate variability during

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the Late Pleistocene (e.g. Sánchez Goñi et al., 1999; Martrat et al., 2007). But the exact phase relations to marine systems, regional variations in vegetation response, and exact locations of refugia are still poorly known mostly due to the complications of obtaining records in key regions and with independent age control.

Southern Europe encompasses five lacustrine pollen records spanning more than the last two glacial/interglacial cycles. They are the composite record of Bouchet/Praclaux in southern France, spanning the last ∼ 450 ka (Reille et al., 2000); Valle di Castiglione in central Italy, spanning the last ∼ 300 ka (Follieri et al., 1988, 1989); Ioannina in western Greece, spanning the last ∼ 480 ka (Tzedakis, 1994); Kopais, in southeastern Greece spanning the last ∼ 500 ka (Okuda et al., 2001); and Tenaghi Philippon, the ∼ 1.35 million year old European lacustrine record from north-eastern Greece (Tzedakis et al., 2006; Pross et al., 2015). In the Near East long continental sedimentary sequences have been studied in Lake Van (eastern Turkey) spanning the last ∼ 600 ka (Litt et al., 2014), in Lake Urmia (north-western Iran) spanning ∼ 200 ka (Djamali et al., 2008) and in lake Yamounneh (Lebanon) spanning the last ∼ 400 ka (Gasse et al., 2015). However, these sediment cores have not been studied with high temporal resolution, which is a precondition for a deeper understanding of the palaeoenvironmental and palaeoclimatic evolution of terrestrial ecosystems (Brauer et al., 2007; Magny et al., 2013; Moreno et al., 2015).

Southern European long pollen records have caught the attention of many researchers, as these archives are arguably among the best available sources of information for past vegetation and climate changes (e.g. Tzedakis et al., 1997, 2001; Pross et al., 2015). Molecular genetic data revealed considerable divergence between populations of many arboreal species in southern refugial centers in Iberia, Italy, the Balkans, and Greece. Arboreal refugia and migration paths, identified by both biogeographical, palaeobotanical and phylogeographical studies (Petit et al., 2005; Cheddadi et al., 2006; Magri et al., 2006; Médail and Diadema, 2009; Tzedakis, 2009; Tzedakis et al., 2013) sometimes confirmed the speculated locations (e.g. Bennett et al., 1991) and their link to modern biodiversity hotspots but most mechanisms have to be still fully

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understood. Under this perspective it is essential to compare the locations of refugia and those of regional hotspots of plant biodiversity.

Located in a strategic position between higher-latitude and lower-latitude climate systems, Lake Ohrid is at the border between Former Yugoslavian Republic of Macedonia (FYROM) and Albania. As one of the Biosphere Reserves of the United Nations Educational, Scientific, and Cultural Organization (UNESCO) is a transboundary World Heritage site in the Balkans. It is thought to be the oldest extant lake in Europe with an uninterrupted lacustrine sedimentation probably starting between 1.2 and 1.9 Ma (Wagner et al., 2014; Lindhorst et al., 2015). The sensitive ecosystem response of the Dessarete lakes Ohrid and Prespa to climate variability during the last glacial–interglacial cycle has been documented in several studies dealing with terrestrial vegetation composition and land cover (Lézine et al., 2010; Wagner et al., 2009, 2010; Panagiotopoulos, 2013; Panagiotopoulos et al., 2014), with macrophytes and phytoplankton communities (Panagiotopoulos et al., 2014; Cvetkovska et al., 2015a, b), and with stable isotope studies (Leng et al., 2010). These findings illustrate the value of the "sister" lakes Ohrid and Prespa as environmental archives. Combined with the lakes' high biological endemism (Albrecht and Wilke, 2008; Föller et al., 2015) and the potential for independent age control through numerous volcanic ash layers (Sulpizio et al., 2010; Leicher et al., 2015), Lake Ohrid is a prime target to obtain a long continental record of multiple glacial/interglacial cycles, and for studies on past and present biodiversity and evolution.

The SCOPSCO (Scientific Collaboration on Past Speciation Conditions in Lake Ohrid) science international team carried out a deep drilling campaign in spring 2013 in the framework of the International Continental Scientific Drilling Program (ICDP). The aim of this initiative is an interdisciplinary analysis of environmental and climate variability under different boundary conditions throughout the Pleistocene. Initial results, based on the DEEP borehole in the lake centre, show approximately 1.2 Ma of continuous lake sedimentation with clear glacial–interglacial signatures represented in the sediment properties (Wagner et al., 2014). Here we report new palynological data

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from the upper ~ 200 m of the DEEP core from Lake Ohrid, representing vegetation dynamics over the past ~ 500 ka.

Specific objectives of this study are: (1) outlining of the flora and vegetation changes occurred in the last half million years in the area surrounding Lake Ohrid; (2) understanding of the glacial and interglacial vegetation dynamics; (3) correlation of the vegetation changes with benthic and planktic marine isotope stratigraphy.

Considering the core length, in this paper we aim to provide a comprehensive overview of millennial-scale vegetation dynamics during glacial–interglacial stages at Lake Ohrid before analysing intervals at high-resolution. The aim of this study is not in fact to discuss in detail the features of either interglacial or glacial periods. This subject, well developed in previous works (e.g. Tzedakis et al., 2004, 2009; Tzedakis, 2007; Fletcher et al., 2010; Margari et al., 2010; Moreno et al., 2015) mostly using high-resolution diagrams not yet available for Lake Ohrid core, will be soon considered in detailed papers.

2 Site setting

Lake Ohrid (40°54′ to 41°10′ N, 20°38′ to 20°48′ E) is a transboundary lake located in the Balkan Peninsula within the Dinaride–Albanide–Hellenide mountain belt, at the border between Albania and FYROM. It is the deepest and the largest tectonic lake in Europe. It is located in a deep tectonic graben, with still tectonically active faults running parallel to the N–S orientation of the lake (e.g. Hoffmann et al., 2012).

Lake Ohrid has a sub-elliptical shape, it is 30.3 km long and 15.6 km wide and is located at an altitude of 693 m a.s.l. It has a water surface of ~ 360 km^2, a maximum water depth of 293 m (Lindhorst et al., 2015), and a watershed area of ~ 1400 km^2. The lake is surrounded by the Mokra Mountains to the west (maximum altitude 1514 m) and the Galičica Mountains to the east (maximum altitude 2265 m). The water body of the lake is fed by 50 % of sub-lacustrine karstic flow, and 50 % by surface inflow; river runoff is at present ~ 20 % to the total inflow and was even lower prior to 1962, when the River

Sateska was diverted into the northern part of Lake Ohrid. Major fluvial inflows are from the rivers Daljan, Sateska, Cerava and Voljorek.

The river Crni Drim is the lake emissary and artificially controlled for its outflow. The karst aquifers are charged by precipitation and by the 150 m higher Lake Prespa, located 20 km to the east and separated by the mountain ridge of Galičica from Lake Ohrid. Because of the large extent of the karst system and the hydrological connection with Lake Prespa, the exact spatial distribution of the Lake Ohrid drainage basin is hard to determine (Watzin et al., 2002; Poposka and Bonacci, 2007; Wagner et al., 2009). If Lake Prespa and its tributaries are included in the catchment of Lake Ohrid, its area is calculated to 3921 km^2 (Portal Unesco, http://opendata.unesco.org/project/41304-549RER4000/).

The bedrock around the lake mainly consists of low to medium-grade metamorphosed Paleozoic sedimentary rocks and Triassic limestones intensely karstified along the eastern coast. The western shoreline is characterized by Jurassic ophiolites of the Mirdita Zone. Cenozoic sediments including Pliocene and Quaternary deposits are mainly found southwest of the lake (Wagner et al., 2009; Hoffmann et al., 2012).

Climatic conditions are strongly influenced by the proximity to the Adriatic Sea, and the water bodies of Lakes Ohrid and Prespa, which reduces the temperature extremes due to the presence of high mountain chains (Wagner et al., 2009; Hoffmann et al., 2012). An average precipitation for the Lake Ohrid watershed of ∼ 900 mm has been determined by Popovska and Bonacci (2007). Temperatures range from ∼ 10.5 to 22.3 °C in summer and −2.3 to 6.6 °C during winter. Prevailing wind directions are controlled by the basin morphology and have northern and southern provenances.

Studies on regional flora and vegetation are rather scarce in international literature. The main source of information is from a detailed survey carried out in Galičica National park (Matevski et al., 2011), the mountain ridge separating lakes Ohrid and Prespa. Concerning the flora, the Mediterranean and Balkan elements dominate, but also several Central European species are widespread in the area. The vegetation is orga-

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nized in altitudinal belts, which develop from the lake level (700 m) to top mountains (> 2200 m) as a result of the topography.

In riparian forests, the dominant species is *Salix alba*. Extrazonal elements of Mediterranean vegetation are present at lower altitudes, while most forests are formed by deciduous elements. The forests appear to be rather diversified. A first belt is dominated by different species of both deciduous and semi-deciduous oaks (*Quercus cerris*, *Q. frainetto*, *Q. petraea*, *Q. pubescens*, and *Q. trojana*) and hornbeams (*Carpinus orientalis*,*Ostrya carpinifolia*). Proceeding towards higher altitudes, mesophilous/montane species such as *Fagus sylvatica* (beech), *Carpinus betulus*, *Corylus colurna*, *Acer obtusatum* are present.*Abies alba* and *A. borisii-regis* mixed forests grow at the upper limit of the forested area, and a sub-alpine grassland with *Juniperus excelsa* is found above 1800 m in the Mali i Thate mountains to the south-east. Alpine pasturelands and grasslands are found over the timberline, currently at around 1900 m (Matevski et al., 2011). The western slopes of Galičica mountains facing Lake Ohrid are steep. The mountain's highest peaks arise from karst plateaus located at an altitude of ~ 1600/1700 m, which have been intensely grazed in the past and are now being slowly reforested.

Picea excelsa shows a disjointed distribution in the Balkans and is not present in the region of Ohrid. It is present in Mavrovo National Park (FYROM) with populations rather small-sized that can even be counted to an exact figure (Matevski et al., 2011). The same applies to *Pinus heldreichii*. Sparse populations of *Pinus* sp. pl. (Klaus, 1989) are considered to be Tertiary relicts and are located in the wider region of Lake Ohrid. These include populations of *Pinus peuce* at high elevation in the Voras mountains in Greece (to the south–east of Lake Ohrid) (Dafis et al., 1997), and in Mavrovo (to the north) and Plelister (to the east) National Parks in FYROM (http://www.exploringmacedonia.com/national-parks.nspx). *Pinus nigra* forests are widespread in Grammos mountains, to the South-West of the lake (Dafis et al., 1997).

Lake Ohrid is well-known for its rich local macrophytic flora, consisting of more than 124 species. Four successive zones of vegetation characterizes the lake shores: the

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zone dominated by floating species such as *Lemna trisulca*, mainly diffused in canals, the *Phragmites australis* discontinuous belt around the lake, the zone dominated by *Potamogeton* species, and the zone dominated by *Chara* species (Imeri et al., 2010).

3 Material and methods

Details about core recovery, the core composite profile, and sub-sampling are provided by Wagner et al. (2014) and Francke et al. (2015). From the DEEP site (ICDP site 5045-1) in the central part of Lake Ohrid (41°02′57″ N, 020°42′54″ E, Fig. 1), 1526 m of sediments with a recovery of > 95 % down to 569 m b.l.f. (meter below lake floor) have been recovered from seven different boreholes at a water depth of 243 m. Until today, a continuous composite profile down to 247.8 mcd (meter composite depth) with a recovery of > 99 % has become available, and sub-sampling was carried out in 16 cm resolution (Francke et al., 2015).

3.1 Core chronology

The DEEP core chronology down to 247.8 mcd (Francke et al., 2015) is based on radiometric ages of nine tephra layers (1st order tie points), and on tuning of biogeochemical proxy data to orbital parameters (2nd order tie points; Laskar et al., 2004) and to the global benthic isotope stack LR04 (3rd order tie points; Lisiecki and Raymo, 2005). Finally, the age model for the sediment cores was refined by a comparison with the age model of the downhole logging data by Baumgarten et al. (2015). Correlation of the tephra layers to well-known eruptions of Italian volcanoes and a re-calibration of radiometric ages from the literature has been carried out by Leicher et al. (2015).

3.2 Pollen analysis

A total of 311 sediment samples at 64 cm interval down to the depth of 197.55 m have been chemically processed for palynology in order to establish an overview diagram

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(in the following named skeleton diagram) spanning the past ∼ 500 ka. According to the age model by Francke et al. (2015) the mean resolution between two samples is ∼ 1600 years.

For each sample, 1/1.5 g of dry sediment was treated with cold HCl (37 %), cold HF (40 %), and hot NaOH (10 %). In order to estimate the pollen concentration, a tablet containing a known amount of *Lycopodium* spores (Stockmarr, 1971) was added to each sample. To draw pollen percentage diagrams, different pollen basis sums (PS) have been used, following the criteria listed by Berglund and Ralska-Jasiewiczowa (1986). Terrestrial pollen percentage has been calculated excluding *Pinus* from the PS due to its high overrepresentation in large part of the samples. *Pinus* percentage has been calculated on its sum plus the PS sum.

Oak pollen has been divided in three types according to morphological features following Smit (1973): *Quercus robur* type, which comprehends deciduous oaks, *Quercus ilex* type including the evergreen oaks minus *Q. suber*, and *Q. cerris* type, comprehending semi-deciduous oaks and *Q. suber*. Further identifications follow Beug (2004), Chester and Raine (2001) and Reille (1992, 1995, 1998). *Juniperus* type comprehends pollen grains of *Cupressus*, *Juniperus* and *Taxus*. Pollen curves/diagrams (Figs. 2, 3 and 4) were drawn using C2 program (Juggins, 2003). Ages are expressed in thousands of years BP (ka BP). Pollen zone boundaries were established with the help of CONISS (Grimm, 1987). The number of pollen zones where limited to the glacial/interglacial transitions and major interstadial phases. Further subdivision will take place during subsequent high-resolution studies.

4 Results and discussion

We present data in two pollen diagrams: (i) a simplified percentage pollen diagram based on the sediment depth scale and including lithostratigraphy of the DEEP site sequence from Francke et al. (2015, Fig. 2); (ii) a pollen diagram showing the percentage

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sums of ecological groups and selected concentration curves drawn according to the age scale (Fig. 3).

In total, 96 % of the samples (296) yielded low-medium to high pollen concentrations allowing a detailed palynological analysis. Mean pollen counts of 821 terrestrial pollen grains have been achieved. The physiognomy of vegetation shows maximum variability: arboreal pollen (AP) ranges from 0 to 99 % (Fig. 2). Total pollen concentration is quite variable, ranging from ca. 4000 to ca. 910 000 pollen grains g^{-1} (Fig. 4). Lower values are found in herb-dominated glacial periods. The pollen state of preservation resulted quite different, but generally allowed a proper identification. The number of identified taxa is 175, comprehending 143 terrestrial plant and 10 water plants.

The main vegetation features are summarized in Table 1. The pollen record was subdivided into 13 main pollen assemblage zones (PAZ, OD- named after Ohrid DEEP core) on the basis of changes in AP vs. non-arboreal pollen (NAP), changes in pollen concentration and major changes in single taxa. We aligned the marine isotope stages (MIS) of Lisiecki and Raymo (2005) (see also Railsback et al., 2015) to the PAZ, as well as the recently updated benthic $\delta^{18}O$ record from ODP Sites 967 and 968 (Konijnendijk et al., 2015), and the planktonic $\delta^{18}O$ composite curves from the Mediterranean (MEDSTACK; Wang et al., 2010) using independent age scales.

4.1 Vegetation and climatic features of the skeleton diagram

A close look at the Lake Ohrid pollen record reveals distinct characteristics for glacial and interglacial periods during the investigated past 500 ka. Glacial periods are generally characterized by dominance of NAP (e.g. Poaceae, Chenopodiaceae and *Artemisia*). An exception to this behaviour is represented by older glacial phases (OD-12, OD-11 and OD-9, Table 1) when *Pinus* was quite diffused. Interglacial periods are characterised by expansions of woodland organized in vegetation belts (e.g. forests with *Abies*, *Picea*, *Quercus robur* type, *Q. cerris* type). This general pattern of glacial/interglacial alternations is at times punctuated by minor expansions of AP during glacials and accordingly by forest opening during interglacials. This is in agreement with previous studies from Greece, e.g. Ioannina (Tzedakis, 1994; Tzedakis et al., 2002; Roucoux et al., 2011) and Tenaghi Philippon (e.g. Milner et al., 2012; Fletcher et al., 2013) and from central Italy (Follieri et al., 1998) suggesting a sensitive response of vegetation to climate change on a regional scale in SE Europe. At Lake Ohrid, most tree taxa show a rather continuous presence, even during glacial phases, suggesting that Ohrid region has been a plant refugium. The investigation on dynamics of specific taxa, on time of extinctions and the detection of possible refuge areas are among the issues that must be refined by ongoing high-resolution studies.

A clear correspondence between the climate signals provided by our terrestrial pollen record and marine oxygen isotope records (Fig. 4) is apparent, even if the limits between pollen zones and marine isotope stages are often not always identical (Figs. 2 and 3).

Glacial periods (PAZ OD-12, 11, 9, 7, 5, 4, 2, Table 1) are generally characterized by dominance of Poaceae, *Artemisia*, Chenopodiaceae that are indicative of open environments around the lake. Poaceae can all be ascribed to herbs, at times perennial. *Artemisia* and Chenopodiaceae, which are typically components of steppe – desert environments, consist of shrub and sub-shrub species. In OD-12/11 and OD-9, high percentages of *Pinus* point to the expansion of conifer forests like those currently growing at very high elevations in the surroundings of the lake.

In contrast, interglacials (PAZ OD-13, 10, 8, 6, 3, 1, Table 1) are marked by expansions of woods dominated by *Abies*, *Picea*, *Quercus robur* type and *Q. cerris* type. This pattern is at times punctuated by minor expansions of AP during glacial periods and by forest opening during interglacial ones.

The so far obtained results indicate marked intra-interglacial vegetation variability with clear vegetation successions attributed to climate change (Fig. 3). The most abundant taxon is *Pinus* that, even if overrepresented, was widespread in the region. Long-term vegetation dynamics correspond accurately to the glacial and interglacial periods, even if admittedly the established chronology for the Lake Ohrid DEEP record could be further improved with tuning to higher-resolution proxy data (see Zanchetta et al., 2015), with the detection of other tephra layers and the general improving of analyses obtained for the record.

In addition, most interstadials and several higher order variability has been previously reported from SE Europe, i.e., Ioannina (MIS6: Roucoux et al., 2011) and Tenaghi Philippon (MIS8: Fletcher et al., 2013). Ongoing high-resolution studies will help defining dynamics of specific taxa, investigating extinctions and detecting possible refuge areas.

The pollen diagram shows that, in the past 285 ka (PAZ OD-7 to OD-1), non-forested periods (herb-dominated) were prevailing and that the duration of glacial conditions was longer than between 500 and 285 ka. Interglacial phases show wetter and cooler conditions in the lower part of the diagram (PAZ OD-13 to OD-8, 500–285 ka) as indicated by the dominance of conifers, while in the upper part (PAZ OD-3 and OD-1, 126 ka-present) there was an increase in aridity and a "general" increasing trend in temperature indicated by the presence of mesophilous broadleaved trees. In OD-6 (106–81 ka) a balanced alternation of the two vegetation "types" can be observed.

This general trend is visible in the expansion of montane trees present in OD-10 (roughly corresponding to MIS11), and the expansion of mesophilous and Mediterranean taxa in the present and penultimate interglacials (Fig. 3). The pre-penultimate interglacial (OD-8, 328–285 ka, cf. MIS9) show increased mesophilous trees. The penultimate interglacial (OD-6, 245–189 ka, cf. MIS7) shows intermediate features, with balanced presence of montane and mesophilous taxa. This trend seems to be confirmed also by herbs: Poaceae and Cyperaceae decrease, while *Artemisia* and Chenopodiaceae increase towards the top of the diagram. Steppes seem to characterize the two last glacial periods as it happens in other records (Combourieu-Nebout et al., 2015).

OD-12 (488–455 ka) shows a dominance of AP and overwhelming presence of pine pollen. This suggests that this glacial phase could have been cold but not very dry so that conifer montane taxa such as *Pinus*, *Picea* and *Abies* were growing in the region. In the following zone OD-11 (455–421 ka), stronger glacial conditions are evidenced

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by decreased AP and increased Poaceae. The curve of *Hippophaë*, the only arboreal plant with increasing percentages (Fig. 2), confirms this interpretation. The climate of this glacial phase was anyway wetter than the following ones, as evidenced by the permanence of both trees and the expansion of Cyperaceae.

The passage to the following interglacial (OD-10, 421–367 ka) is marked by an important and multi-millennial-long expansion of *Abies* (accompanied by*Quercus robur* type) followed by a ~ 10 ka-long expansion of *Picea* (accompanied by*Quercus cerris* type). This vegetation pattern indicates that the first part of this interglacial was warmer and wetter than the second one. Moreover, this long-term succession is not represented in the rest of the diagram, pointing to the unique character of MIS 11. Both fir (*Abies*) and spruce (*Picea*) could have occupied the montane belt (with pines on higher elevations), while deciduous oaks (*Quercus robur* type) first, and subsequently semi-deciduous oaks (*Quercus cerris* type), were growing at lower elevations.

Glacial conditions were attained during zone OD-9, 367–328 ka (cf. MIS10) even if oscillations of mesophilous trees occurred and alternated with herb expansions. Cichorioideae, together with Asteraceae undiff., characterized the herbaceous vegetation, although their values may be increased in the pollen profile because of taphonomic issues still to be fully investigated.

The following interglacial OD-8, 328–285 ka (cf. MIS9) shows a tree-phase widespread mesophilous vegetation expansion. *Quercus robur* type prevailed in the first and longer phase, while *Q. cerris* type at the end of the zone indicating a successive change from warmer and wetter to cooler and dryer conditions interrupted by short cool events (NAP increases).

OD-7, 285–245 ka (cf. MIS8) shows low AP percentages (pioneer vegetation mainly consisting of *Juniperus* type is rather abundant) and increased values of Poaceae. Even if Poaceae pollen could have come from the *Phragmites* lacustrine vegetation belt, such high values are mainly ascribed to the presence of regional grasslands that are typical for glacial periods in SE Europe (e.g. Tzedakis et al., 2001; Pross et al., 2015).

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OD-6 (245–189 ka) shows a very high interglacial variability, with three expansions of trees interrupted by two herb expansions. This interglacial, possibly corresponding to MIS7, has a vegetation behaviour quite different from that of MIS9 and MIS11. MIS7 at Lake Ohrid is marked by warmer and wetter conditions as evidenced by decreasing *Abies* and increasing *Picea* percentages. The first NAP increase is characterized by many taxa with similar values (Poaceae, Chenopodiaceae, *Artemisia* and other Asteroideae); the second one by Poaceae and the first strong increase of *Artemisia* percentage in the diagram.

A long glacial phase is represented in OD-5 (189–161 ka) and OD-4 (161–126 ka). The limit between the two open formations is marked by a change from grassland-dominated environment (Poaceae and Cyperaceae) to steppe-dominated (*Artemisia*) one. Dry conditions are also indicated by decreasing *Quercus robur* type and increasing *Q. cerris* type together with *Juniperus* type and *Hippophaë* percentages. The second part of MIS6 (OD-4) appears to be the driest phase of the recorded diagram. This is in good agreement with hydro-acoustic data and sediment core analyses from the northeastern corner of Lake Ohrid, which revealed that during MIS6 the water surface of the lake was 60 m lower than today (Lindhorst et al., 2010). Similarly, sedimentological data from the DEEP core (Francke et al., 2015) shows that an accumulation of mass movement deposits (MMD) occurred during the second part of MIS6, which might be also indicative of low lake levels.

OD-3, 126–70 ka (cf. MIS5) is an interglacial characterized by less variability than the previous OD-6. Mesophilous communities prevailed on the montane vegetation. *Quercus robur* type and *Q. cerris* type values are rather similar. *Picea* is very rare and *Fagus* shows the highest values of the entire record. Similarly to all previous interglacials, the vegetation seems to be organized in altitudinal belts. Periods with open vegetation are featured by expansions of *Artemisia*, Chenopodiaceae and Poaceae.

The last glacial period, i.e., MIS4-2, is represented in PAZ OD-2 (70–12 ka). It has a rather high variability, evidenced, already at this step of analysis, by important oscillations of most trees.

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The present interglacial is featured by the strong and stable expansion of *Quercus robur* type accompanied by *Q. cerris* type and relatively low montane taxa such as *Abies* and *Fagus*. The uppermost samples show opening of the landscape by humans with evidence of crops and spreading of fruit trees such as *Juglans* (included in Juglandaceae in Fig. 2). The reduced presence of *Picea* matches both the palynological data from Lake Prespa for the last glacial (Panagiotopoulos et al., 2014) and the present-day vegetation features of the region, where spruce is represented by relic populations in few forested areas.

4.2 Comparison with other proxies and outlook

In Fig. 4 alignment of the Total Organic Carbon (TOC), Total Inorganic Carbon (TIC), AP percentages and AP+NAP concentrations from Lake Ohrid (and "ecogroup" curves of Fig. 3) with both Tenaghi Philippon AP% (Tzedakis et al., 2006) and marine isotope curves shows a very good general agreement between the different records. TOC and AP + NAP (pollen of terrestrial plants) concentration as well as AP% show the same main changes, indicating that there is a strict relation between the plant biomass and the organic carbon deposited in the lake. TIC increases are mostly in phase with vegetation changes too. The main discrepancies between both TIC/TOC and pollen data are found during glacial phases OD-12 (488–455 ka) and OD-9 (367–328 ka).

The similarity between Lake Ohrid and Tenaghi Philippon curves is striking. All the main changes in forest cover match, and they are both corresponding to marine records too. There are some differences in the timing of interglacial phases start. DEEP core benefited in fact of the presence of several tephra layers (see Fig. 2, Leicher et al. 2015) that were used to establish the chronology. The main difference with Tenaghi Philippon is in the fact that arboreal taxa show a continuous presence at Lake Ohrid, even during the glacials, while at Tenaghi Philippon they often disappear to spread again during the interglacials, often with a certain delay. This behaviour could anyway have been expected considering the differences in water availability at the two sites. In Greece, not only Tenaghi Philippon, but also Kopais (Okuda et al., 2001) areas, resulted not

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to be ideal refugia for mesophilous trees. A quite different situation is found at Ioannina (western Greece), a refugial site for temperate trees featuring sub-Mediterranean climate and vegetation in the last ~ 480 ka (Tzedakis, 1994; Tzedakis et al., 2002).

Aside a close correspondence with Tenaghi Philippon AP curve %, Fig. 4 also shows a close correspondence between our pollen data and the Mediterranean benthic and planktic composite curves (Wang et al., 2010; Konijnendijk et al., 2015). Compared to the global isotope stack (Lisiecki and Raymo, 2005), additional detail in the pollen diagram is clearly representative of regional Mediterranean conditions and of the influence of moisture availability on the expansion of plants. Both marine deep and surface water features show additional warm phases during interglacial that are also observed in the pollen data. For example, the tripartite forest during MIS7 are well reflected in the pollen data, but likely overprinted by the effect of ice volume in the global benthic isotope stack. Completion of the downcore analysis of the DEEP core from Lake Ohrid will allow for a more accurate correlation of the entire sequence to the orbitally tuned Mediterranean isotope records, and provide a finer tuning of the present age model (Francke et al., 2015) to independently dated records in the Mediterranean region were available.

5 Conclusions

The 500 ka long DEEP pollen record from Lake Ohrid represents a continuous documentation of the vegetation and climate history of the western Balkan region. Palynological data are supported by many sedimentological proxies highlighting the need of a multi-disciplinary approach in palaeoenvironmental studies (see all the articles of this special issue).

The richness of pollen diversity and continuity along this long-time series point to the particular climatic and environmental conditions that make Lake Ohrid a hotspot of biodiversity. This has deep roots in the past, as the lake has probably acted as a permanent water reservoir providing wetness to its surroundings even during dramatic dry or cold climatic phases. In fact trees never disappeared from the investigated area.

The main novelty of this pollen record from the Balkan Peninsula relies on the following summarized evidences:

- The continuous record of glacial–interglacial vegetation successions shows that refugial conditions occurred in Lake Ohrid area. A detailed article on trees extinction, whose timing and patterns needs accurate check and refined analyses, is in preparation (Donders et al., 2015).

- A clear shift from relatively cool/humid interglacial conditions prior to 285 ka BP, to warmer and drier ones during recent interglacial periods (last ∼ 130 ka), suggests changing seasonality patterns toward a more Mediterranean-type climate. During the interglacial period occurred between 245 and 189 ka, a very high interglacial variability is found. Glacial features, generally characterized by grasslands until 245 ka BP and then by steppes, also confirm this climate shift.

- Similarities and dissimilarities with other southern European and Near Eastern pollen records, even if already visible, will be better defined with the improvement of analyses through ongoing high-resolution studies.

- Tephrostratigraphic alignment of Lake Ohrid with the new Tenaghi Philippon record (Pross et al., 2015) will provide a better understanding of climate gradients (temperature and precipitation) in the Balkans.

- A close correspondence of interglacial and glacial climate and vegetation evolution with regional benthic and planktic isotope data is apparent. The terrestrial pollen record is integrating temperature data from the marine stratigraphy with clear indication of humidity/dryness changes.

Author contributions. This article is the fruit of a strict cooperative work among palynologists who all contributed to the Lake Ohrid pollen analysis and its interpretation. The manuscript was

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written by L. Sadori with substantial contribution of T. H. Donders and A. Koutsodendris. A. Masi (c.a.) was responsible of data management and refined diagrams drawn by T. H. Donders and A. Koutsodendris. All coauthors contributed to the writing of this manuscript.

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Table 1. Main vegetational features of Lake Ohrid DEEP core pollen assemblage zones (OD-PAZ) and related chronological limits. The basis sum for AP and NAP taxa does not include *Pinus* (see text).

PAZ	Zone description
OD-1 depth limits (m) 5–0 age limits (ka) 12–0 duration (ka) 12 pollen samples n. 9 mean pollen count 354	Mesophilous tree taxa prevail. Forests are characterized by *Quercus robur* type (22–43 %) and *Q. cerris* type (2–21 %). Montane taxa are quite scarce and mainly represented by *Abies* and *Fagus.* Riparian and Mediterranean trees are not abundant too. Poaceae are dominant among herbs. Pollen concentration is high.
OD-2 depth limits (m) 29–5 age limits (ka) 70–12 duration (ka) 58 pollen samples n. 28 mean pollen count 228	Open vegetation (steppe) with low/medium values of *Pinus* (9–77 %) and sparse presence of many montane and mesophilous taxa. Among them *Q. robur* type is worth of mention. *Artemisia* is the most abundant taxon and is accompanied by other herbs like Poaceae, Chenopodiaceae and Cyperaceae. Pollen concentration shows medium values.
OD-3 depth limits (m) 49–29 age limits (ka) 126–70 duration (ka) 56 pollen samples n. 32 mean pollen count 663	Alternation of periods characterized by mesophilous/montane trees and open vegetation. Forests are mainly characterized by expansion of *Q. cerris* type (2–33 %) and *Quercus robur* type (4–40 %) together with *Abies* and*Fagus*, this last reaching the highest values of the diagram in this zone. Riparian and Mediterranean trees are present. *Artemisia*, Poaceae and Chenopodiaceae characterize the open vegetation. Pollen concentration is high.
OD-4 depth limits (m) 62–49 age limits (ka) 161–126 duration (ka) 35 pollen samples n. 21 mean pollen count 335	Open vegetation (steppe) with medium/high values of *Pinus* (14–83 %). *Juniperus* (0–55 %) and *Hippophaë* (0–5 %) are important woody taxa. Mesophilous taxa are present even if with low values. Herbs are overwhelming: *Artemisia* shows a sudden increase, while Poaceae and Cyperaceae are reduced; Chenopodiaceae are abundant. Pollen concentration shows medium values.
OD-5 depth limits (m) 81–62 age limits (ka) 189–161 duration (ka) 28 pollen samples n. 29 mean pollen count 362	Open vegetation with medium values of *Pinus* (6–75 %), *Juniperus* (0–9 %) and *Hippophaë* Many mesophilous taxa are present even if with low values. Herbs are overwhelming: Poaceae, *Artemisia,* Chenopodiaceae and Cyperaceae are abundant. Pollen concentration has medium values.
OD-6 depth limits (m) 106–81 age limits (ka) 245–189 and duration 56 pollen samples n. 39 mean pollen count 1520	Alternation of coniferous and mesophilous forests with grassland (steppe) formations. Main conifer taxa are *Pinus* (24–99 %), *Abies* (0–77 %) and *Picea* (0–67 %); *Q. cerris* (0–21 %) is the dominant mesophilous taxon, being more abundant than *Q. robur* type (0–30 %). Poaceae are accompanied by high values of Chenopodiaceae, Cichorioideae and *Artemisia.* Pollen concentration is quite variable, oscillating from almost the highest to almost the lowest values of the record.
OD-7 depth limits (m) 125–106 age limits (ka) 285–245 duration (ka) 40 pollen samples n. 27 mean pollen count 606	Open vegetation with high values of pioneer taxa (mainly *Juniperus*). *Pinus* is very abundant (10–87 %). Poaceae are very abundant, accompanied by Chenopodiaceae and *Artemisia*. Pollen concentration is very low.

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Table 1. Continued.

PAZ	Zone description
OD-8 depth limits (m) 144–125 age limits (ka) 328–285 duration (ka) 43 pollen samples n. 30 mean pollen count 824	Mesophilous tree taxa prevail. Forests are characterized by *Quercus robur* type (5–55 %) and *Q. cerris* type (0–50 %). Riparian and Mediterranean trees are worth of mention. Poaceae are dominant among herbs. Pollen concentration is high.
OD-9 depth limits (m) 156–144 age limits (ka) 367–328 duration (ka) 39 pollen samples n. 18 mean pollen count 510	Open vegetation with relatively high values of pioneer taxa. *Pinus* (60–98 %), *Juniperus* type and *Hippophaë* are rather abundant. *Picea* (0–43 %) and *Abies* (0–63 %) are mainly found in the middle of the zone. Peaks of mesophilous taxa are also observed. Poaceae, Chenopodiaceae, Asteroideae, Cichorioideae and *Artemisia* are very abundant. Pollen concentration is low.
OD-10 depth limits (m) 175–156 age limits (ka) 421–367 duration (ka) 54 pollen samples n. 29 mean pollen count 1710	Forests characterized first by *Quercus robur* type (0–43 %) and *Q. cerris* type (0–40 %) then by long-term successions of *Abies* (1–80 %), and *Picea* montane woods. Poaceae are most dominant among the herbs. Pollen concentration is high.
OD-11 depth limits (m) 182–175 age limits (ka) 455–421 duration (ka) 34 pollen samples n. 12 mean pollen count 789	Open vegetation with relatively high values of pioneer taxa. *Pinus* (28–98 %) and *Hippophaë* are very abundant. *Picea* (0–67 %) and *Abies* (0–26 %) are mainly found in the lowermost samples of the zone. Poaceae, Cyperaceae, Chenopodiaceae, Asteroideae, Cichorioideae and *Artemisia* are very abundant. Pollen concentration is the lowest of the entire record.
OD-12 depth limits (m) 193–182 age limits (ka) 488–455 duration (ka) 33 pollen samples n. 15 mean pollen count 1585	Forests dominated by *Pinus* (58–98 %), *Abies* (2–82 %) and *Picea* (1–60 %) are alternating with open vegetation dominated by Poaceae, Cyperaceae, Chenopodiaceae, Cichorioideae and *Artemisia*. Pollen concentration is relatively low.
OD-13 depth limits (m) 198–193 age limits (ka) 500–488 duration 12 pollen samples n. 7 mean pollen count 342	Mesophilous and montane tree taxa prevail. Forests first with *Abies* (min. 11 %, max. 51 %) and then with *Quercus robur* type (min. 16 %, max. 54 %). Poaceae are dominant among herbs. Pollen concentration is high.

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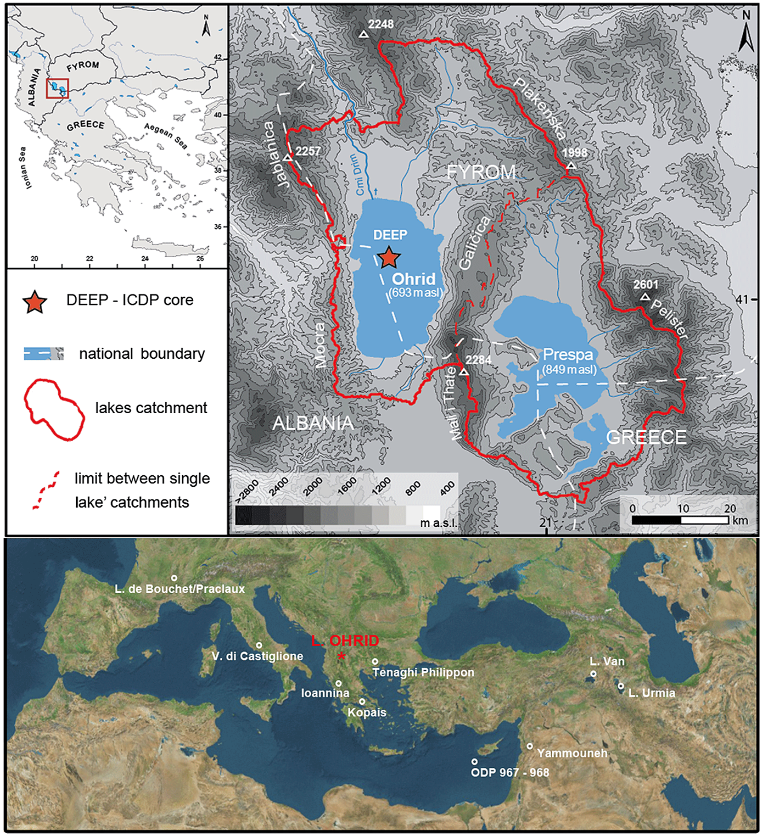

Figure 1. Map of Lake Ohrid modified from Panagiotopoulos (2013) and locations of terrestrial and marine records discussed in the text.

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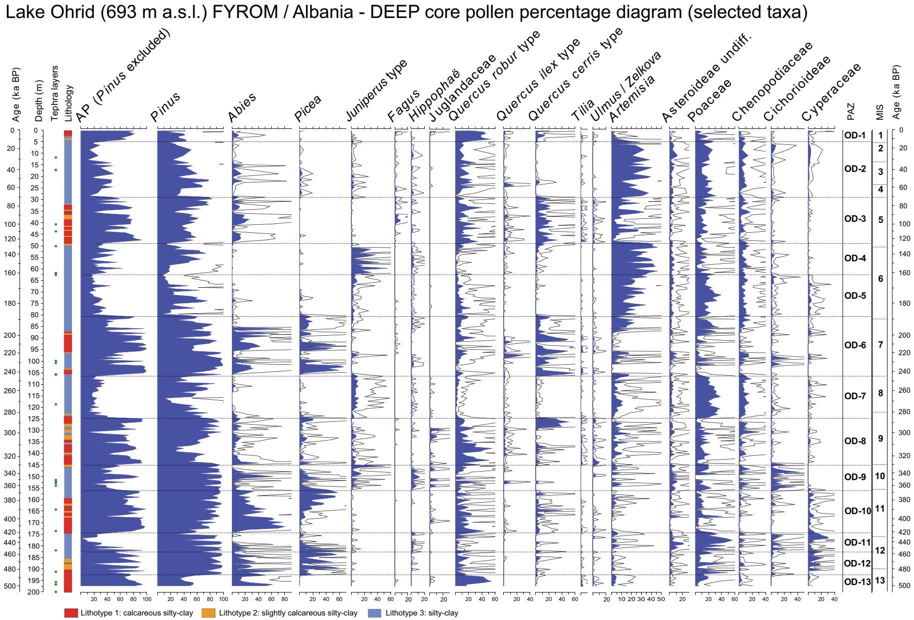

Figure 2. Lake Ohrid (FYROM), DEEP core. Pollen percentage diagram of selected taxa against depth scale. Lithology and tephra layers adapted from Francke et al. (2015).

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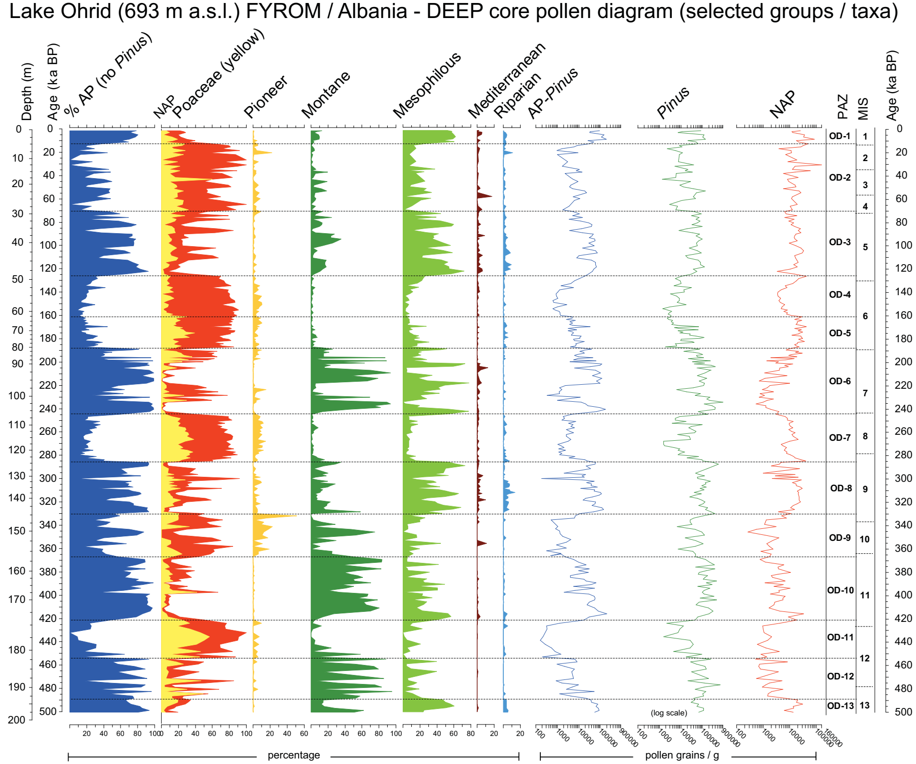

Figure 3. Lake Ohrid (FYROM), DEEP core. Pollen diagram of selected ecological groups (%) and concentration curves against chronology (Francke et al., 2015). Ecological groups: montane trees (*Abies*, *Betula*,*Fagus*, *Ilex*, *Picea*, *Taxus*), mesophilous trees (*Acer*, *Buxus*, *Carpinus betulus*, *Castanea*, *Carya*, *Celtis, Corylus, Fraxinus excelsior/oxycarpa*, *Ostrya/Carpinus orientalis*, *Pterocarya*, *Hedera*,*Quercus robur* type, *Quercus cerris* type, *Tilia*, *Tsuga*, *Ulmus*, *Zelkova*); mediterranean trees (*Arbutus*, *Fraxinus ornus, Cistus*, *Olea*, *Phillyrea*, *Pistacia*, *Quercus ilex*, *Rhamnus*); riparian trees (*Salix*, *Platanus*, *Populus*, *Alnus*, *Tamarix*); pioneer shrubs (*Ephedra*, *Juniperus* type, Ericaceae, *Hippophaë*).

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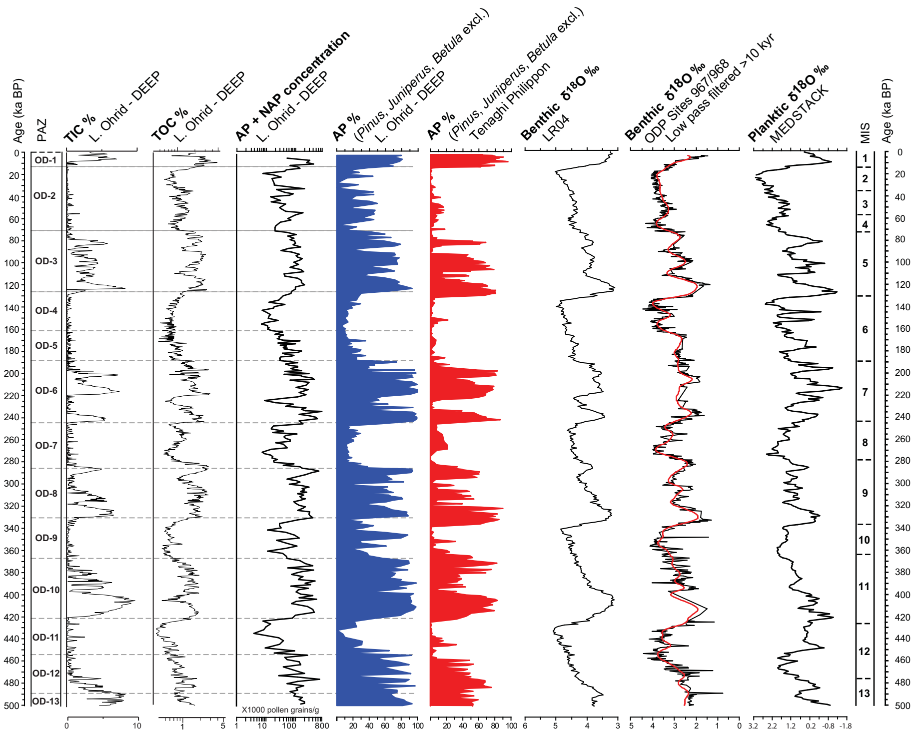

Figure 4. Comparison of selected proxies from Lake Ohrid with other records spanning the last 500 ka drawn against original age models. Lake Ohrid: TOC, TIC (Francke et al., 2015); AP percentages and concentrations (this study). Tenaghi Philippon: AP % excluding *Pinus*, *Betula*, *Juniperus* (Wijmstra, 1969 and Wijmstra and Smit, 1976; age model from Tzedakis et al., 2006). Marine records: LR04 $\delta^{18}O$ benthic stack (Lisiecki and Raymo, 2005); stacked benthic $\delta^{18}O$ data for ODP Sites 967 and 968 from the Eastern Mediterranean (Konijnendijk et al., 2015); MEDSTACK planktic $\delta^{18}O$ data (Wang et al., 2010).

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