VEGETATION AND CLIMATE RECONSTRUCTION DURING THE LAST INTERGLACIAL COMPLEX: THE POLLEN RECORD OF LAKE OHRID (ALBANIA/FYROM), THE OLDEST EUROPEAN LAKE.

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ABSTRACT:

This thesis is focussed on the palaeonvironmental and climatic changes occurred during the period between 130 and 70 ka (including the whole Last Interglacial Complex), with the aims to investigate the long-term climate variability on environment, on the basis of high resolution pollen data from Lake Ohrid sediments (Albania/F.Y.R.O.M. border), the oldest lake in Europe and one of most ancient in the world. The climate reconstruction obtained from pollen data is based on a wider interval, 160-70 ka.

Lake Ohrid is located in a key region at the confluence of central European and Mediterranean climate influences and as already demonstrated by previous studies, has an important role for the study of the climatic and environmental changes occurred during the millennia in the Balkan and European areas.

The investigated pollen material comes from the sediments retrieved in spring 2013 in the frame of the project SCOPSCO (Scientific Collaboration on Past Speciation Conditions in Lake Ohrid) whose drilling was financed by the ICDP (International Continental Scientific Drilling Program). During the drilling campaign 6 parallel cores have been collected from the depocenter of Lake Ohrid obtaining an extraordinary composite sequence 569 m long (DEEP).

The upper 247.8 m of DEEP core have been dated using tephrostratigraphic information and tuning of biogeochemical proxy data to orbital parameters and covers the last 637 ka. In the framework of this careful temporal establishment, an even more precise chronology for the Last Interglacial Complex, and in particular for the transition between MIS6 and 5, was obtained by comparing pollen data from the same period with other DEEP and Mediterranean proxies. This make Lake Ohrid extremely important because for the other records from Mediterranean and European area such chronological constrains are not available and so the chronologies are less precise.

The pollen analysis results come from the uppermost 200 m of the DEEP core (covering the last 500 ka) and revealed a succession of non-forested and forested periods clearly connected with glacial–interglacial cycles of the marine isotope stratigraphy.

Among the different glacial-interglacial cycle, the new high-resolution pollen stratigraphy of the Last Interglacial Complex shows the classical alternation of periods characterized by forest (interstadials, warm and wet periods) and open vegetation (stadials, cold and dry periods), clearly resembling the well-known vegetational and climate succession of other European records.

Concerning the Last Interglacial (or Eemian, 128-112 ka, roughly equivalent to MIS5e), pollen analysis and climate quantitative reconstructions identify three key phases with a slight different timing, with an initial phase characterized by a sudden warming (propagation of mesophilous forests), then a decrease of temperatures associated with wet conditions (expansion of *Carpinus betulus*) and at the end a progressive establishment towards cold and dry conditions until the termination of Eemian at 112 ka, confirming what other previous studies on European records said, namely Eemian was not a stable period.

Several abrupt events are in also identified, during the successive stadials and interstadials (Early Last Glacial), probably correlated to the succession of cold events recorded in the Greenland ice core records, associated to a weakening of the North Atlantic Meridional Overturning Circulation.

This work provides a new pollen reference sequence for the Last Interglacial Complex in Europe and concerning climate reconstruction provides new information for a period (160-70 ka, from the last part of Riss Glaciation to the beginning of Würm Glaciation) still poorly investigated in Europe, mostly in the south (< 45° lat. N), where only one record has been studied for the whole interval, with high resolution time.

According to my results, Lake Ohrid can be considered a key role site for the investigation of the climatic changes occurred in centennial and millennial scale in a region of mid-altitude between European and Mediterranean areas, providing furthermore new evidence for the connection between the Europe and Northern Hemisphere climate oscillations.

RÉSUMÉ:

Le réchauffement global est au cœur des débats scientifiques actuels et soulève de nombreuses questions quant à la dynamique des variations climatiques et aux impacts possibles sur notre

environnement. Une meilleure compréhension de la variabilité climatique dans le passé s’avère donc nécessaire et de nombreux efforts ont été entrepris depuis quelques décennies dans différents domaines de la climatologie actuelle et de la paléoclimatologie pour mieux comprendre la variabilité du climat au cours du temps.

Comme le montre les études basées sur les sédiments marins, les données continentales (flore et faune) et carottes de glace, le climat varie au cours du temps. Le Quaternaire est ainsi caractérisé par des cycles climatiques rapides et de grande amplitude, les cycles interglaciaires-glaciaires dont, depuis le Pléistocène moyen, la période est d’environ 100 000 ans.

Dans l'interglaciaire actuel, l'Holocène, l'impact anthropique a pu avoir masqué le changement climatique. Dans le monde entier, l’impact de l'activité anthropique est de plus en plus important et les activités humaines peuvent constituer une menace non seulement pour la biodiversité, et les écosystèmes. Selon les données actuelles, l'Holocène peut être près de la fin de son parcours naturel et une nouvelle période glaciaire pourrait commencer bientôt, si ce n'était pour un réchauffement climatique progressif.

Pour comprendre les changements climatiques actuels et futurs, il est primordial étudier l'évolution de la végétation et du climat pour certaines périodes clés du passé, notamment celles caractérisées par peu ou pas d’impact humain. Dans ce cadre, le dernier interglaciaire (ou Eémien, 128-112 ka) est une période particulièrement importante pour la communauté des paléo-environnementalistes, car très proche de l'Holocène.

Cette thèse est centrée sur les changements paléoenvironnementaux et climatiques survenus dans le période entre 130 et 70 ka (qui comprend l'ensemble du dernier complexe interglaciaire), pour étudier la variabilité du climat à long terme sur l'environnement, sur la base des données de pollen à haute résolution provenant des sédiments du lac Ohrid (Albanie / F.Y.R.O.M), le plus ancien lac d'Europe et l'un des plus anciens du monde. La reconstruction du climat obtenue à partir des données polliniques est basée sur un intervalle plus large, 160-70 ka.

Le lac Ohrid est situé dans une région clé, à une zone de confluence entre influences climatiques d'Europe centrale et méditerranéenne. Le matériel pollinique provient des sédiments prélevés en 2013, dans le cadre du projet SCOPSCO (Scientific Collaboration On Past Speciation Conditions in Lake Ohrid) dont le carottage a été financé par l'ICDP (International Continental Scientific Drilling Program). Pendant la campagne de carottage, 6 carottes parallèles ont été prélevées à partir de l'épicentre du lac, obtenant une séquence composite «extraordinaire» de 569 m (DEEP).

Les 247.8 m supérieurs de la carotte DEEP ont été datés par téphrostratigraphie et tuning des proxies biogéochimiques et des paramètres orbitaux: ils couvrent les derniers 637 ka. Nous avons amélioré le modèle d'âge pour le Dernier Complexe Interglaciaire et en particulier pour la transition entre MIS6 et 5, en comparant les données polliniques de la même période avec d'autres proxies de la carotte DEEP et de la Méditerranée. Cela rend le lac Ohrid extrêmement important car pour les autres enregistrements de la région Méditerranéenne et Européenne, de telles contraintes chronologiques ne sont pas disponibles et donc les chronologies sont moins précises.

L'analyse des premiers 200 m de la carotte DEEP, couvrant les derniers 500 ka, a été étudiée avec une résolution de 1,6 ka. La séquence a révélé une alternance entre des ouvertures forestières et périodes boisées reflétant une cyclicité glaciaires-interglaciaires comparable à celle de la stratigraphie des isotopes marins. Parmi les différents cycles glaciaires-interglaciaires, l'analyse pollinique à haute résolution du Dernier Complexe Interglaciaire montre l'alternance classique de périodes caractérisées par la forêt (interstades, périodes chaudes et humides) et la végétation ouverte (stades, et périodes sèches), ressemblant clairement à la succession végétale et climatique bien connue des autres séquences européennes.

Concernant le Dernier Interglaciaire (ou Eémien, 128-112 ka, plus ou moins équivalent à MIS5e), l'analyse pollinique et les reconstructions quantitatives climatiques basées sur ces dernières identifient trois phases clés: une phase initiale caractérisée par un réchauffement soudain (propagation des forêts mésophiles), puis une diminution des températures associées à des conditions humides (expansion de *Carpinus betulus*) et à la fin un établissement progressif vers des conditions froides et sèches jusqu'à la fin de Eémien à 112 ka, confirmant l'hypothèse déjà avancée par plusieurs études antérieures basées sur des séquences polliniques européennes , à savoir que l'Eémien n'était pas une période climatiquement stable.

D'autres changements climatiques sont également visibles dans la région du lac Ohrid entre 112-70 ka. Ces derniers sont probablement liés à la succession d'événements froids enregistrés dans les carottes de glace du Groenland, associé à un affaiblissement de l'AMOC (Atlantic Meridional Overturning Circulation).

Ce travail a permis de fournir une nouvelle séquence de référence pollinique pour le Dernier Complexe Interglaciaire en Europe. Ce travail a également permis de quantifier les paléoclimats pour la période 160-70 ka, (de la dernière partie de la glaciation de Riss au début de la glaciation de Würm) encore peu étudiée en Europe, principalement dans le sud (<45 ° lat. N), où un seul enregistrement a été étudié pour toute la période, avec une résolution temporelle élevée.

Sur la base de ces résultats, le lac Ohrid apparait comme un site clé pour l'étude des changements climatiques survenus à une échelle centenaire et millénaire dans une région de moyenne altitude entre les régions européennes et méditerranéennes, fournissant en outre des nouvelles informations sur la connexion entre les oscillations climatiques de la région méditerranéenne et de l'Hémisphère du Nord.

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INTRODUCTION:

In the recent years, global warming has become the focus of scientific debates, raising several questions about the dynamics of climate changes and their possible impact on the environment. Nowadays the impact of anthropogenic activities (i.e. greenhouse gas, intensive land-use) on climate is increasing causing possible disastrous consequences in future (e.g. Houghton et al., 1996; Ruddiman et al., 2016).

As widely demonstrated studying deep-sea sediments, continental proxies (e.g. lacustrine sediments, speleothems) and ice cores, climate varies naturally (e.g. Berger, 1978; Imbrie et al., 1993; Petit et al., 1999). During the last 2.75 million year, glacial-interglacial cycles have alternated due to changes on Earth's orbital parameters (precession, obliquity and eccentricity; Hays et al., 1976; Imbrie et al., 1992; Shackleton et al., 1984; Tzedakis et al., 1997; Raymo et al., 1989). The progress of global warming should be contradicted because the current Interglacial, the Holocene, could be over the end of its naturally course and a new glacial phase could be forthcoming (e.g. Change et al., 2001; Houghton et al., 1996; IPCC, 1996 and following ones; Ruddiman et al., 2015). Indeed, for analogy with the closest analogous of current interglacial (for its orbital configuration at the time) namely MIS 19 (Marine Isotope Stage, Giaccio et al., 2015; Oliveira et al., 2017), we actually would be at the gate of a new ice age. MIS 19 interglacial lasted 10.8 ± 3.7 ka, comparable to the time elapsed since the onset of the Holocene. However, greenhouse gases concentrations during MIS 19 were significantly lower than those of the late Holocene (e.g. Giaccio et al., 2015) during which, in all parts of the Earth, greenhouse gases are increasing and a consequent temperature stability is registered rather than a shift toward glaciation (e.g. Change et al., 2001; Houghton et al., 1996; IPCC, 1996; Ruddiman et al., 2015).

For the interpretation of the current climate and environment and to infer possible future scenarios, it's important to distinguish between natural and anthropogenic factors, but this is becoming increasingly difficult. For this reason the solution is to investigate the evolution of vegetation and climate variability in certain key periods of the past, where human impact was absent.

Under this light, the study of an interglacial (Eemian), similar to the present one, human impact included, can be even more important than the investigation of an interglacial (MIS 19) more similar from an astronomical point of view. As already mentioned, in fact, the future of our World could have a better analogue in the Eemian.

In this framework, the Last Interglacial Complex (LIC, 130–80 ka, Govin et al., 2015; Turon, and references therein), the terrestrial equivalent of Marine Isotope Stage 5 (MIS 5) of the marine benthic isotope stratigraphy (Shackleton et al., 2003), provides interesting hints to interpret the present-day environment and to infer its potential future changes. In particular, within it, the Last Interglacial (LI or Eemian, 130-110 ka, Turner, 2002), roughly equivalent of Marine Isotope Substage 5e (MIS 5e, Shackleton et al., 2003; Sánchez-Goñi et al., 1999, 2002, 2007, 2012) is considered a key period for the community of researchers. According to different studies based on pollen data, the LI were warmer (up to 2 ˚C above present in Northern Hemisphere, CLIMAP Project Members, 1984; Bauch and Erlenkeuser, 2003) and more humid than today (Guiot, 1990; 1993; Kukla et al., 2002; Fauquette et al., 1999; Klotz et al., 2003). These characteristics make it the new best analogue of the Holocene, considering that humidity and temperature increasing in the near future may find a good simulation in its sediments.

The Eemian was characterized by glacial ice sheet reduction (Emiliani, 1955; Shackleton et al., 2003) and high sea level (Shackleton, 1969). These conditions favored the development of forested vegetation in Europe, until the inception of the Last Glaciation (e.g. Stirling et al., 1998; Gallup et al., 2002). According to the available pollen data, the Last Interglacial was characterized in southern Europe by deciduous forests (e.g. Allen et al., 2009; Beaulieu and Reille, 1984, 1992a and 1992b; Follieri et al., 1988; Milner et al., 2016; Pickarski et al., 2015a; Tzedakis, 1999, 2003; Tzedakis and Bennet, 1995; Tzedakis et al., 2003 and 2006; Wijmstra, 1969; Wijmstra and Smit, 1976) easily identifiable in records by a clear vegetation succession. It is indeed preceded and followed by a steppic taxa vegetation typical of cold and dry environments (Turner and West, 1968).

Besides the Eemian interglacial, the terrestrial stratigraphy of the LIC comprises a succession of stadials (cold and dry conditions) and interstadials (warm and wet conditions) periods, which constitute the Early Last Glacial (commonly named Early Würm in Europe).

This thesis is focused on the palaeonvironmental and climatic changes occurred during the period between 130 and 70 ka (including the whole Last Interglacial Complex), with the aims to investigate the long-term climate variability on the environment, on the basis of high resolution pollen data from Lake Ohrid sediments, located in the Balkan Peninsula (Albania / F.Y.R.O.M. border) at 693 m a.s.l. The climate reconstruction obtained from pollen data is based on a wider interval, 160-70 ka (from the last part of Riss Glaciation to the beginning of Würm Glaciation) still poorly investigated in south Europe (< 45° lat. N), where only one record has been studied with high resolution time.

Fill the gap on the knowledge of high resolution studies during this key periods is becoming crucial for the comprehension of regional and global climate changes occurred over time. Indeed while previously it was thought that LIC and especially LI had a climate quite stable, now pervasive short-term (i.e., centennial to millennial scale) climatic variability is become apparent from several Mediterranean continental and marine records (e.g. Drysdale et al., 2007; Klotz et al., 2004; Milner et al., 2016; Mokeddem et al., 2014; Regattieri et al., 2014, 2015, 2016a, 2017). This climate fluctuations are related to glacial advance/retreat detected in the northern Atlantic Ocean (Bond events: Bond et al., 1992, Bond and Lotti, 1995; Heinrich events: Bond et al. 1993; Broecker, 1994; Surface ocean cooling: McManus et al., 1994; Oppo, 2006) and in the Greenland ice cores (Dansgaard-Oeschger events: Dansgaard et al., 1993).

Lake Ohrid sediments come from an extraordinary composite sequence 569 m long (DEEP core) retrieved in the frame of the project SCOPSCO (Scientific Collaboration on Past Speciation

Conditions in Lake Ohrid), whose drilling was financed by the ICDP (International Continental Scientific Drilling Program). The project was created in order to: (1) obtain a continuous record containing information about the origin and the age of the lake, (2) investigate the regional seismic and tectonic history, and (3) evaluate the influences of geological and climatic events on biotic evolution which led to the extraordinary endemic biodiversity (300 species) of the catchment area.

Preliminary results confirmed the exceptionality of Lake Ohrid. Its long continuous sedimentation history (more than 100 ka, Albrecht and Wilke, 2008), probably starting between 1.9 and 1.2 Ma (Wagner et al., 2014; Lindhorst et al., 2015) makes it the oldest lake in Europe and one of the most ancient in the world (Wagner et al. 2014; Lindhorst et al., 2015). This distinctive characteristic suggests that Lake Ohrid can be considered a key role site for the investigation of the climatic changes occurred through the millennia in Mediterranean area, as already shown by sedimentary records recovered in previous drilling campaigns (e.g. Lezine et al., 2010; Sulpizio et al., 2010; Vogel et al., 2010; Wagner et al., 2008, 2014, and 2017).

The upper 247.8 m of DEEP core have been previously investigated in order to obtain lithological, sedimentological and (bio) geochemical data. The age model is based on 11 tephra layers and on tuning of bio-geochemical proxy data to orbital parameters. Results reveal an undisturbed and continuous archive of data spanning the last 637 ka (see Wagner et al., 2017).

Data of this thesis derive from the study of pollen grains extracted from the lacustrine sediment of Lake Ohrid by a long routine chemical treatment, consisting of a series of acid and basis attacks (HCl 37%, HF 40% and NaOH 10%) to obtain a residue enriched in pollen suitable for observation and identification at transmitted light optical microscope. Pollen rain preserved in anoxic sediments is an invaluable investigative tool to reconstruct past environments (e.g. Fægri and Iversen, 1989; Birks et al., 2016) and quantify climate changes (e.g. Cheddadi et al., 1998; Guiot, 1990; Peyron et al., 2013), due to the relation between pollen grains production and climate conditions. Indeed, climate strongly influences the distribution and composition of vegetation, because every plant tolerates different ranges of temperature and moisture (Woodward, 1987).

Until today several pollen studies from lacustrine records have been made for the LIC period in Europe: Les Echets (eastern France, Beaulieu et Reille, 1984), Ribains (S-E France, Beaulieu and Reille, 1992b; Kukla et al., 2002), La Grande Pile (N-E France, Beaulieu and Reille, 1992b; Woillard 1978), Bouchet/Praclaux (southern France, Reille and Beaulieu, 1990; Reille et al., 1998), Mondsee (N-W Austria, Müller, 2000), Bispingen (northern Germany, Muller 1974), Furamoos (Southern Germany, Muller et al., 2003), Valle di Castiglione (central Italy, Follieri et al., 1988), Lago di Vico (central Italy, Magri and Sadori, 1999), Lagaccione (central Italy, Magri 1999), Lago Grande di Monticchio (southern Italy, Allen et al., 2009; Brauer et al 2007), Ioannina (western Greece, Frogley and Tzedakis 1999; Tzedakis, 1994a, 2003), Tenaghi Philippon, (N-E Greece, Milner et al., 2013; Tzedakis et al., 2006) and Kopais (S-E Greece, Tzedakis, 1999; Okuda et al., 2001) and Lake Prespa (transboundary lake between Albania, FYROM and Greece, Panagiotopoulos et al., 2014). While, in the near East, Lake Van (Litt et al., 2014; Pickarski et al., 2015) in eastern Turkey, Lake Urmia (Bottema, 1986; Djamali et al., 2008) in north-western Iran and Lake Yamounneh (Gasse et al., 2015) in northern Lebanon are the only long records with LIC. However, only few of these records have a sufficient temporal resolution to resolve short-term climatic oscillations within the LI and the onset of the Last Glacial., Thanks to the detailed chronology (see Francke et al., 2016; Wagner et al., 2017; Zanchetta et al., 2016) and the high time resolution analysis (roughly one sample every 400 years), this work on Lake Ohrid sediments is a valuable contribution to the knowledge of the period.

The thesis is organized as a collection of 5 articles (of which one in submission, consequently it may vary in their definitive version) from journals present in Scopus and in Web of Science (5). Four of them are published or submitted to journal classified Q1 in SJR (Scientific Journal Rankings).

The first CHAPTER (1) is composed by two articles (Bertini et al., 2016; Sadori et al., 2016), published respectively in Alpine and Mediterranean Quaternary 29 and Biogeosciences 13. In

Sadori et al. (2016) pollen data of the top 200 m of the DEEP sequence covering the last 500 ka and five glacial/ interglacial cycles (the sample resolution is 1600 years) are reported. I personally contributed with pollen identification and counting, analyzing 36 samples for Last Interglacial Complex (LIC, MIS 5) and 17 samples for Penultimate Glacial (MIS 6). In Bertini et al., 2016, the authors (myself included) summarized the main project results and described the protocol for laboratory and optical microscope analysis adopted for the entire research/project.

In CHAPTER (2) the article published in Biogeosciences 13 (Zanchetta et al., 2016) is presented. It focuses on the improvement of chronology for MIS 5 trough comparison of other data from Lake Ohrid and other Mediterranean sequences. Thanks to this new age model a more precise correlation with other records is possible. I personally contributed to the article with my MIS 5 high-resolution data and with interpretation and writing.

In CHAPTER (3) the article submitted to Quaternary Science Review (Sinopoli et al., 2018) is presented. It contains the high-resolution (400 years, 143 samples) analysis of the Last Interglacial Complex at Lake Ohrid. In the article pollen data are presented and compared with other pollen records and proxies from Mediterranean and North Atlantic areas. With this article I contributed to provide a new reference climatic series for southern Europe and to enhance the hypothesis of presence of forest refuges in the southern Balkans. I performed pollen identification and counting, writing most of the text. The article was sent back in the present, revised form, on 17 October.

In CHAPTER (4) the article in submission (Sinopoli et al., 2018) in which climatic quantifications using a multi-method approach are made on the basis of pollen results described in CHAPTER 3 is included. In Europe, for the Last Interglacial Complex, few records were investigated for climatic quantification and they are principally located to the north of Mediterranean (see Brewer et al., 2008). With this article I contributed to improve climatic data for the Mediterranean region and in particular for southern Europe. I performed climate reconstruction using R and writing most of the text.

In CHAPTER (5) all data obtained during the PhD course are reported and summarized.

In appendix I include the list of other publications / conference presentations I have produced during my PhD course.

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CHAPTER 1:

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

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Abstract. Lake Ohrid is located at the border between FYROM (Former Yugoslavian Republic of Macedonia) 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, 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 Scientific 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 depocentre of Lake Ohrid. The study is the fruit of a cooperative work carried out in several European palynological laboratories. The age model of this part of the core is based on 10 tephra layers and on tuning of biogeochemical proxy data to orbital parameters.

According to the age model, the studied sequence covers the last ~500 000 years at a millennial-scale resolution (~1.6 ka) and records 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 the marine isotope stratigraphy. The record shows a progressive change from cooler and wetter to warmer and drier interglacial conditions. This shift in temperature and moisture availability is visible also in vegetation during glacial periods.

The period corresponding to MIS11 (pollen assemblage zone OD-10, 428–368 ka BP) is dominated by montane trees such as conifers. Mesophilous elements such as deciduous and semi-deciduous oaks dominate forest periods of MIS5 (PASZ OD-3, 129–70 ka BP) and MIS1 (PASZ OD-1, 14 ka BP to present). Moreover, MIS7 (PASZ OD-6, 245–190 ka) shows a very high interglacial variability, with alternating expansions of montane and mesophilous arboreal

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taxa. Grasslands (open vegetation formations requiring relatively humid conditions) characterize the earlier glacial phases of MIS12 (PASZ OD-12, 488–459 ka), MIS10 (corresponding to the central part of PASZ OD-10, 428–366 ka) and MIS8 (PASZ OD-7, 288–245 ka). Steppes (open vegetation formations typical of dry environments) prevail during MIS6 (OD-5 and OD-4, 190–129 ka) and during MIS4-2 (PASZ OD-2, 70–14 ka).

Our palynological results support the notion that Lake Ohrid has been a refugium area for both temperate and montane trees during glacials. Closer 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 at 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 1960s when the pioneer pollen study of Wijmstra (1969) at Tenaghi Philippon (Greece) was published. The study of long lacustrine pollen records from southern Europe is 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 understanding 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 the Late Pleistocene (e.g. Sánchez Goñi et al., 1999; Tzedakis et al., 2004b). 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, 1994b), Kopais, in south-eastern 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 centres 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; Liepelt et al., 2009; 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 still have to be fully understood. From 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 the Former Yugoslavian Republic of Macedonia (FYROM) and Albania. As one of the biosphere reserves of the United Nations Educational, Scientific, and Cultural Organization (UNESCO), it 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., 2013, 2014), with macrophytes and phytoplankton communities (Panagiotopoulos et al., 2014; Cvetkoska 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), the Lake Ohrid record is a prime target to study past and present biodiversity and evolution.

The SCOPSCO (Scientific Collaboration on Past Speciation Conditions in Lake Ohrid) international science 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 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) to outline the flora and vegetation changes that occurred in the last half million years in the area surrounding Lake Ohrid, (2) to understand the glacial and interglacial vegetation dynamics, and (3) to correlate 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. Existing high-resolution pollen studies focusing on different time intervals (e.g. Tzedakis et al., 2004b, 2009; Tzedakis, 2007; Fletcher et al., 2010; Margari et al., 2010; Moreno et al., 2015) offer a more detailed picture of ecosystem dynamics in the Mediterranean region. High-resolution studies using the exceptional Lake Orhid archive are in progress for selected intervals (e.g. MIS 5–6, MIS 11–12 and MIS 35–42).

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 (Fig. 1). It is the deepest and 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).

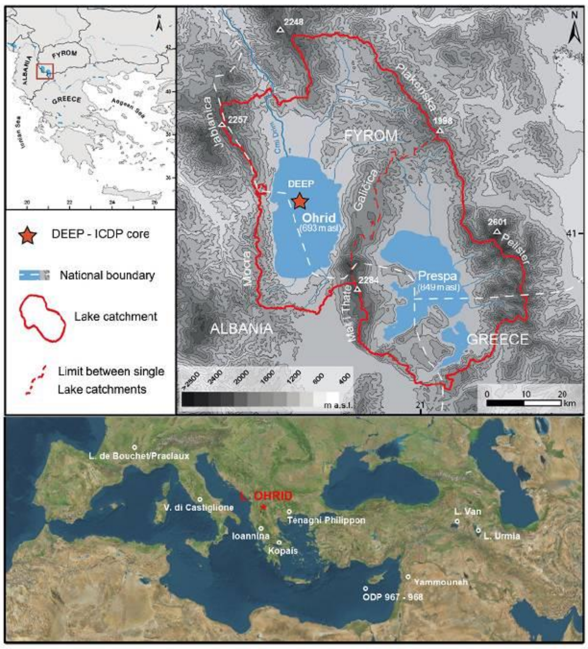

Figure 1. Map of Lake Ohrid modified from Panagiotopoulos (2013) and locations of terrestrial and marine records discussed in the text.

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 50 % by sub-lacustrine karstic flow and 50 % by surface inflow; river runoff is at present ~ 20 % of the total inflow and was even lower prior to 1962, when the Sateska River 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 its outflow is artificially controlled. Lake Ohrid is separated from Lake Prespa, which is situated at 849 m a.s.l. (~ 150 m higher), by the Galičica mountain range (Fig. 1). The two lakes are hydrologically connected through underground karst channels. Diatom palaeoecology shows that, despite the hydrological connectivity, the lake ecosystems respond independently to external forcing (Cvetkoska et al., 2015b). 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; Popovska 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 reduce 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 from −2.3 to 6.6 °C in 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 the international literature. The main source of information is from a detailed survey carried out in Galičica National Park (Matevski et al., 2011). Concerning the flora, the Mediterranean and Balkan elements dominate, but several central European species are also widespread in the area. The vegetation is organized into altitudinal belts, which develop from the lake level (700 m) to the 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* and *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 pasture lands and grasslands are found over the timberline, currently at around 1900 m (Matevski et al., 2011). The western slopes of the 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 relics and are located in the wider region of Lake Ohrid. These include populations of *Pinus peuce* (Macedonian pine) 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 Pelister (to the east) National Parks in FYROM (Panagiotopoulos, 2013; Panagiotopoulos et al., 2013; http://www.exploringmacedonia.com/national-parks.nspx). *Pinus peuce* (Alexandrov and Andonovski, 2011) shows a high ecological adaptability. Cold mountain climate and high air humidity are the most suitable conditions for Macedonian pines. They naturally grow mainly on silicate terrains and, less often, on carbonate ones at an elevation of 800–900 up to 2300–2400 m a.s.l., while the most favourable habitats occur between 1600 and 1900 m altitude. *Pinus nigra* forests are widespread in the 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 characterize the lake shores: the 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. (2016). 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 below lake floor (m b.l.f.) have been recovered from seven different boreholes at a water depth of 243 m. Until today, a continuous composite profile down to 247.8 m composite depth (mcd) with a recovery of > 99 % has become available, and sub-sampling was carried out at 16 cm resolution (Francke et al., 2016).

3.1 Core chronology

The DEEP core chronology down to 247.8 mcd (Francke et al., 2016) is based on radiometric ages of 11 tephra layers (first-order tie points), and on tuning of biogeochemical proxy data to orbital parameters (second-order tie points; Laskar et al., 2004). The second-order tie points were obtained by tuning minima in total organic carbon (TOC) and TOC / TN against increasing summer insolation and winter season length. The timing of increasing summer insolation and winter season length caused cold and dry conditions in the Balkan Peninsula (Tzedakis et al., 2006; Francke et al., 2016), which may have led in Lake Ohrid to restricted primary productivity during summer and prolonged mixing and better decomposition of organic matter during winter. This likely resulted in low TOC and a low TOC / TN ratio (Francke et al., 2016). 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 with well-known eruptions of Italian volcanoes and a re-calibration of radiometric ages from the literature have been carried out by Leicher et al. (2015).

3.2 Pollen analysis

Sample processing and pollen microscope analysis are the fruit of strict cooperative work by several investigators across many European laboratories. Prior to the pollen analysis, considerable time was invested in assessing and standardizing the treatment protocol and pollen identification issues. More specifically, (1) we joined previous lists of taxa that were derived from older studies in Lake Ohrid and the western Balkans and produced a final list that has been accepted by all the analysts; (2) we thoroughly elaborated on systematic issues like synonyms and different degrees of pollen determination, particularly focusing on the identification of problematic taxa; (3) we shared pollen pictures of key taxa (e.g. oak types) and of dubious ones; (4) we also performed analyses of samples from the same core depth in different laboratories. Samples were mostly distributed in batches of consecutive samples; and (5) finally, close checks were performed at the intervals where two different analysts' samples met in order to avoid any potential identification bias.

A total of 306 sediment samples at 64 cm intervals down to the depth of 197.55 m taken from the DEEP core have been chemically processed for palynology in order to establish an overview diagram (named the skeleton diagram hereafter) spanning the past ~ 500 ka. According to the age model by Francke et al. (2016), 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, two tablets containing a known number of *Lycopodium* spores (Stockmarr, 1971) were 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 percentages have been calculated excluding *Pinus* from the PS due to its high overrepresentation in a large number of samples. The *Pinus* percentage was calculated on a different pollen sum which includes pines.

Oak pollen has been divided into three types according to morphological features following Smit (1973): *Quercus robur* type, which includes deciduous oaks, *Quercus ilex* type including the evergreen oaks minus *Q. suber*, and *Quercus cerris* type, including semi-deciduous oaks and *Q. suber*. Further identifications follow Beug (2004), Chester and Raine (2001) and Reille (1992, 1995, 1998). *Juniperus* type includes pollen grains of *Cupressus*, *Juniperus* and *Taxus*. Pollen curves/diagrams (Fig. 2, 3 and 4) were drawn using the 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). Given the millennial temporal resolution of the skeleton diagram and considering the ongoing and planned high-resolution studies, we assigned 13 (i.e. OD-1 to OD-13) Pollen Assemblage SuperZones (PASZ, sensu Tzedakis, 1994a) that correspond to major shifts in glacial–interglacial vegetation. This approach allows for the definition of new pollen zones and subzones within these superzones as high-resolution (centennial) data from the Lake Ohrid archive will emerge.

4 Results and discussion

We present data in two pollen diagrams: (i) a percentage pollen diagram (main taxa) based on the sediment depth scale and including lithostratigraphy and tie points used to assess chronology of the DEEP site sequence (Francke et al., 2016, Fig. 2); (ii) a pollen diagram showing the percentage sums of ecological groups and selected concentration curves drawn according to the age scale (Fig. 3).

In total, 296 samples (97 % of the total analysed) yielded low–medium to high pollen concentrations allowing a detailed palynological analysis. Samples with counts less than 80 terrestrial pollen grains were excluded from the diagram. Mean pollen counts of 824 terrestrial pollen grains have been achieved. The physiognomy of vegetation shows maximum variability: arboreal pollen (AP) ranges from 19 to 99 % (Fig. 2). The total pollen concentration of terrestrial taxa 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. Pollen preservation was good, allowing most times identification of individual taxa. The number of identified taxa is 175, encompassing 143 terrestrial and 10 aquatic plants.

The main vegetation features are summarized in Table 1. The pollen record was subdivided into 13 main pollen assemblage superzones (PASZ, OD – named after the Ohrid DEEP core) on the basis of changes in AP versus non-arboreal pollen (NAP), changes in pollen concentration and major changes in single taxa. The most abundant taxon is *Pinus*. Given the uncertainties on the origin of the high pollen percentages of *Pinus*, exceeding 95 % in some samples, we decided to remove *Pinus* from the pollen sum (Figs. 2, 3 and 4, Table 1) used as the basis for all percentage calculations. The only exception is in Fig. 3, where we also present the AP–NAP diagram with *Pinus* included in the pollen sum.

4.1 Vegetation and climatic inferences based on the skeleton diagram

Climate variability paces the pronounced intra-interglacial vegetational shifts inferred from the pollen record, while different patterns of ecological succession emerge during interglacials (Fig. 3).

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

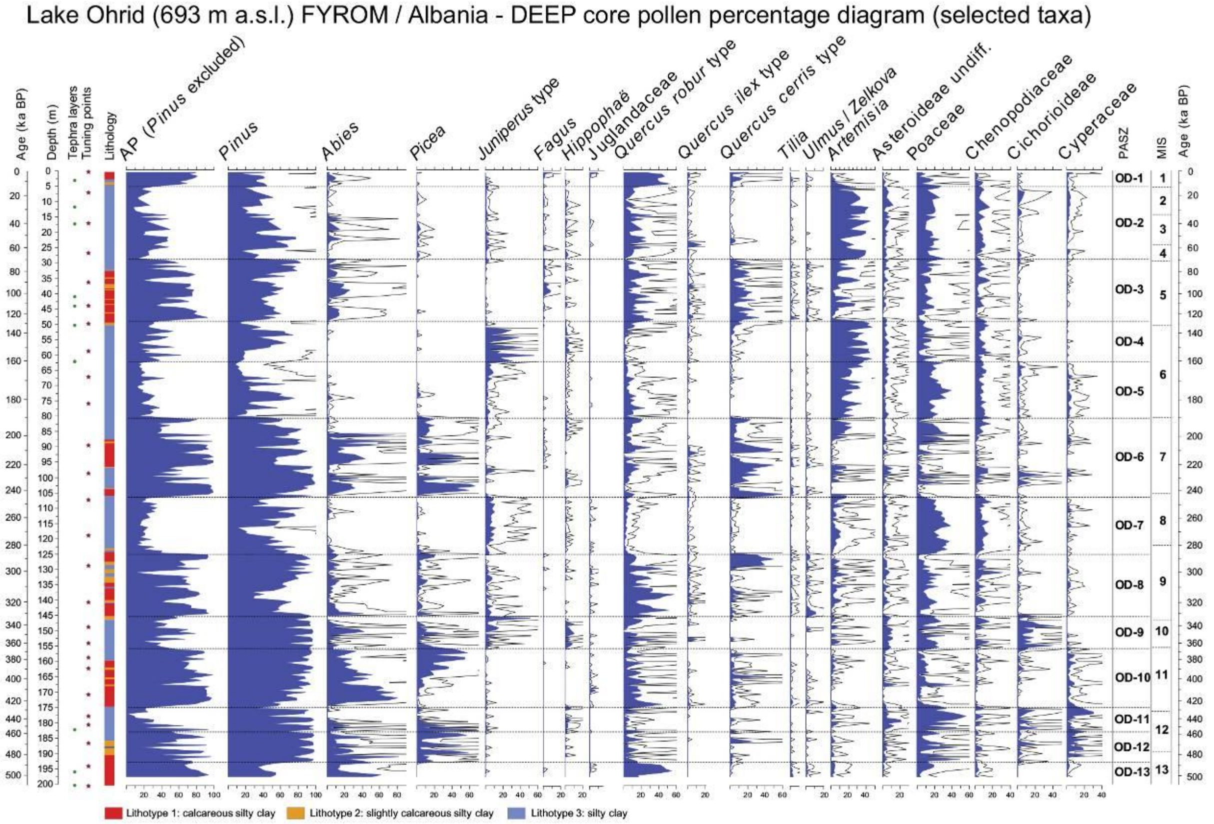

Figure 2. Lake Ohrid (FYROM), DEEP core. Pollen percentage diagram of selected taxa against depth scale. Lithology, tephra layers and tuning points adapted from Francke et al. (2016).

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 some higher-order variability have been previously reported from south-eastern Europe, i.e. Ioannina (MIS6: Roucoux et al., 2011) and Tenaghi Philippon (MIS8: Fletcher et al., 2013). Ongoing high-resolution studies will help define dynamics of specific taxa, revealing extinctions and detecting possible new refuge areas.

A close look at the Lake Ohrid pollen record reveals distinct characteristics for glacial and interglacial phases 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 found during older glacial phases (OD-12, OD-11 and OD-9; Table 1) when *Pinus* pollen show high percentages and medium/high concentrations that appear reduced only at the end of OD-11 (Figs. 3, 4). Interglacial/interstadial periods are characterized by expansions of woodland organized in vegetation belts (e.g. forests with *Abies*, *Picea*, *Quercus robur* type, *Q. cerris* type) and by increases in AP–*Pinus* pollen concentration. This general pattern of glacial–interglacial alternations is at times punctuated by minor expansions of AP during glacials and accordingly by forest opening (stadials) during interglacial complexes. This is in agreement with previous studies from Greece, e.g. Ioannina (Tzedakis, 1994b; Tzedakis et al., 2002; Roucoux et al., 2008, 2011) and Tenaghi Philippon (e.g. Milner et al., 2012; Fletcher et al., 2013; Pross et al., 2015), and from central Italy (Follieri et al., 1998), suggesting a sensitive response of vegetation to climate change on a regional scale in south-eastern Europe. At Lake Ohrid, most tree taxa show a rather continuous presence, even during glacial phases, suggesting that the Ohrid region has been a plant refugium. The investigation of dynamics of specific taxa and 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

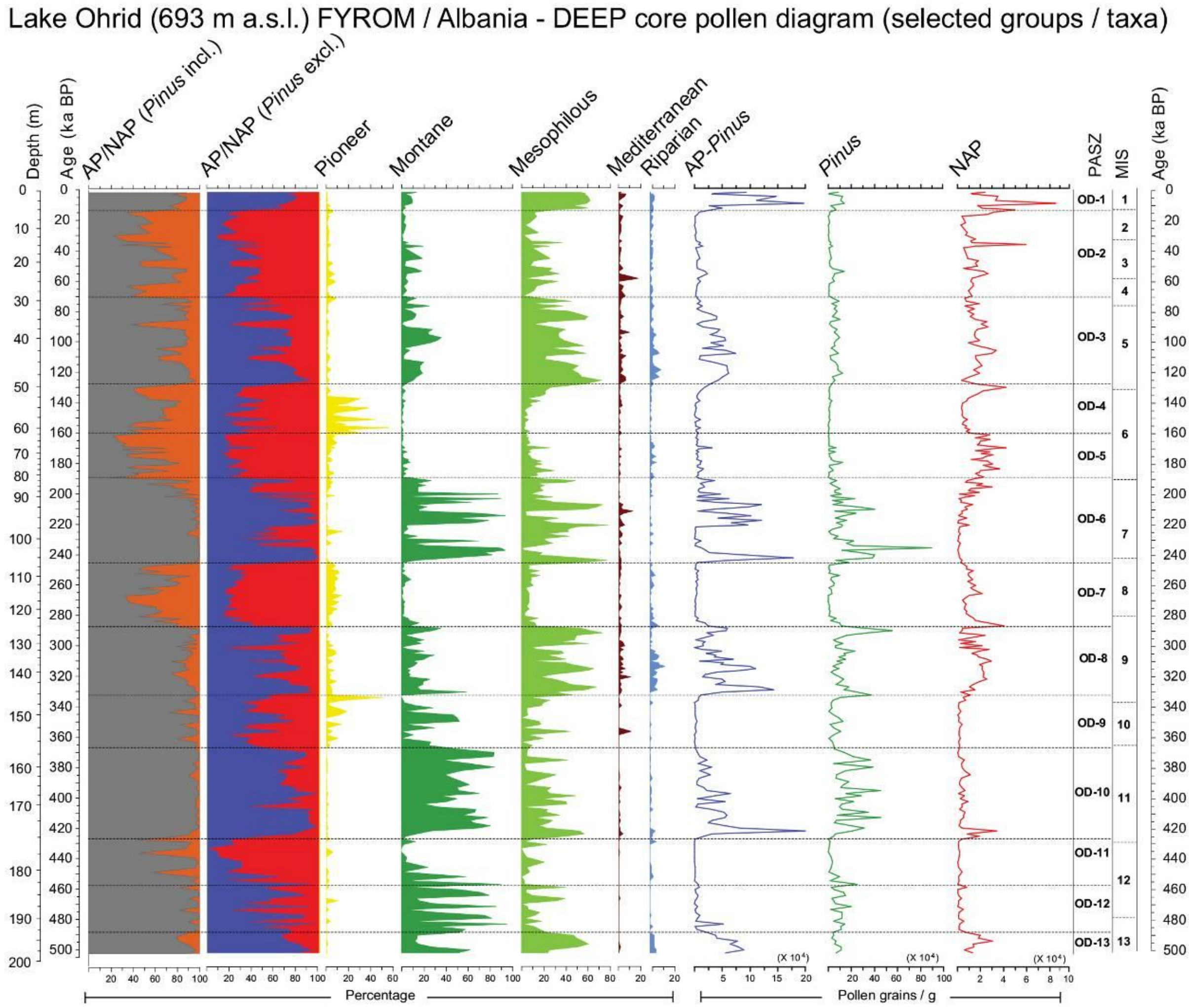

Figure 3. Lake Ohrid (FYROM), DEEP core. Pollen diagram of selected ecological groups (%) and concentration curves against chronology (Francke et al., 2016). Ecological groups: montane trees (*Abies*, *Betula*, *Fagus*, *Ilex*, *Picea*, *Taxus*); mesophilous trees (*Acer*, *Buxus*, *Carpinus betulus*, *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*).

pollen zones and marine isotope stages are often not identical (Figs. 2, 3).

Glacial periods (PASZ OD-12, 11, 9, 7, 5, 4, 2, Table 1) are generally characterized by dominance of Poaceae, *Artemisia*, and Chenopodiaceae that are indicative of open environments around the lake. Poaceae probably include aquatic macrophytes from the lacustrine belt and herbs from grassland formations in the catchment of Lake Ohrid. *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* can either point to the local presence of widespread thickets like those currently growing at very high elevations in the surroundings of the lake, or to transport from a long distance in a barren land. Another aspect to consider is that a large lake such as Ohrid could partially resemble the marine realm, leading to over-representation of pollen grains that float easily. But this should be a constant factor in the analysed records, unless big changes in the lake surface occurred. The available seismic data, not completely processed yet, suggest anyway (K. Lindhorst and S. Krastel, personal

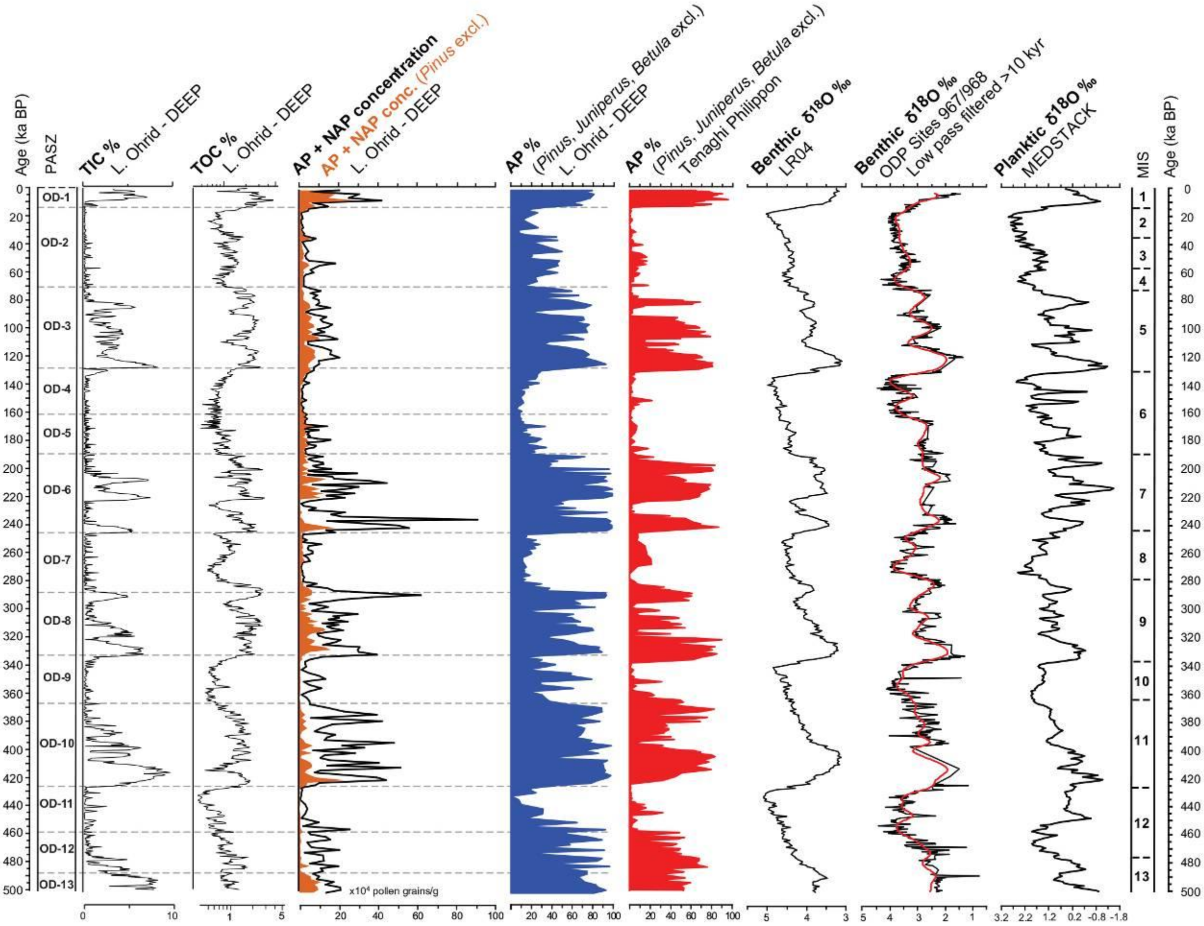

Figure 4. Comparison of selected proxies from Lake Ohrid with other records spanning the last 500 ka drawn against original age models. Lake Ohrid: total organic carbon, TOC, total inorganic carbon, TIC (Francke et al., 2016); total pollen concentration of terrestrial plants (AP + NAP) and the same without *Pinus*, AP percentages (this study). Tenaghi Philippon: AP % excluding *Pinus*, *Betula* and *Juniperus* (Wijmstra, 1969 and Wijmstra and Smit, 1976; age model from Tzedakis et al., 2006). Marine records: LR04 δ^{18}O benthic stack (Lisiecki and Raymo, 2005); stacked benthic δ^{18}O data for ODP sites 967 and 968 from the eastern Mediterranean (Konijnendijk et al., 2015); MEDSTACK planktic δ^{18}O data (Wang et al., 2010).

comments, 2015) that the lake size was not significantly different prior to 330 ka.

In contrast, interglacial complexes (PASZ OD-13, 10, 8, 6, 3 and 1, Table 1) are marked by expansions of woods dominated by *Abies*, *Picea*, the *Quercus robur* type and the *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 pollen diagram shows that, in the past 285 ka (PASZ OD-7 to OD-1), non-forested periods (herb-dominated) prevailed and that their duration was longer than between 500 and 285 ka. Forest phases show wetter and cooler conditions in the lower part of the diagram (PASZ OD-13 to OD-8, 502–288 ka) as indicated by the dominance of conifers, while in the upper part (PASZ OD-3 and OD-1, 129 ka–present) there was a "general" increasing trend in temperature indicated by the presence of mesophilous broadleaved trees. In OD-6 (245–190 ka) a balanced alternation of the two vegetation "types" can be observed.

This general trend is visible in the reduction of montane trees present in OD-10 and 12 (roughly corresponding to MIS11 and 13) and the expansion of mesophilous and Mediterranean taxa in the present and penultimate interglacials (Fig. 3). The pre-penultimate interglacial (OD-8, 333–288 ka, cf. MIS9) shows increased mesophilous trees. The penultimate interglacial (OD-6, 245–190 ka, cf. MIS7) shows intermediate features, with balanced presence of montane and mesophilous taxa. This trend seems to be con-

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

PASZ		Zone description
OD-1	Depth limits (m) 5–0 Age limits (ka) 14–0 Duration (ka) 14 Pollen sample no. 9 Mean pollen count 353	Mesophilous tree taxa prevail. Forests are characterized by the *Quercus robur* type (22–43 %) and the *Q. cerris* type (2–21 %). Montane taxa are quite scarce and mainly represented by *Abies* and *Fagus*. Riparian and mediterranean trees are not abundant either. Poaceae are dominant among herbs. Pollen concentration is high.
OD-2	Depth limits (m) 29–5 Age limits (ka) 70–14 Duration (ka) 56 Pollen sample no. 26 Mean pollen count 270	Open vegetation (steppe) with low/medium values of *Pinus* (9–77 %) and sparse presence of many montane and mesophilous taxa. Among them the *Q. robur* type is worth mentioning. *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) 48–29 Age limits (ka) 129–70 Duration (ka) 59 Pollen sample no. 31 Mean pollen count 660	Alternation of periods characterized by mesophilous/montane trees and open vegetation. Forests are mainly characterized by expansion of the *Q. cerris* type (2–33 %) and the *Q. robur* type (4–40 %) together with *Abies* and *Fagus*, this last one 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) 62–48 Age limits (ka) 160–129 Duration (ka) 31 Pollen sample no. 21 Mean pollen count 352	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) 80–62 Age limits (ka) 190–160 Duration (ka) 30 Pollen sample no. 28 Mean pollen count 320	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) 106–80 Age limits (ka) 245–190 Duration (ka) 55 Pollen sample no. 41 Mean pollen count 1484	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 the *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) 288–245 Duration (ka) 43 Pollen sample no. 27 Mean pollen count 605	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.
OD-8	Depth limits (m) 145–125 Age limits (ka) 333–288 Duration (ka) 45 Pollen sample no. 31 Mean pollen count 804	Mesophilous tree taxa prevail. Forests are characterized by the *Quercus robur* type (5–55 %) and the *Q. cerris* type (0–50 %). Riparian and mediterranean trees are worth mentioning. Poaceae are dominant among herbs. Pollen concentration is high.
OD-9	Depth limits (m) 155–145 Age limits (ka) 366–333 Duration (ka) 33 Pollen sample no. 16 Mean pollen count 438	Open vegetation with relatively high values of pioneer taxa. *Pinus* (60–98 %), the *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.

Table 1. Continued.

PASZ		Zone description
OD-10	Depth limits (m) 175–155 Age limits (ka) 428–366 Duration (ka) 62 Pollen sample no. 31 Mean pollen count 1665	Forests characterized first by the *Quercus robur* type (0–43 %) and the *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) 183–175 Age limits (ka) 459–428 Duration (ka) 31 Pollen sample no. 12 Mean pollen count 810	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) 193–183 Age limits (ka) 488–459 Duration (ka) 29 Pollen sample no. 16 Mean pollen count 1513	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) 502–488 Duration (ka) 14 Pollen sample no. 7 Mean pollen count 342	Mesophilous and montane tree taxa prevail. Forests first with *Abies* (11–51 %) and then with the *Q.robur* type (16–54 %). Poaceae are dominant among herbs. Pollen concentration is high.

firmed also by herbs: Poaceae and Cyperaceae decrease, while *Artemisia* and Chenopodiaceae increase towards the top of the diagram. Steppes and steppe forests seem to characterize the last two glacial periods.

OD-12 (488–459 ka) shows a dominance of AP and the overwhelming presence of pine pollen. This suggests that this period, corresponding to the first part of the MIS12 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 lake basin. In the following zone OD-11 (459–428 ka), stronger glacial conditions are evidenced by decreased AP and increased herbs. 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 relative humidity recorded at Lake Ohrid during the second part of MIS12 (OD-11) is consistent with the high endemism and biodiversity of the site. The buffering capacity of the lake has to be considered together with the possibility that a part of pine pollen could be from *Pinus peuce*, a species with high ecological plasticity, which currently has only a relict distribution and is adapted to cold and moist conditions (Aleksandrov and Andonovski, 2011). The surrounding area of the lake could have acted as a refugium for conifers such as Macedonian pines. The relatively low abundance of the xerophytic Mediterranean "ecogroup" also supports this view.

If we do not consider pine, the passage to the following interglacial (OD-10, 428–366 ka) is marked by an important and multi-millennial-long expansion of *Abies* (accompanied by the *Quercus robur* type) followed by a ∼ 10 ka-long expansion of *Picea* (accompanied by the *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, which has also been documented in Praclaux (de Beaulieu et al., 2001) and in the central European lowlands (Koutsodendris et al., 2010), 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 at higher elevations or in poor soils), while deciduous oaks (*Quercus robur* type) first, and subsequently semi-deciduous oaks (*Quercus cerris* type), were most likely growing at lower elevations.

Glacial conditions prevailed during zone OD-9, 366–333 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 that still need to be further investigated.

The following interglacial OD-8, 333–288 ka (cf. MIS9), shows a three-phase widespread mesophilous arboreal expansion. The *Quercus robur* type prevailed in the first and longer phase, while the *Q. cerris* type at the end of the zone indicated a successive change from warmer and wetter to cooler and drier conditions interrupted by short cool events (NAP increases).

OD-7, 288–245 ka (cf. MIS8) shows low AP percentages (pioneer vegetation mainly consisting of the *Juniperus* type is rather abundant) and increased values of Poaceae. Even if Poaceae pollen could originate 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 south-eastern Europe (e.g. Tzedakis et al., 2001; Pross et al., 2015).

OD-6 (245–190 ka) shows a very high forest variability, with three expansions of trees interrupted by two herb expansions. This interglacial/interstadial complex, 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 suggested 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 in the *Artemisia* percentage in the diagram.

A long glacial phase is represented in OD-5 (190–160 ka) and OD-4 (160–129 ka). The limit between the two open formations is marked by a change from a grassland-dominated environment (Poaceae and Cyperaceae) to a steppe-dominated (*Artemisia*) one. Dry conditions are also indicated by a decreasing *Quercus robur* type and an 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 diagram. This is in good agreement with hydro-acoustic data and sediment core analyses from the north-eastern 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., 2016) show that an accumulation of thin mass movement deposits (MMD) occurred during the second part of MIS6, which might be also indicative of low lake levels.

Forests of OD-3, 129–70 ka (cf. MIS5) are characterized by less variability than the previous OD-6 interglacial/interstadial complex. 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 PASZ OD-2 (70–14 ka). It has a rather high variability, evidenced, already at this step of analysis, by important oscillations of most trees.

The present interglacial is characterized by the strong and prominent expansion of the *Quercus robur* type accompanied by the *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 FYROM, where spruce is represented by relic populations in few forested areas. During the penultimate glacial (MIS6), *Picea* populations were probably too near to their tolerance limit to survive. The importance of ecological thresholds for temperate trees was carefully investigated in three Greek records located in contrasting bioclimatic areas (Ioannina, Kopais, Tenaghi Philippon; Tzedakis et al., 2004a). This turned out to be crucial to understand the importance of local factors in modulating the biological response to climatic stress that occurred in the last glacial and to comprehend the present-day distribution of arboreal species in the Balkans.

4.2 Comparison with other proxies and outlook

In Fig. 4 alignment of the TOC, 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 tight coupling 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 (488–459 ka) and OD-9 (368–333 ka).

The similarity between Lake Ohrid and Tenaghi Philippon curves is striking. All the main changes in forest cover match, and they both correspond to marine records too. There are some differences in the timing of the onset of interglacial phases. DEEP core chronology benefited in fact from the presence of several tephra layers (see Fig. 2, Leicher et al., 2015). 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 the Kopais (Okuda et al., 2001) areas, resulted in not being ideal refugia for mesophilous trees (Tzedakis et al., 2004a). 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, 1994b; Tzedakis et al., 2002, 2004a).

Besides a close correspondence to the 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; Railsback et al., 2015), 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 interglacials that are also observed in the pollen data. For example, the tripartite forests 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 with the orbitally tuned Mediterranean isotope records, and provide a finer tuning of the present age model (Francke et al., 2016) to independently dated records in the Mediterranean region where 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 complemented by many sedimentological proxies highlighting the need for a multi-disciplinary approach in palaeoenvironmental studies (see all other 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 contributed to the high plant diversity encountered at Ohrid at present. This has deep roots in the past, as the lake has probably acted as a permanent water reservoir providing moisture 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 is summarized by the following key findings.

- The continuous record of glacial–interglacial vegetation successions shows that refugial conditions occurred in the Lake Ohrid area. Tree extinction, whose timing and patterns need accurate checks and refined analyses, will be focused on in a dedicated study.
- A clear shift from relatively cool/humid interglacial conditions prior to 288 ka BP, to warmer and drier ones during recent interglacial periods (last ~ 130 ka), suggests changing patterns toward a more Mediterranean-type climate. During the period that occurred between 245 and 190 ka (MIS7), a very high forest variability is found during interglacials and interstadials. 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.
- A close correspondence of interglacial and glacial climate and vegetation evolution to regional benthic and planktic isotope data is apparent. The Ohrid pollen record integrates temperature data from the marine stratigraphy, with a clear indication of humidity/dryness changes.

Author contributions. This article is the product of strict cooperative work among palynologists who all contributed to the Lake Ohrid pollen analysis and its interpretation. The manuscript was written by L. Sadori with substantial contribution of T. H. Donders, A. Koutsodendris and K. Panagiotopoulos. A. Masi (c.a.) was responsible for data management and refined diagrams drawn by T. H. Donders and A. Koutsodendris. All coauthors contributed to the writing of this paper.

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ALL TOGETHER NOW: AN INTERNATIONAL PALYNOLOGICAL TEAM DOCUMENTS VEGETATION AND CLIMATE CHANGES DURING THE LAST 500 KYR AT LAKE OHRID (SE EUROPE)

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ABSTRACT: Lake Ohrid (Balkan peninsula) is the oldest European extant lake and one of the deepest and largest. Such a unique, terrestrial natural archive is especially relevant for both paleoenvironmental and paleoclimatic reconstructions but also for genetic studies. In the frame of the International Continental Scientific Drilling Program (ICDP), a deep drilling campaign was carried out within the scope of the Scientific Collaboration on Past Speciation Conditions in Lake Ohrid (SCOPSCO) project in 2013. Here, we present the summary of palynological analyses carried out in the upper 200 m of the overall 569 m long DEEP site sediment succession from the central part of the lake. These studies, performed by an international palynological team, document the main floristic, vegetation and climate changes during the last ca 500 kyr, at a millennial-scale resolution (~1.6 kyr). The continuous sediment infill permitted to trace multiple non-forested/forested phases as a response to Glacial/Interglacial cycles as well as to sub-Milankovitch climate changes. The pollen record, corresponding with marine isotope stages MIS 13 to MIS 1, points to a progressive change from cooler and wetter to warmer and drier interglacials. New palynological studies are underway to reconstruct vegetational and climatic conditions over older intervals as well as to obtain high resolution data for some key intervals such as MIS 5-6, MIS 11-12, MIS 35-42. The complete record of changes in flora composition and vegetation during both glacials and interglacials will furnish indispensable insights for understanding the role of refugia, ecosystem resilience and maintenance of terrestrial biodiversity in the Mediterranean area.

Keywords: Lake Ohrid, pollen, flora, vegetation, climate, Pleistocene, Balkan peninsula

1. INTRODUZIONE

In 2013, within the frame of the International Continental Scientific Drilling Program (ICDP), a deep drilling campaign was carried out as part of the Scientific Collaboration on Past Speciation Conditions in Lake Ohrid (SCOPSCO) project, on the Balkan peninsula (Fig. 1). Several sites in Lake Ohrid (LO in the following), with the deepest one having a depth of some 568 m, were drilled to address several scientific aims (Wagner et al., 2014). Most important is to define both the depositional context and the range of past natural variability and magnitude of climate changes within a coherent chronologic frame.

Previous molecular clock analyses of DNA on endemic genera (e.g. *Dina*, Hirudinea, Erpobdellidae) that have evolved within the lake suggested, by estimating the onset of intralacustrine diversification, a time frame of approximately 2-3 Ma (Trajanovski et al., 2010). However recent evidence indicates an age of 1.2-1.9 Ma for the origin of LO (Wagner et al., 2014; Lindhorst et al., 2015). The occurrence of freshwater endemic species (including both flora and fauna taxa) was also a prime motivation for the study of present conditions at LO in order to observe their response to the increasing anthropogenic pressure in the lake. Based on field surveys, monitoring data, published records, expert interviews, conservation concerns and associated major threats were traced (e.g. Kostoski et al., 2010).

Palynology, together with a large amount of geological and stratigraphical investigations (Franke et al., 2016) was applied to the study of the LO sedimentary succession since 2014, especially to provide evidence on the history of changes of both flora composition and vegetation structure. Both items are indispensable for climate deductions as well as to assess the distribution

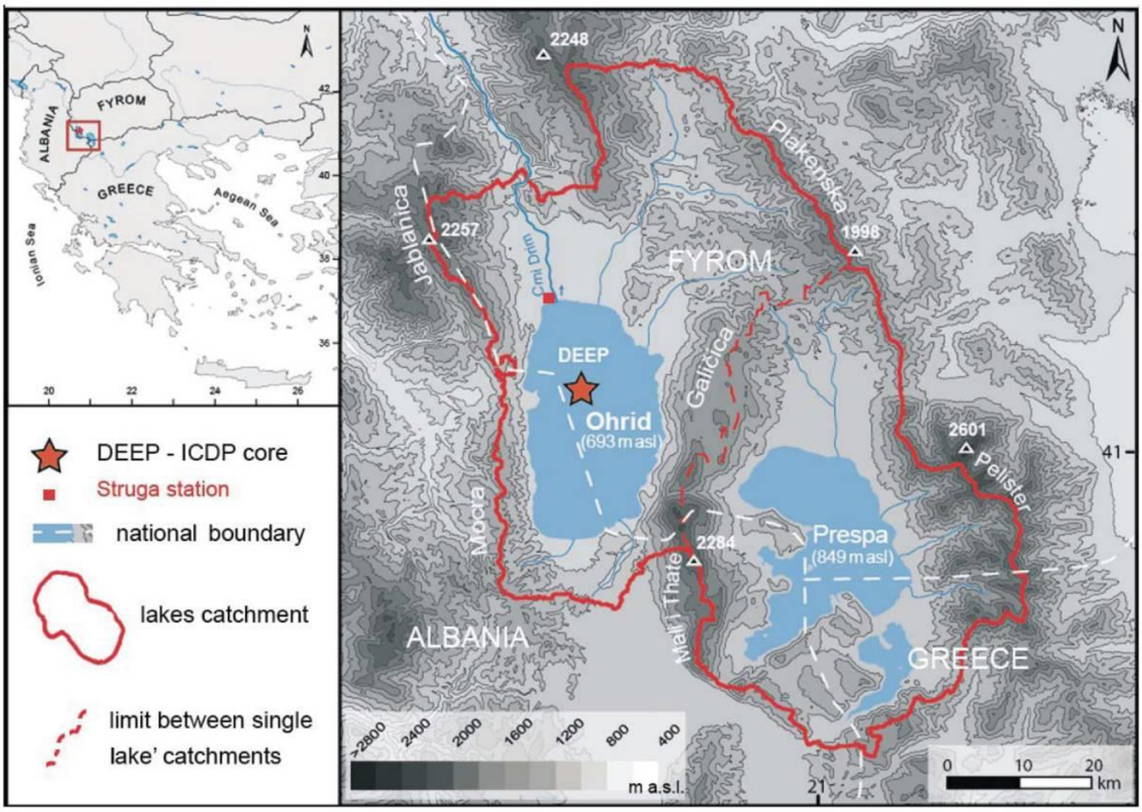

Fig. 1 - Location map of Lake Ohrid (modified from Panagiotopoulos, 2013).

of plant refugia in southern Balkans, i.e. one of the three Mediterranean refuge areas so far identified along with southern Iberian Peninsula and southern Italy. Such evidence is especially relevant to get a better understanding of the role played by (glacial) refugia in vegetation dynamics during the Pleistocene in Europe (e.g. Médail & Diadema, 2009; Fletcher et al., 2013; Tzedakis et al., 2013 and references therein). Here we summarize and discuss the first results of palynological studies, carried out by an international team of palynologists, from the upper part of the DEEP site sediment succession and covering the last 500 kyr (Francke et al., 2016; Sadori et al., 2016). The palynology work schedule for the year 2016 is also presented.

2. GENERAL SETTING

Lake Orhid (40°54′-41°10′ N and 20°38′-20°48′ E; Fig. 1) is located at the border between Albania and the Former Yugoslav Republic of Macedonia (FYROM), at an altitude of 693 m above sea level (a.s.l.). The ICDP deep drilling campaign took place using the Deep Lake Drilling System (DLDS) operated by the Drilling, Observation and Sampling of the Earths Continental Crust (DOSECC) consortium, in spring 2013. More than 2100 m of sediments were recovered from four different drill sites (Figs 2, 3); onsite core processing comprised analyses of core catcher material and magnetic susceptibility measurements. All cores were shipped to the University of Cologne for in progress and future analyses (Figs 4, 5; i.e. lithological, sedimentological, and biogeochemical). The main drill site in the central part of the lake (Fig. 1; 41°02'57" N, 20°42'54" E) permitted to recover 1526 m of core in total (DEEP site 5045-1) in six overlapping holes down to a maximum composite depth of 569 m. For more details see Francke et al. (2016) and references therein.

2.1. Present features

Lake Ohrid, 30.3 km long and 15.6 km wide, covers an area of ca 360 km^2 (Fig. 1); its maximum water depth is 293 m. LO is mainly fed by groundwater from karstic sources in the relatively small natural catchment area of 1042 km^2, which was artificially enlarged to 1487 km^2 in 1962 (Matzinger et al., 2006). However the occurrence of several surface springs and possibly also some subaquatic inflows from the nearby Lake Prespa (10 km to the east, at 849 m a.s.l., i.e. around 150 m above LO from which is separated by the Galičica mountain range) are responsible for a larger effective size of the catchment (Stankovic, 1960; Matzinger et al., 2006; Fig. 1). The surface outflow of LO is the river Crni Drim in the northern part of the lake, which accounts for 63% of the water loss, with the remaining 37% accounted for by

Fig. 2 - The barge at the deep site at lake Ohrid (photo courtesy S. Schorr).

Fig. 3 - The HBI boat/Core handing at Lake Ohrid on April 2013. On board researchers of Cologne university: B. Wagner, N. Leicher and F. Wild. (photo courtesy S. Schorr)

Fig. 4 - Cores in the refeer at the University of Cologne (a, b), (photo courtesy S. Schorr)

Fig. 5 - Core description and processing at the University of Cologne. At work N. Leicher and colleagues. (photo courtesy S. Schorr).

evaporation (Watzin et al., 2002). The current lake state is oligotrophic, due to the large water volume and the low nutrient availability (Wagner et al., 2010). The thermopluviometric diagram of the Struga meteorological station shows the main climate features for the close area located North of LO, at an altitude of 694 m (Figs. 1, 6). The average annual temperature is here 11.3 °C. The annual precipitation amounts to 878 mm. July is the warmest and driest month, with an average temperature of 20.5 °C and 42 mm of rain. Most of the precipitation falls in November, averaging 114 mm. January is the coldest month, with temperatures averaging 2.0 °C. This climate is considered to be Cfb (temperate rainy climate, warm summers) according to the Köppen-Geiger climate classification (e.g. Kottek et al., 2006). The catchment vegetation (see Fig. 7a and b for some panoramic views) is distributed mainly in altitudinal belts, from the lake level (700 m) to the top of mountains (>2200 m), with mixed deciduous oak forest, beech forest at lake level followed at higher elevation by mesophilous/montane species; mixed forests at the upper limit of the forested area and alpine pasturelands and grasslands are found over the timberline, currently at around 1900 m (Matevski et al., 2011). The presence of glaciers is documented on top of the Galičica Mountains during glacial periods (Ribolini et al., 2011).

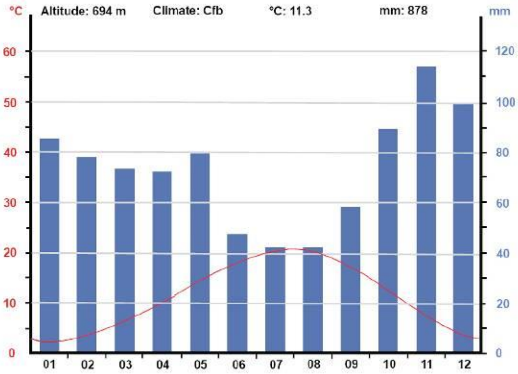

Fig. 6 - The thermopluviometric diagram of Struga metereological station (Fig. 1) at the north side of Lake Ohrid (data from http://en.climate-data.org/location/29778/).

Fig. 7 - View of the present vegetation around Lake Ohrid. (a) Saint John at Kaneo; (b) The rocky southeastern shore of the lake.

2.2. Geological and stratigraphical framework

The LO morphostructure with high mountains to the west ("Mokra Mountain" Chain, up to 2156 m) and east ("Galičica Mountain" Chain, up to 2254 m) (Fig. 1) is mainly the result of a pull-apart like opening of the basin during the late phases of the Alpine orogeny (Aliaj et al., 2001; Hoffmann et al., 2010). The oldest bedrock (Devonian) is present in the northeastern part of the basin whereas Triassic carbonates and siliciclastics occur in the southeast, east, and northwest (e.g., Wagner et al., 2009; Hoffmann et al., 2010; Vogel et al., 2010). Jurassic and Cretaceous metamorphic and magmatic rocks crop out in the west (Hoffmann et al., 2010). Quaternary lacustrine and fluvial deposits cover the plains to the north and to the south (Hoffmann et al., 2010; Vogel et al., 2010) overlaying Pliocene continental mudstones and claystones. The tectonic activity in the area is attested, until present day, in the lateral parts of LO (Reicherter et al., 2011; Lindhorst et al., 2012; Wagner et al., 2012) by several earthquakes (NEIC database, USGS) and mass wasting deposits (Lindhorst et al., 2016).

2.3. Summary of main project results

Most of the data collected by various investigators, during the 2 years following the core-drilling period since 2013, have been focused on lithology, sedimentology, tephrostratigraphy, and (bio-) geochemistry (see for all details Wagner et al., 2014, Francke et al., 2016 and references therein, Leicher et al., 2016). Here we summarize those results from studies carried out in cores from the central part of the lake giving, in the next paragraph, special emphasis to the palynological contribution (Sadori et al., 2016) concerning the upper 200 m of the overall 569 m long DEEP site sediment succession.

1. The DEEP site sediment succession (in Francke et al., 2016) consists of hemipelagic sediments including several tephra layers and rare mass wasting deposits (< 5 cm). They were organized, on the basis of the initial core description and the calcite content, into three main lithotypes (1-3). Lithotypes 1 and 2 deposits comprise calcareous and slightly calcareous silty clay respectively, whereas lithotype 3 deposits consist of clastic, silty clayey material.
2. The tectono-sedimentary structure of the basin as reconstructed by Lindhorst et al. (2015) includes three main seismic units overlying the acoustic basement associated with fluvial deposits and lacustrine sediments. The seismic facies analysis revealed a prominent cyclic pattern associated with Glacial/Interglacial cycles with a mean sedimentation rate of 0.41 mm yr^{-1} for the last 430 kyrs.
3. According to the age model based on radiometric ages of eleven tephra layers (1st order tie points) and

on tuning of biogeochemical proxy data to orbital parameters (2^{nd} order tie points; Laskar et al., 2004), the upper portion of the sedimentary succession, 247.8 m thick, covers the last 637 kyr (Francke et al., 2016, Leicher et al., 2016).

4. According to the isotopes ($\delta^{18}O$ and $\delta^{13}C$) from the upper ca 247.5 m of sediments, LO experienced a period of general stability between MIS 15 to 13. Wetter climate conditions characterized both MIS 11 and MIS 9. The successive interglacials were marked by progressively drier conditions (Lacey et al., 2016).

3. THE PALYNOLOGICAL CONTRIBUTION

The first SCOPSCO palynological meeting was held at the *Dipartimento di Biologia Ambientale* in Rome (Italy) on 8 and 9 January 2014. It led to the composition of an international palynological team with 12 European scientists from 5 countries under the supervision and coordination of Laura Sadori (University of Rome). In order to provide coherent flora and vegetation data, indispensable for both successive quantification analyses to infer regional paleoclimatic signals and to ensure comparability of results among the different laboratories, common protocols for both chemical-physical and microscope analyses were discussed and established. Moreover cross-check analyses on selected pollen samples by more than one analyst were adopted.

3.1. Protocol for laboratory analyses

Each sample, previously described for its main visual lithological features was weighed and 0.5 to 1.5 g of dry sediment were chemically treated. In order to estimate the pollen concentration, two tablets containing a known amount of *Lycopodium* spores (Stockmarr, 1971) were added in this first step to ensure that all palynomorphs will be treated similarly. The different chemical attacks (see below) were each time followed by both washing of sediment with distilled water and decantation. HCl (37%) was used to remove the carbonate fraction of the sediment as well as to dissolve the *Lycopodium* tablets. HF (40%) was used to remove silicates and hot NaOH (10%) to disperse organic matter and remove humic acids. At the end some drops of glycerol were added to the residue.

For the present work 306 sediment samples, at 64 cm interval down to the depth of 197.55 m of the DEEP core have been processed.

3.2. Protocol for optical microscope analysis

The list of pollen flora taxa, the counts, diagrams, bibliographic and photographic documentation are available to all components of the palynological team in a shared cloud folder. Here several general articles on both modern and ancient pollen taxa are also available. Special emphasis was given to selected taxa in order to facilitate their morphological identification and taxonomy. The difficulty and even the impossibility to always precisely discriminate, at the optical microscope, the different deciduous, semi-deciduous and evergreen components of the genus *Quercus* has long been discussed as they obviously produce some limitations for the ecological and climatic reconstructions. Beug (2004), Chester & Raine (2001), Reille (1992, 1995, 1998) and Smit (1973) documentation and criteria were carefully evaluated. Finally we decided to apply an informal subdivision, which possibly represents, at present, the best compromise for analyses at the optical microscope despite it was originally defined by electron microscope analyses (Smit, 1973). Accordingly, oak pollen has been divided in three main types: *Quercus robur* type (including all deciduous oaks), *Quercus ilex* type (including all the evergreen oaks minus *Q. suber*) and *Quercus cerris* type (including semi-deciduous oaks plus *Q. suber*). *Juniperus* type was established to include pollen grains of *Cupressus*, *Juniperus* and *Taxus*.

Further efforts are being made to collect materials in view of the ongoing studies on the oldest intervals in the sedimentary core, especially pictures of pollen grains belonging to taxa having a good spread in the Mediterranean area during Pliocene and Early Pleistocene and now showing a disjunct geographical distribution. For the interval under examination, special attention was paid to trace the occurrence and abundance of some taxa such as *Carya*, *Cathaya*, *Cedrus*, Hamamelidaceae, *Liquidambar*, *Pterocarya*, *Tsuga*, *Zelkova*.

3.3. The time schedule

The project unfolds over three main steps. The two first allow the study of the entire sedimentary succession at low resolution (from the top down to 200 m, i. e. the present study and from 200 m to the bottom core, respectively), in relatively short time. According to the age model by Francke et al. (2016) the mean resolution between two samples from the upper portion is ~1600 years. Being the first step just accomplished (Sadori et al., 2016), the study of the interval between 200 m and the bottom core has started (Step 2). At the same time higher resolution analyses (Step 3) are also in progress in the sedimentary portions corresponding to MISS 5-6, 10-12, 35-42.

3.4. Palynological results and discussion

Palynological analyses pointed out a rich palynoflora including 175 taxa (153 terrestrial plants including 10 freshwater plants). Quantitative data high enough to trace different pollen diagrams were possible in 296 of the 306 available samples (see, figs 2, 3 and table 1 in Sadori et al., 2016). Samples with final counts less than 80 pollen grains (in addition to *Pinus*) were excluded. Mean pollen counts of 824 terrestrial pollen grains have been achieved. Pollen concentration is quite variable, ranging from ca. 4000 to ca. 910,000 pollen grains g^{-1}. Pollen grains do no exhibit major mechanisms of degradation but bisaccate pollen, especially *Pinus*, is often fragmented. Dinoflagellate cysts are sporadically present. Significant reworking phenomena were absent, as also indicated by the lithology, except of very few, thin mass movement deposits (Francke et al., 2016). Pollen assemblages in the upper 200 m are characterized by a general good richness, which however fluctuates in its values in dependence of both climate (being lower during glacials and higher during interglacials) and time interval (e.g. richness in NAP notably increases in the younger intervals). The main floristic features are summarized below. Trees are mainly represented by *Pinus* pollen. Among other Pinaceae taxa, *Abies* and *Picea* are present throughout; *Tsuga* is scattered and *Cedrus* as well as *Cathaya* are absent. Deciduous broadleaved trees are represented mainly by *Quercus* spp. followed by *Carpinus betulus*, *Ostrya*/*Carpinus orientalis*, *Ulmus*, *Zelkova*, *Acer*, *Tilia* and *Juglans*. Among the only sporadically present taxa we number *Celtis* and *Carya*. Among Mediterranean trees, *Quercus ilex* type is dominant with *Phillyrea, Pistacia,* plus the pioneer shrub *Hippophaë*. *Betula* and especially *Fagus* occur in a discontinuous way. Herbaceous/non arboreal taxa are particularly represented by pollen of Asteraceae, especially *Artemisia*, Poaceae and Amaranthaceae. Moreover Cyperaceae, Caryophyllaceae, Ranunculaceae, *Helianthemum*, Plantaginaceae. Polygonaceae, Rubiaceae, Euphorbiaceae, Dipsacaceae, Gentianaceae, Rosaceae and Caprifoliaceae also occur but discontinuously and at low frequencies. Pteridophyta are generally well represented. Algal taxa are principally represented by *Pediastrum* and *Botryococcus*, though discontinuously.

The analysis of changes in pollen concentration and percentages of both single taxa and arboreal pollen sum (AP) versus non-arboreal pollen sum (NAP), is summarized in Fig. 8. In the text *Pinus* percentages refer to a pollen sum including all AP (plus *Pinus*) and NAP; all the other taxa were calculated with respect to the pollen sum of AP (but *Pinus* excluded) and NAP.

A prevalent contraposition between non arboreal pollen (including Poaceae, Amaranthaceae, *Artemisia*) and woodland (including *Abies*, *Picea*, *Quercus robur* type, *Quercus cerris* type) taxa is well evident throughout the sedimentary succession (Fig. 8). Such pattern reflects the vegetational response to the succession of Glacial/Interglacial cycles between MIS 13 and MIS 1 (Francke et al., 2016). Moreover, minor expansions of AP during glacials as well as forest opening during interglacials pointed out interstadials and stadials, respectively.

Glacials at LO

At LO (Fig. 8), pollen zones OD-12, OD-11, OD-9 and OD-7 roughly corresponding to older glacials MIS 12, MIS 10 and MIS 8 exhibit Poaceae as the most abundant NAP taxon, followed sometimes by Cyperaceae (MIS 12) or Amaranthaceae (MIS 10), and subsequently by Asteroideae, Cichorioideae, *Artemisia* and *Hippophaë* (particularly abundant during MIS 10); *Pinus* as a whole, shows a large occurrence in both concentration and percentage values, exhibiting striking relatively millennial-scale variations in addition to the glacial -interglacial cycles. It fluctuates between 28% and 98%. Montane coniferous taxa show significant fluctuations too as expressed by *Picea* (range 0%- 67%) and *Abies* (range 0%-63%). MIS 8 is marked with respect to MIS 12 and 10 by a peculiar increase of both *Juniperus* and *Artemisia*. The younger glacials are marked by successive distinct patterns in the abundances of some taxa. From MIS 6 onwards a progressive decrease of *Pinus*, as well as of *Abies* and *Picea*, parallels a notable increase of *Artemisia* followed by Poaceae and Amaranthaceae. A relevant increase of *Juniperus* (up to 55%) marks the top of MIS 6.

The establishment of harsh climate conditions possibly promoted various environmental changes; it is a fact that montane taxa, after MIS 6, never reach previous values. The successive, younger glacials are especially characterized by the dominance of *Artemisia* followed by Poaceae and Amaranthaceae; *Pinus* still well represented in percentages, shows a remarkable decrease in concentrations since MIS 6. *Abies* shows a slight percentage increase just after the onset of MIS 5 whereas *Picea* occurs sporadically and in low values.

Overall total pollen concentration during glacials is lower than in interglacials; probably the larger expansion of open environments (i.e. herbaceous taxa) or even bare soils, which favored enhanced phases of erosion and transport of clastic material in the basin may have diluted the pollen content. Such depositional processes are expressed by the rather exclusive occurrence of lithotype 3 sediments, except lithotype 1 in MIS 8 (Francke et al., 2016).

Interglacials at LO

The climate signature in the depositional environment is well expressed by the dominance of a peculiar and diverse pattern with respect to that dominant during glacials. In fact during interglacials lithotypes 1 and 2 sediments prevail with rare occurrences of lithotype 3 sediments. A progressive overall shift from cooler and wetter to warmer and drier interglacials was pointed out.

As a whole the strong chronological frame for LO enables precise terrestrial-marine correlations using the comparison with the main coeval regional sites (e.g. Follieri et al., 1989; Okuda et al., 2001; Tzedakis et al., 2004; 2006; Brauer et al., 2007; Roucoux et al. 2008, 2011; Litt et al., 2014; Pross et al., 2015) and synchronization of single Marine Isotope Stages (Zanchetta et al., 2016). A striking feature of LO respect to the other long terrestrial pollen records of Europe and Near East, is the relatively continuous presence of taxa from all major vegetation belts despite the significant Glacial/Interglacial variability throughout the profile.

In particular, similar patterns of vegetation development during the last Glacial/Interglacial cycles are testified by previous palynological studies (Panagiotopoulos et al., 2014) on the adjacent Lake Prespa (Fig. 1) for the last 92 ka. Similar forested phases, dominated by deciduous trees indicative of higher temperatures and moisture availability, developed during both MIS 5 and MIS 1. Open landscapes during lower temperatures and moisture availability phases were prevalent during MIS 4, 2, and also 3 despite the significant presence of temperate trees. With respect to Prespa, the longer LO pollen record provides a unique documentation of the history of flora composition and vegetation structure here updated to the MIS 13 p.p. According to the summary AP vs NAP diagram (Fig. 8) an overall progressive enlargement of the open vegetal formations is quite evident since MIS 13, with a major rise to dominance of steppe formations with *Artemisia* (Fig. 8) occurring from the MIS 7/MIS 6 transition onwards. The quite long glacial MIS 6 is especially marked by a sig-

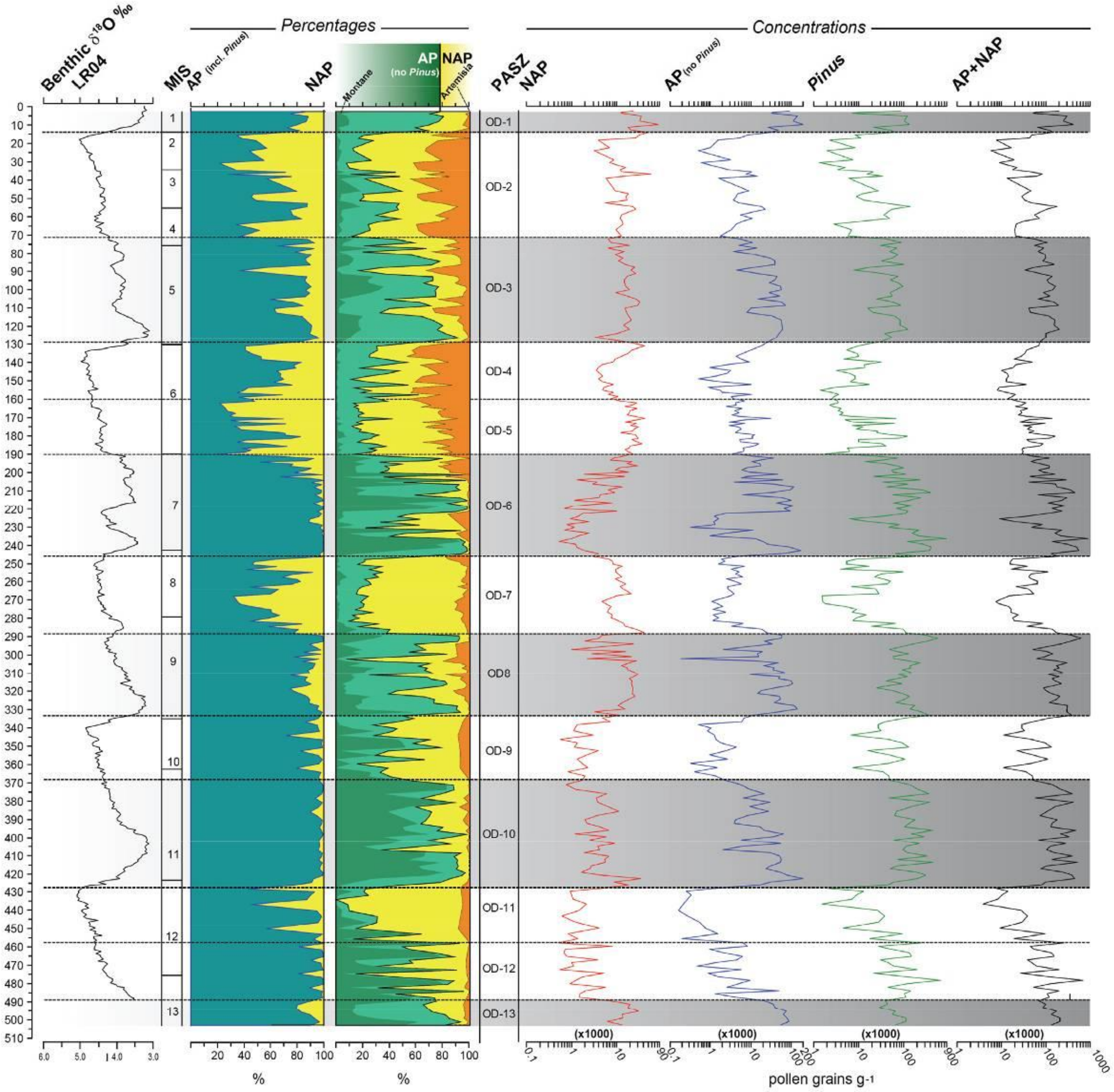

Fig. 8 - Summary pollen data of Lake Ohrid (FYROM), DEEP core against chronology (Francke et al., 2016). From the left: marine records, LR04 $\delta^{18}O$ benthic stack (Lisiecki and Raymo, 2005); terrestrial records, percentages summary pollen diagrams, and selected concentration pollen curves. AP: Arboreal Plants; NAP: Non Arboreal Plants; MIS: Marine Isotope Stages; PASZ: Pollen Assemblage SuperZones.

nificant increase for *Artemisia,* which reaches values up to ca 47%. Ongoing pollen-based climate reconstructions will be able to establish the magnitude of changes in temperatures but especially in the regime of precipitations. The persistent dry conditions during MIS 6 probably enhanced intense erosive processes. After this significant paleoenvironmental and paleoclimate change, probably the major of the last 500 kyr, we observe a general reduction of the altitudinal coniferous taxa (*Abies* and *Picea*) particularly evident during interglacials. Possibly a progressive and generalized decrease in the humidity values plays a major role in the reorganization of vegetation assemblages. Such a prominent event is traceable for *Picea* (see fig. 2 in Sadori et al., 2016) which became subordinated with respect to *Abies* since MIS 6. The knowledge of both the stratigraphic distribution and the past change in the abundances of previous taxa is really helpful to assess their current spatial distribution under the effects of different ecological processes (e.g., competition, survival, biological diversity) within forest communities as well as to choose correct preservation and conservation strategies.

4. CONCLUSION

LO is a unique continental site including at least the last 1.2 Ma history of changes on the Balkan peninsula, a key area of the Mediterranean. The productive collaboration among the different components of the international palynological team provided effective implementation of the SCOPSCO project being a long and continuous pollen record for the last 500 kyr produced in a short period of time for the standard time requested by palynological analyses. The achievement of this first step (Step 1) as well as the ongoing collaboration aimed at the completion of the entire record by the end of 2016 (Step 2) and to the implementation of high resolution studies in key intervals (Step 3) are truly relevant, the full pollen record permitting to trace by the analysis over multiples Glacial/Interglacial cycles

i. the climate variability since 1.2 Ma when subtropical ecosystems disappeared from the central Mediterranean area,
ii. the history of taxa migration and extinctions under the effects of regional to global events
iii. the role of refugia areas over time.

The palynological evidence along with the geological, micropaleontological and stratigraphical data, now well documented by a large number of studies, provide indispensable elements of knowledge for the reconstruction of the late Quaternary paleoclimatic changes in the eastern Mediterranean area within a strong chronologic frame. Such an integrated approach has paramount importance as it permits to trace a comprehensive paleoenvironmental history of LO which is needed to both its appropriate present management and in the context of predicting its future.

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Aligning and synchronization of MIS5 proxy records from Lake Ohrid (FYROM) with independently dated Mediterranean archives: implications for DEEP core chronology

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Abstract. The DEEP site sediment sequence obtained during the ICDP SCOPSCO project at Lake Ohrid was dated using tephrostratigraphic information, cyclostratigraphy, and orbital tuning through the marine isotope stages (MIS) 15-1. Although this approach is suitable for the generation of a general chronological framework of the long succession, it is insufficient to resolve more detailed palaeoclimatological questions, such as leads and lags of climate events between marine and terrestrial records or between different regions. Here, we demonstrate how the use of different tie points can affect cyclostratigraphy and orbital tuning for the period between ca. 140 and 70 ka and how the results can be correlated with directly/indirectly radiometrically dated Mediterranean marine and continental proxy records. The alternative age model presented here shows consistent differences with that initially proposed by Francke et al. (2015) for the same interval, in particular at the level of the MIS6-5e transition. According to this new age model, different proxies from the DEEP site sediment record support an increase of temperatures between glacial to interglacial conditions, which is almost synchronous with a rapid increase in sea surface temperature observed in the western Mediterranean. The results show how a detailed study of independent chronological tie points is important to align different records and to highlight asynchronisms of climate events. Moreover, Francke et al. (2016) have incorporated the new chronology proposed for tephra OH-DP-0499 in the final DEEP age model. This has reduced substantially the chronological discrepancies between the DEEP site age model and the model proposed here for the last glacial-interglacial transition.

1 Introduction

Since the demonstration of a strong astronomical control on the oxygen isotope composition ($\delta^{18}O$) preserved in the shells of foraminifera collected from marine sediments (e.g. Hays et al., 1976) and the construction of composite reference records (e.g. Martinson et al., 1987; Lisiecki and Raymo, 2005), the marine isotope signal has been extensively used as a reference for chronological tuning of continental successions (e.g Tzedakis et al., 1997, 2001) and to infer, for instance, the response of regional vegetation to climate forcing on a global scale. $\delta^{18}O$ reference records are of-

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ten based on benthic foraminifera, with appropriate species offset corrections, and are primarily interpreted as first order indicators of global ice volume. Therefore, these records can provide information on glacial–interglacial variations in Earth's climate conditions, even if heavily contaminated by the effect of deep-water temperature variability (e.g. Shackleton, 2000; Skinner and Shackleton, 2006), and by translation these records can also be used for inferring sea-level oscillations (Shackleton, 1987; Waelbroeck et al., 2002).

However, when marine records are used for tuning terrestrial archives there is an implicit assumption of synchronicity between climatic events recognized in marine proxies and those in terrestrial archives, often identified using different proxies. Under scrutiny such a relationship may not be sustainable, as terrestrial and marine proxies could indicate different processes at local and global scales, with different responses to climatic forcing. For instance, marine pollen studies indicate that broad land–sea correlations and average ages of respective stages are generally correct, but that there may be significant offsets in the precise timing of terrestrial and marine stage boundaries (e.g. Shackleton et al., 2003; Tzedakis et al., 2003) when, e.g., pollen and benthic foraminifera δ^{18}O were directly compared. These offsets can offer complementary information, which will not be recognized and understood if tuning is the only tool used for chronological control (Blaauw, 2012; Sanchez-Goni et al., 2013). However, correlation between the terrestrial and marine realm is a fundamental task for understanding how climate systems work at different timescales and the nature of climate change impacts on the Earth system.

The development of U / Th-based speleothem studies in the last 20 years may bypass the necessity to synchronize continental archives with marine records for supporting terrestrial chronologies, especially if similar proxies are used (e.g. stable isotopes, Regattieri et al., 2014). Considering that marine chronologies, beyond the limit of radiocarbon dating methods, are often based on astronomical assumptions, it is now also common to transfer independently dated speleothems chronologies to marine records (Bar-Matthews et al., 2000; Almogi-Labin et al., 2009; Drysdale et al., 2007, 2009; Grant et al., 2012; Ziegler et al., 2010; Hodell et al., 2013; Marino et al., 2015; Jiménez-Amat and Zahn, 2015). This can be somewhat problematic, as the assumption of synchronicity between speleothem and marine proxy records is not necessarily straightforward (e.g. Zhornyak et al., 2011). Moreover, different approaches to correlate chronologies from speleothem-based proxy records and marine proxies have been proposed (e.g. Drysdale et al., 2009; Ziegler et al., 2010; Grant et al., 2012; Marino et al., 2015; Jiménez-Amat and Zahn, 2015).

An increasing number of studies are now devoted to the use of tephra layers for correlation and synchronization of archives (see e.g. Lowe, 2011 for an extensive review). In the Mediterranean region, the use of tephra layers as chronological and stratigraphic markers (Wulf et al., 2004, 2008; Zanchetta et al., 2011, 2012a, b; Blockley et al., 2014; Albert et al., 2015; Giaccio et al., 2015) has largely improved our ability to synchronize archives and proxies, and to recognize leads and lags between different paleoclimate records (e.g. Regattieri et al., 2015). Therefore, the parsimonious use of tuning based on independently dated archives, along with the strong stratigraphic constraint afforded by tephra layers is perhaps the most rigorous way to provide a chronological reference for archives which lack an independent chronology (e.g. Regattieri et al., 2016). However, tephrostratigraphic and tephrochronological work also depends on the accuracy of existing data, and radiometric ages provided for proximal and distal deposition of the same tephra can vary by up to several thousand years. For example the Y-3 tephra is a widespread marker in the central Mediterranean (Zanchetta et al., 2008), for which an age range of ca. 31–30 ka has been proposed for the supposed proximal deposits (e.g. Zanchetta et al., 2008) but this age range has been recently challenged by Albert et al. (2015) who dated distal Y-3 deposits to be between 28.7–29.4 ka.

Here we attempt to compare different proxy series from MIS 5 (ca. 130–80 ka; cf. Railsback et al., 2015) from the "DEEP" core composite profile, drilled in Lake Ohrid (Fig. 1) within the framework of the ICDP-SCOPSCO project (Wagner et al., 2014a, b), with recent radiometrically dated continental records in the central Mediterranean, to further constrain the age model of the DEEP record for this period. The major aims are to understand (1) which proxies are most useful for correlating different archives during specific intervals of time; (2) which proxies can provide fundamental information on time-lag relationships between specific environments, and (3) which proxies can be confidently considered as an expression of local-to-regional climatic change. The approach employed here is different from that previously used to produce a chronology for the DEEP site composite long record, which is based on tephrostratigraphy, cyclostratigraphy and/or orbital tuning through the marine isotope record (Baumgarten et al., 2015; Francke et al., 2015, 2016). In contrast, our approach provides more detailed insights into the chronological framework of a discrete time period, and aims to contribute to the synchronization of paleoclimate records in the Mediterranean region.

2 Site description

Lake Ohrid originated in a tectonic graben and formed during the latest phases of uplift of the Alps (Stankovic, 1960). It is located on the border between Macedonia (FYROM) and Albania and covers an area of 358 km^2 at an altitude of 693 m a.s.l. (Fig. 1). It is about 30 km long and 15 km wide, with a maximum water depth of 293 m (Lindhorst et al., 2015). The topographic watershed of Lake Ohrid comprises an area of 2393 km^2 incorporating Lake Prespa, which is situated 10 km to the east of Lake Ohrid at an altitude of

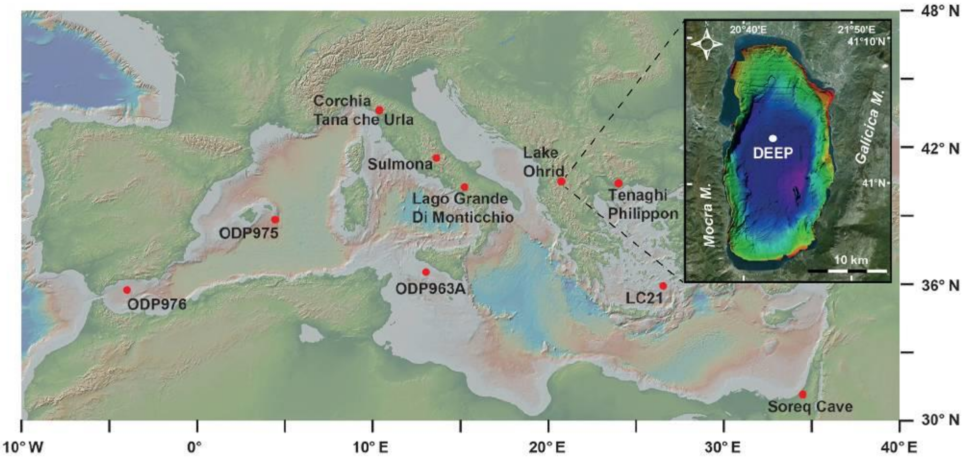

Figure 1. (a) site quoted in the text; **(b)** DEEP site drilling location within Lake Ohrid.

848 m a.s.l. (Popovska and Bonacci, 2007). The two lakes are connected via karst aquifers that pass through the Galičica and Suva Gora mountain ranges. Karst springs depleted in nutrients and minerogenic load represent the primary hydrologic inputs to Lake Ohrid (55 %) and up to 50 % of these karst waters originate from Lake Prespa (Anovski et al., 1992; Matzinger et al., 2007). Direct precipitation on the lake surface, river and direct surface runoff account for the remaining 45 % of the hydrologic input into Lake Ohrid. The surface outflow (60 %) through the river Crn Drim in the northern corner and evaporation (40 %) represent the main hydrologic outputs (Matzinger et al., 2006). The theoretical hydraulic water residence time is estimated to be ca. 70 years (Matzinger et al., 2006). Due to its sheltered position in a relatively deep basin surrounded by high mountain ranges and to the proximity of the Adriatic Sea, the climate of the Lake Ohrid watershed shows both Mediterranean and continental characteristics (Watzin et al., 2002). The average annual air temperature for the period between 1961 and 1990 is +11.1 °C, with a maximum temperature of +31.5 °C and a minimum temperature of −5.7 °C. The average annual precipitation amounts to 800–900 mm (Popovska and Bonacci, 2007), and the prevailing wind directions follow the N–S axis of the Ohrid valley.

The lake is thought to be the oldest lake in continuous existence in Europe, with current age estimates varying between ca. 1.2 and 5 million years from geological investigations and between 1.5 and 3.0 Ma from molecular clock analyses of endemic taxa (Trajanovski et al., 2010). Preliminary analyses from SCOPSCO DEEP core sediments confirm a limnological age for Lake Ohrid of > 1.2 Ma (Wagner et al., 2014a, b; Baumgarten et al., 2015). The peculiar hydrological conditions of the lake and the presence of > 300 endemic species make Lake Ohrid a hotspot of biodiversity and a site of global significance (Albrecht and Wilke, 2008; Föller et al., 2015).

3 Material and methods

The "DEEP" core was retrieved in the central basin of Lake Ohrid (41°02′57″ N and 020°42′54″ E, Fig. 1) at 243 m water depth, in a basement depression with an estimated maximum thickness of sediment fill of 680 m (Lindhorst et al., 2015). Seismic data show that the upper ∼ 400 m comprises undisturbed sediments without unconformities or erosional features, thus supporting a continuous sediment record (Wagner et al., 2014a, b). At the DEEP site (ICDP label 5045-1), six parallel holes were drilled to a maximum sediment depth of 569 m below lake floor (b.l.f.). Pelagic or hemi-pelagic sediments characterize the uppermost 430 m of the sediment column (Francke et al., 2016). Below 430 m blf, shallow water facies became increasingly dominant, including peaty layers, coarser sediments with shell remains, and distinct sandy layers. The correlation of the core segments of the individual holes revealed an overall recovery of almost 100 % for the upper ca 248 m (Francke et al., 2016). Mass movement deposits have thicknesses of < 3 cm, are not erosive, and are very rare in the section studied here, which spans from ca. 53 to 29 metres core composite depth or the period from ca. 140 to 70 ka according to the age model proposed by Francke et al. (2016).

Proxy data used here comprise total inorganic carbon (TIC), total organic carbon (TOC), and biogenic silica (B-SiO_2) from Francke et al. (2016), the stable isotope composition of total inorganic carbon ($\delta^{18}O_{TIC}$ and $\delta^{13}C_{TIC}$) from Lacey et al. (2016) and pollen data from Sadori et al. (2016). Analytical procedure and related errors, in addition to individual sampling resolutions, are discussed in the cited papers. $\delta^{18}O_{TIC}$ and $\delta^{13}C_{TIC}$ data are present only between 128 and 78 ka, where there was sufficient TIC for isotope analysis (Lacey et al., 2016). The investigated interval includes three prominent tephra layers, which were visually identified af-

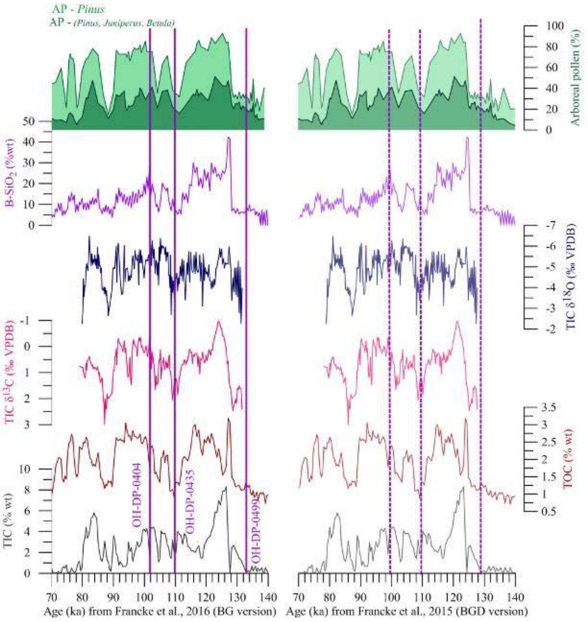

Figure 2. DEEP site proxy series plotted on age models from Francke et al., 2016 (left) and Francke et al. (2015; right). From top: B-SiO$_2$ after Francke et al. (2016), AP % (Arboreal Pollen, without considering *Pinus* spp. pollen grains) after Sadori et al., 2016; TIC δ^{13}C after Lacey et al. (2016); TIC δ^{18}O after Lacey et al. (2016); TOC and TIC % after Francke et al. (2016). Violet lines indicate tephra layers.

ter core opening and are characterized by prominent peaks in XRF-scanning data (Francke et al., 2016). A detailed description of these tephra layers, as well as analytical procedures for their geochemical fingerprinting, can be found in Leicher et al. (2016). Most of these tephras have already been described for other cores from Lake Ohrid and nearby Lake Prespa (Lezine et al., 2010; Wagner et al., 2008; Sulpizio et al., 2010a, b; Vogel et al., 2010; Damaschke et al., 2013). In Fig. 2 all Lake Ohrid data are plotted versus the age, according to the model established by Francke et al. (2016). Other Mediterranean records (Fig. 3) are plotted using their own published age models. Correlation with MISs is given but acknowledged to be likely inaccurate as there may not necessarily be an identical correspondence between marine and terrestrial proxies. Moreover, we use the term "transition" instead of "termination" for the passage between glacial and interglacial periods, as suggested by Kukla et al. (2002), because the definition of "termination" should be reserved for benthic isotopic records where it has been defined (e.g. Broecker and van Donk, 1970). Govin et al. (2015) have recently suggested to use the term "penultimate deglaciation" to refer to the climatic transition occurring between full glacial and interglacial conditions. The two terms are often used interchangeably. Following the definition of Govin et al. (2015) our approach is to align the δ^{18}O records at the regional scale. However, according to Govin et al. (2015), the term "synchronization" should be used when tephra layers are used. Therefore, in our tuning exercise here proposed, we align using regional proxies and we synchronize using tephra layers.

4 Results and discussion

Figure 2 shows the correlation of selected proxy series from the DEEP site. The general structure of the different proxies shows a relatively good agreement, as already discussed in other contributions of this themed issue (Francke et al., 2016; Lacey et al., 2016; Just et al., 2016). Interglacial sediments are typically characterized by calcareous and slightly calcareous silty clay, while clastic, silty clayey material dominates in the glacial periods (Francke et al., 2016). However, although orbital-scale sedimentological variability and sedimentation rates appear to remain fairly constant, differences are apparent when the cores are examined at higher resolution. The transition between MIS6 and the Last Interglacial (i.e., MIS5e) is of particular interest. In the original Biogeosciences Discussion paper by Francke et al. (2015) the age model used for the DEEP site assumed an age of 129 ± 6 ka for the tephra layer OH-DP-0499, which was correlated to P11 tephra (Rotolo et al., 2013; Leicher et al., 2016) and used as 1st order independent chronological tie point (cf., Francke et al., 2016). Using this model, all the proxy data show a prominent change starting at ca. 124–125 ka (Fig. 2a). $\delta^{18}O_{TIC}$ shows decreasing values starting at ca. 128 ka, followed by a second, more pronounced step from ca. 124–125 ka (Fig. 2a). TIC percentage starts to increase almost synchronous to the first $\delta^{18}O_{TIC}$ step, but with a prominent rate of increase from ca. 125 ka. TOC shows a similar pattern, but with a slightly earlier and more gradual increase (Francke et al., 2015, 2016). The behaviour of these three proxies can be explained by an initial step of warming at the end of the glaciation, with an increase of primary productivity possibly connected with a change in the efficiency of recycling of organic matter within the lake (e.g. burial vs. bottom oxygenation). This early signal of warmer temperature is also confirmed by $\delta^{13}C_{TIC}$, which shows a small decrease at the same time TIC percentage begins to increase, and by pollen data, which shows a synchronous small increase of arboreal pollen percentage (AP %; Fig. 2). Interestingly, TIC percentage and isotopes show a short inversion just before the start of the second prominent step (Fig. 2). This second step is also well marked by a strong increase in B-SiO$_2$, indicating a definite transition to interglacial conditions.

The comparison of DEEP proxy data during the MIS6-MIS5 transition with regional records (Fig. 3) shows some interesting features, which highlight the timing and evolution of the glacial/interglacial transition at Lake Ohrid and may represent the starting point for tuning consideration.

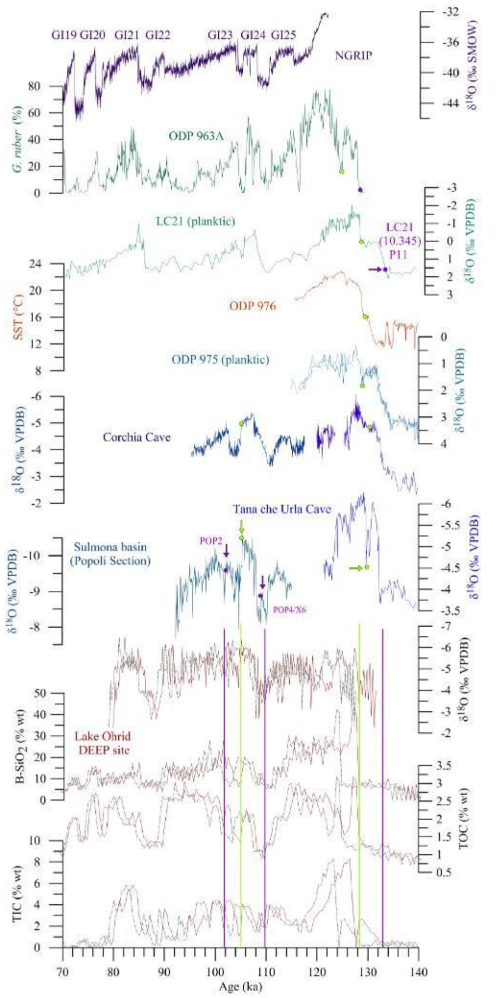

Figure 3. Comparison of selected DEEP proxies (TIC δ^{18}O after Lacey et al. (2016), B-SiO$_2$ after Francke et al. (2016), TOC and TIC % after Francke et al., 2016) with regional to extra regional record. From the bottom: δ^{18}O from Sulmona paleolake (POP section, Regattieri et al., 2015); δ^{18}O from Corchia Cave (CC5 Drysdale et al., 2009; CC28 Drysdale et al., 2007) and Tana che Urla Cave (Regattieri et al., 2014); ODP-975 planktic δ^{18}O (*G. ruber* darker; *G. bulloides*, lighter, after Marino et al., 2015); ODP-976 Alkenone SST (data from Martrat et al., 2014 and age model after Marino et al., 2015); LC21 planktic δ^{18}O (*G. bulloides* Grant et al., 2012); ODP-963A *G. ruber* abundance (Sprovieri et al., 2006); δ^{18}O from NGRIP ice core (NGRIP member, 2004). Violet dots indicates correlated tephra layers (LC21 10.345/P11 on core LC21 and ODP-963A, POP2 and POP4/X6 on Sulmona Basin δ^{18}O record, Regattieri et al., 2015); green dots indicate correlated points used for tuning. Arrows and lines (violet = tephras, green = tuning point) indicate age tuning points. See text and Table 1 for details. Dotted lines are the same proxies, but plotted using the Franke et al. (2015) age model.

A majority of Mediterranean δ^{18}O planktonic records show a two-stepped MIS6-MIS5 transition (e.g. Paterne et al., 2008; Grant et al., 2012; Martrat et al., 2014; Marino et al., 2015 and references therein). Figure 3 shows data from site ODP-975 compiled by Marino et al. (2015). In Marino et al. (2015), the well-documented intermediate-water connection between the eastern and western Mediterranean Sea allowed for the ODP-975 δ^{18}O planktonic record to be tuned with the δ^{18}O planktonic record of the LC21 core in Eastern Mediterranean (Marino et al., 2015; Figs. 1, 3). LC21 had previously been chronologically anchored to Soreq cave U / Th speleothem chronology, based on the assumption that speleothem δ^{18}O from Soreq Cave strictly reflects changes in the isotopic composition of the eastern Mediterranean surface water (Bar-Matthews et al., 2003; Grant et al., 2012). Marino et al. (2015) subsequently propagated the ODP-975/LC21 chronology to the core ODP-976, producing an Alkenone Sea Surface Temperature (SST) record starting from the data obtained by Martrat et al. (2014; Figs. 1, 3). Therefore, planktonic δ^{18}O records of LC21 and ODP-975 and SST from ODP-976 are all anchored to the same chronologies derived by tuning with Soreq Cave speleothems (Grant et al., 2012; Marino et al., 2015).

A similar two-stepped pattern for the MIS6-MIS5 transition is also observed in δ^{18}O of two well-dated speleothems from the Apuan Alps in central Italy (Fig. 1) collected in the Corchia and Tana che Urla caves (Drysdale et al., 2009; Regattieri et al., 2014). A potential tie point for tuning between the DEEP site and these speleothem records is represented by a small inflection that is evident in the DEEP $\delta^{18}O_{TIC}$ data (green line in Fig. 3), in both speleothem δ^{18}O series (Tana Che Urla and Corchia) and in LC21 and ODP975 δ^{18}O planktonic records (green dots in Fig. 3). The end of this inflection is easily identifiable and robustly U / Th dated at Tana che Urla at 129.6 ± 0.9 ka (Regattieri et al., 2014). The use of this tie point for the DEEP core would have several important implications. Firstly, the old DEEP age model of Francke et al. (2015) underestimated the chronology of the transition by ca. 4–5 ka. Secondly, the distinct step recorded by all the DEEP proxies at 124 ka (Fig. 2) would coincide with the phase of highest rate of rising temperature recorded in the Western Mediterranean, according to the new chronology for ODP-976 SST record (Marino et al., 2015; Figs. 3, 4). Therefore, aligning the DEEP time series with other Mediterranean chronologies indicates that the rapid temperature increase observed at ca. 129–128 ka in the SST of ODP-976 is almost coincident to the sharp increase in TIC %, TOC %, AP %, and B-SiO$_2$ values and to the sharp decrease in $\delta^{13}C_{TIC}$ and $\delta^{13}C_{TOC}$ (Fig. 4).

To strengthen the proposed correlation of events during the MIS6-5e transition, we also consider the position of the tephra layer P-11 from Pantelleria Island in different records (Fig. 3, red dots; Paterne et al., 2008; Caron et al., 2010; Vogel et al., 2010), which is correlated with the tephra layer OH-DP-0499 recognized in the DEEP core (Leicher et al.,

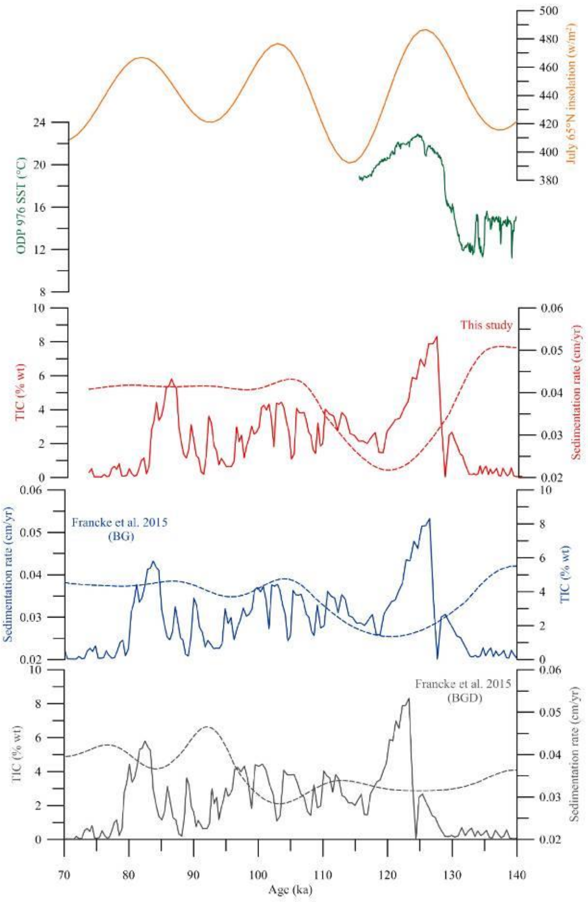

Figure 4. From bottom: TIC (% wt) and sedimentation rate of DEEP site plotted on age models from Francke et al. (2015, Discussion version, grey); Francke et al. (2016, blue); this study (red); Alkenone SST (°C) for core ODP-976 (Marino et al., 2015, green); Summer (July) insolation at 65° N (orange; Berger and Loutre, 1991).

2016; Fig. 2). As shown in Fig. 3, this tephra layer occurs at the base of the first small, but pronounced, increase of TIC in the Ohrid record. In the ODP-963A record from the central Mediterranean (Fig. 3; Sprovieri et al., 2006; Tamburrino et al., 2012) this tephra layer (here correlated with ODP3 layer) corresponds to the first increase in the abundance of *Globigerinoides ruber* (a warm foraminifera taxa) after the end of MIS6. In core LC21 from the eastern Mediterranean, a pantelleritic tephra (Satow et al., 2015) was found at the beginning of the first decrease of *G. ruber* δ^{18}O (Fig. 3). This also corresponds to the position of P-11 in the δ^{18}O *G. bulloides* record from core KET82-22 in the Ionian Sea (Paterne et al., 2008), although this record has a low resolution compared to LC21. Overall, P-11 occupies the same "climatostratigraphic" position in every one of these records. According to the speleothem-based chronology proposed for core LC21, the Pantelleritic layer was dated at ca. 133.5 ± 2 ka (Grant et al., 2012; Satow et al., 2015). This would be slightly older (although statistically indistinguishable) compared to the age reported from the Unit P at Pantelleria (ca. 129 ± 6 ka, Rotolo et al., 2013), which is regarded as proximal counter part of this tephra layer (Paterne et al., 2008) and that was used for the first age model of the DEEP core (Francke et al., 2015). This age represents an average over different sets of dating, and thus has a large error (Rotolo et al., 2013). However, we have to note that even if the stratigraphic correlation between P-11 and the pantelleritic layer in LC21 is obvious, chemical data used for tephrostratigraphy are not unambiguous and could indicate a different dispersion of ash with different chemistry, as result of a zoned magma chamber (Leicher et al., 2016). Taking these considerations into account, it seems reasonable to shift the age model for the MIS6-MIS5e transition at the DEEP site by ca. 4 ka compared to Francke et al. (2015). This shift is supported by a marked increase in the abundance of *G. ruber* in ODP-963A, immediately following the P-11 tephra (Fig. 3), which is indicative of warming conditions and probably correlates with the initial TIC increase observed in the DEEP site record. Following the revision proposed here, which substantially differs from the approach used by Francke et al. (2015), Francke et al. (2016) changed the age of OH-DP-0499 tephra to that of Satow et al. (2015), which alleviated the discrepancies between the two age models for the period corresponding to the penultimate deglaciation (Fig. 4).

In the central Mediterranean, and specifically for Corchia and Tana che Urla caves, speleothem calcite δ^{18}O is principally seen as an indicator of local hydrology and interpreted in terms of "amount of precipitation", with lower/higher values related to increasing/decreasing precipitation (Bard et al., 2002; Drysdale et al., 2004, 2005, 2006, 2007, 2009; Zanchetta et al., 2007, 2014; Regattieri et al., 2014). Changes in precipitation amount, and thus in δ^{18}O of speleothem, have in turn been linked to North Atlantic conditions, with enhanced ocean evaporation and advection toward the Mediterranean (i.e. higher rainfall) during periods of higher ocean SST (e.g. Drysdale et al., 2004). Similar findings have also been found in lake δ^{18}O records (Regattieri et al., 2015, 2016; Giaccio et al., 2015). Based on such evidence, the first decreasing in the $\delta^{18}O_{TIC}$ values of the DEEP record may also be related to increasing precipitation. However, Marino et al. (2015) proposed that the first δ^{18}O decrease in both Mediterranean planktonic foraminifera and speleothems is instead related to a decreasing sea surface salinity (SSS), due to massive iceberg discharge related to Heinrich event 11 (H11), a major deglacial meltwater pulse that may account for about 70 % of the glacial–interglacial sea-level rise. If this is correct then the prominent shift in the $\delta^{18}O_{TIC}$ of the DEEP record at the beginning of the transition is likely related to the progressive lowering of sea surface isotopic composition due to decreasing SSS (i.e. source effect) and not to hydrological changes (i.e., increasing of precipitation).

The designation of additional tuning points during the interglacial appears more complicated. During the first part of MIS5c some common patterns are evident, like the prominent increase in TIC, TOC and B-SiO_2 between ca 124 and 120 ka. We suggest that a good correlation point would be the sharp increase in $\delta^{18}O$ at the transition between GI24 and GS23 visible at Corchia and the DEEP core (Fig. 3, green dots), as well as in the $\delta^{18}O$ record from lacustrine carbonate from the Sulmona basin (POP section, Regattieri et al., 2015). This point is set at ca. 105.1 ka in the CC28 stalagmite record from Corchia Cave (Drysdale et al., 2007) and it is chronologically in agreement with data from the POP section (Figs. 1, 3, Regattieri et al., 2015) and NALPS speleothem records from the northeastern Alps (Boch et al., 2011). We note that the increase in $\delta^{18}O$ slightly precedes the TIC, TOC, and B-SiO_2 decrease. We are not able to give a detailed explanation for this, but we believe that it is more appropriate to use the $\delta^{18}O_{TIC}$ when tuning with other $\delta^{18}O$ records (speleothem and lacustrine). As discussed, we are aware by the fact that $\delta^{18}O$ in speleothems and lacustrine sediments can be affected by several local factors (e.g. Wilson et al., 2015) and unequivocal paleoclimatic interpretation may complicate the use of this proxy for "synchronization" studies (Govin et al., 2015), but the consistent nature of the $\delta^{18}O$ signal observed in different regional archives (e.g. speleothems and lacustrine carbonate) makes the use of $\delta^{18}O$ of carbonate a good candidate for the alignment of the discussed records.

Two robust target points for synchronization are represented by the tephra layers OH-DP-0404 and OH-DP-0435 (Fig. 2), which were independently dated in other records (Table 1). Particularly, both tephras occur in the POP section from the Sulmona Basin (Regattieri et al., 2015) and thus their recalculated ages can be obtained from this age model. Tephra OH-DP-0435 is also used in Francke et al. (2015, 2016) as tie point, and the $^{40}Ar/^{39}Ar$ radiometric age from Iorio et al. (2014) was used.

From the above discussion, we suggest an alternative age model for the MIS 5 DEEP record (Fig. 4) using the tie points shown in Fig. 3 (green and purple arrows) and detailed in Table 1. This new age model was calculated using the Bacon software (Blaauw, 2011), using the same settings employed also for the construction of the DEEP site chronology by Francke at al. (2016). The simulation is limited to the chronological interval for which tie points are available (ca. 140–70 ka).

As noted before, the most significant differences are in the timing of the whole glacial/interglacial transition in the first age model of Francke et al. (2015). However, in the final version of the age model from Francke et al. (2016), incorporating the new age here proposed for the OH-DP-0499 tephra layer, the differences are less evident (Fig. 4). There is a good fit between ca. 115 and 108 and ca. 95–88 ka, whereas ages diverge again at the base of the record. Interestingly, the new model allows for comparison between the Ohrid record and with SST reconstructions from the Western Mediterranean (core ODP-975), which, as previously explained, is an indirectly, radiometrically dated record (Fig. 4). Despite a minor chronological offset, the pattern of TIC variability during the transition is consistent with that of SST.

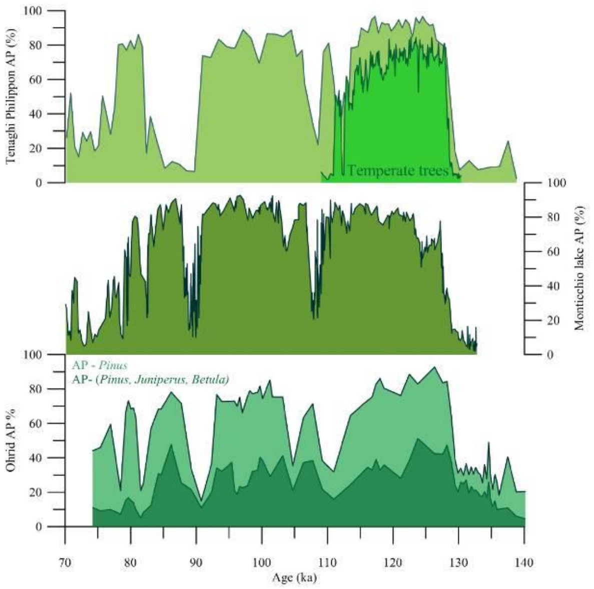

Figure 5. From bottom: DEEP site pollen record (AP-*Pinus* and AP-(*Pinus, Betula and Juniperus*), Sadori et al., 2016) plotted on chronology proposed in this study; Monticchio Lake arboreal pollen (Brauer et al., 2007); Tenaghi Philippon, % of temperate trees from Milner et al. (2012) and total AP from Tzedakis et al. (2006).

Figure 4 also illustrates the change in sedimentation rate in the different age models. It is possible to see that by increasing the number of aligning points the sedimentation rate becomes significantly different, suggesting a faster decrease at the time of the interglacial inception. Sedimentation rate increased again around 120 ka, and then remained stable since ca. 105 ka. We note that the Francke et al. (2016) age model (and most other age models too) are based on the assumption of gradually changing sedimentation rates. This might be true if studying long sequences at low resolution. However, changes in sedimentation rates become more important when examining a sequence at higher resolution. On the long-term scale, and using the chronological tie points of the 11 tephras from the orbital tuning used in the Francke et al. (2015, 2016) age model, relatively constant sedimentation rates are inferred for the DEEP core site record. On closer inspection, however, there might be significant changes, particularly at the MIS6-5e transition, as inferred from the new age model (see also Francke et al., 2016), as it is highly unlikely that a decrease in clastic input from the catchment (prevailing

Table 1. Chronological tie points discussed in this study. DEEP core ages and associated 2σ uncertainties are from Francke et al. (2015, Discussion AM) and Francke et al. (2016, Final AM) age models.

			DEEP core age model				This study					
			Final AM		Discussion AM		New used age		New modelled age		Age differences	
tuning points		mcd depth	Age (ka)	2σ (ka)	age	2σ (ka)	Age (ka)	2σ (ka)	Age (ka)	2σ (ka)	Final	Discussion
tephra	POP2	40.49	101.8	2.4	99.2	3.2	102.0^{d}	2.4	103.6	3	−1.8	−1.8
tuning	end GI24	41.63	104.8	4.2	103.1	3.6	105.4^{c}	0.9	105.4	1.8	−0.6	−2.3
tephra	POP4	43.51	109.8	2.0	109.7	2	109	1.5	109.7	2.4	0.1	0
tuning	TII TCU	48.58	127.7	6.6	124.4	2.7	129.6^{b}	0.9	129.4	2	−1.7	−5
tephra	P11	49.94	133.0	2.0	129.4	6	133.5^{a}	2.0	132.7	2.7	0.3	−3.3

[a] From Satow et al. (2015; after Grant et al., 2012), [b] from Tana che Urla record (Regattieri et al., 2014), [c] from Popoli section record (Regattieri et al., 2015), [d] from Corchia Cave CC28 record (Drysdale et al., 2007).

during glacials, even if partially compensated by a reduced input of organic matter and calcite, and indicated in lithofacies 3 of Francke et al., 2016) is completely, simultaneously and equally compensated by an increase in carbonate precipitation reaching > 80 % during the interglacial (MIS 5e peak, Fig. 4). This means that it is highly likely that there are significant changes in sedimentation rates, which can only be detected by high resolution studies and by a detailed comparison of different records, as indicated in this study.

From Fig. 4 it is also possible to note that the strong increase in SST and TIC occurred slightly before the maximum of summer insolation at 65° N; when the insolation reached its maximum TIC starts to decrease, whereas SST reaches its maximum. A secondary maximum in TIC occurs at ca. 86 ka, ca. 4 ky before the maximum in insolation, whereas the decrease starts at the maximum of insolation.

With the new age model presented here it is also possible to attempt a more precise regional correlation of pollen records. In Fig. 5 pollen records from Tenaghi Philippon, (Fig. 1, Milner et al., 2012, 2013; Pross et al., 2015) and Monticchio (Fig. 1; Brauer et al., 2007) are plotted against the DEEP site pollen record (Sadori et al., 2016). The sharp increase in the AP percentages at ca. 130 ka is almost synchronous in all the mentioned records, and simultaneous to the highest rate of SST increase in the western Mediterranean (Fig. 4). A comparison of the chronology from different records after the end of the Eemian forest phase is more problematic, since the first clear forest opening coincides with the C24 cold event in the North Atlantic (Sánchez-Goñi et al., 1999). In the DEEP core, two tephra layers and a robust alignment point at the end of GI24 probably make this chronology the most reliable, even if in the younger part of the record there are no further alignment points.

The proposed correlation exercise described here can potentially be extended in the future to other sections of the DEEP record. The $\delta^{18}O_{TIC}$ and TIC data contain interesting points for tuning, even if correlations with regional records are not always obvious. However, both have limitation because TIC is particularly low or absent during most of the glacial periods (Lacey et al., 2016; Francke et al., 2016) and seems to be affected by dissolution once a critical threshold is exceeded. Because of preservation/dissolution processes during glacial periods (Lacey et al., 2016; Francke et al., 2016) the selection of correlation points at the beginning of the glacial/interglacial transition would be complex. Moreover, the interglacial periods seem the more appropriate periods for applying the approach presented here. Therefore, a careful selection between proxy data is necessary, because leads and lags are evident when the fine scale is considered. However, the DEEP multiproxy record, along with the presence of regionally important tephra layers, allow us to apply a range of alignment and synchronization approaches.

5 Conclusions

Regional proxy records that have been independently dated support the development of a more detailed chronology for the Lake Ohrid DEEP site record in the interval covering the MIS6/5 transition and the first part of MIS5. The aligning with regional proxies indicates that the most prominent rate of increase of B-SiO$_2$, TIC, TOC, AP %, and $\delta^{13}C_{TOC}$ is concomitant with increasing in temperature in Western Mediterranean cores (Figs. 3, 4), whereas $\delta^{18}O_{TIC}$ and TIC seem also to record an early warming, probably connected with hydrological changes (increasing rainfall). $\delta^{18}O_{TIC}$ may also record a source change in the isotopic composition of oceanic surface waters due to a massive discharge of freshwater resulting from the H11 event (Marino et al., 2015).

During the MIS5 interglacial, different proxy records show generally similar patterns but with evident leads and lags, which can make the selection of the tuning points somewhat more complex. However, the presence of two regionally widespread tephra layers allows a relatively good anchoring of the chronology.

It is important to remark that the approach proposed here can be extended to relatively few intervals of the long DEEP record because independently radiometrically dated records in the Mediterranean region are rare for periods older than the MIS5 (e.g. Bar-Matthews et al., 2000; Drysdale et al., 2004; Giaccio et al., 2015; Regattieri et al., 2016). Therefore, the approach proposed by Baumgarten et al. (2015) and Francke et al. (2016) still appears the most suitable for the definition of general chronological framework of the long record.

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CHAPTER 3:

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Palynology of the Last Interglacial Complex at Lake Ohrid: palaeoenvironmental and palaeoclimatic inferences

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ABSTRACT

In this article, we present new, high-resolution, pollen results obtained from the DEEP site sequence recovered from Lake Ohrid (Albania/FYROM) for the Last Interglacial Complex (LIC), corresponding to Marine Isotope Stage 5 (MIS 5) of the marine isotope stratigraphy. LIC covers the period between 130 and 70 ka and includes the Eemian (Last Interglacial, LI) and the succession of stadial and interstadial phases of the Early Last Glacial.

During the LIC, the pollen record shows an alternation of periods characterized by forest and open vegetation, clearly resembling the well-known vegetational succession of other European records. Our results reveal three key phases for the LI: a first period (128-125 ka) with a rapid increase in temperature and precipitation, a central phase (125–118.5 ka) characterized by a slight cooling, and a late phase (118.5–112 ka), with a decline both in temperatures and precipitation. Besides the LI, we identify four more forested periods dominated by mesophilous trees and intercalated by colder and drier steppe phases, during which, however, most arboreal taxa never disappear.

During the Early Last Glacial we also identify several abrupt events that can be correlated to the succession of cold events recorded in the Greenland ice core records, associated to a weakening of the North Atlantic Meridional Overturning Circulation.

The new high-resolution record indicates that Lake Ohrid is an important site to understand the response of vegetation to fluctuations in regional moisture availability and temperature changes, and thus provides new evidence for the connection between the Mediterranean Region and Northern Hemisphere climate oscillations.

1. Introduction

To evaluate past environmental natural changes and to hypothesize future climate scenarios, the close correlation between plant populations and climate change is used since the last century (Fægri and Iversen, 1989; Birks et al., 2016). Pollen rain, preserved in anoxic sediments, reflects past vegetation and is an invaluable tool for studying the evolution of the environment over time and for following the succession of climatic events.

The Last Interglacial Complex (LIC, 130–80 ka, Govin et al., 2015; Turon, 1984 and references therein), the terrestrial equivalent to Marine Isotope Stage 5 (MIS 5) of the marine benthic isotope stratigraphy (Shackleton et al., 2003), provides interesting hints to interpret the present-day environment and to infer its potential future changes. In particular during the Last Interglacial (LI, or Eemian in the European pollen stratigraphy, Turner, 2002; ca. 130-110 ka), the majority of the Earth experienced a climate warmer than present (e.g. Kukla et al., 2002). Thus, it is considered as a

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possible analogue for the projected global warming, although global climate boundary conditions differ from the current interglacial (Brewer et al., 2008 and references therein). Moreover, unlike the Holocene, the global environmental change that occurred during LI was surely not influenced by long-term impacts due to human-induced CO_2 emission (Ruddiman and Thomson, 2001; Ruddiman, 2003; Ruddiman et al., 2005, 2016), allowing unraveling the background of natural variability during period of "excess" warmth. Besides the Eemian interglacial, the terrestrial stratigraphy of the LIC comprises a succession of stadial and interstadial periods, which constitute the Early Last Glacial (commonly named Early Weichselian in Europe). Several pollen records from continental Europe, Mediterranean and Near East (see Fig. 1) show coherent general trends at the orbital scale for the LIC, particularly for the onset of the main interstadial (i.e., forested) periods. Instead, latitudinal gradients between central and southern Europe are apparent and concern especially the end of the Eemian phase, with interglacial conditions lasting longer in the south (Sánchez-Goñi et al., 2005). However, only few of these records have sufficient temporal resolution to resolve short-term climatic oscillations within the LI and the onset of the Last Glacial. A pervasive short-term (i.e., centennial to millennial scale) climatic variability during the LIC is indeed apparent from a wealth of high-resolution marine and continental records from the North Atlantic and the Mediterranean, especially during the Early Last Glacial but also within the LI, although the latter characterized by lower intensity (e.g. Drysdale et al., 2007; Klotz et al., 2004; Milner et al., 2016; Mokeddem et al., 2014; Regattieri et al., 2014, 2015, 2016a, 2017).

However correlations among different records and definitions of the timing and of the regional expression of these events is still problematic, primarily due to the lack of independent and robust chronologies (e.g. Govin et al., 2015; Zanchetta et al., 2016).

In this article, we present a detailed high-resolution pollen analysis of the LIC (128-70 ka) at Lake Ohrid (LO), which is located at the border between Albania and the Former Yugoslav Republic of Macedonia (FYROM, southern Balkans). LO is an important archive of environmental and climate evolution. A detailed multiproxy biogeochemical record (Wagner et al., 2017 and references therein) is available for the last 640 ka, including low-resolution pollen analyses (Bertini et al., 2016; Sadori et al., 2016) for the last 500 ka. Noteworthy, the LO chronology is based on independent tephrochronology and orbital tuning (Francke et al., 2016). Thus the vegetational changes observed in our record can significantly improve the available knowledge on the timing and patterns of vegetational evolution during the LIC in southern Europe, both on orbital- and on millennial/centennial-scale. Moreover, through direct comparison with the other biogeochemical proxies available from the LO, our record would provide a more comprehensive view of environmental changes during the studied period. This would allow a stronger correlation between changes at the site and variations in regional hydrological patterns and temperature variability known from other records covering the same time span. The new record will also shed light on the role that LO played as glacial refugium for the Balkans and Southern Europe.

2. General setting

2.1. Geographic and geological settings

Lake Ohrid (LO, 40°54′ to 41°10′ N and 20°38′ to 20°48′ E; Fig. 1) is located at 693 m above sea level (a.s.l.) at the southern Balkan Peninsula. It is located within the Dinarides–Albanides–Hellenides mountain chain, a fold and thrust belt formed in the tertiary during the final phase of Alpine orogenesis. Geological studies suggest that the lake has a tectonic origin (Lindhorst et al., 2015). The lake graben structure was formed ca. 2–10 Ma (Lindhorst et al., 2015; Trajanovski et al., 2010). The modern lake basin is tub-shaped, with a N-S orientation. It is 30.3 km long and 15.6 km wide, and thus it is one of the largest existent lakes in Europe. The lake is surrounded by several, N-S oriented mountain ranges, i.e. the Mokra mountains (maximum altitude 1514 m a.s.l.) and Jablanica (maximum altitude 1945 m a.s.l.) to the west, the Mali Thatë to the south (maximum altitude 2028 m a.s.l.), and the Galičica mountains to the east (maximum altitude 2265 m a.s.l.). LO has a volume of ca. 55 km^3 and an average water depth of 164 m, with a maximum depth of 293 m. The water body is mainly fed by karstic inflow, rivers and direct precipitation; while water leaves the lake through the river Crni Drim and by evaporation. LO is also hydrologically connected through underground karst channels with the nearby Lake Prespa, LP (849 m a.s.l., Matzinger et al., 2006; Watzin et al., 2002, Fig. 1). Today LO is oligotrophic. Surface water temperature varies between 6 °C and 26 °C, while bottom water temperatures are fairly constant at 5–6 °C (Popovska and Bonacci, 2007).

2.2. Local climate

The climate of the Ohrid region is characterized by Mediterranean-type conditions, with hot and dry summers and cold and mild winters, but it is also affected by continental influences (Panagiotopoulos et al., 2014). Moisture availability is linked to the penetration of westerly storm tracks across southern Europe, especially during winter, and to Mediterranean cyclogenesis (Dünkeloh and Jacobeit, 2003; Ulbrich et al., 2012). Warm and dryness in summer are related to the expansion of the Azores High (Xoplaki et al., 2003). In addition, local meteorology is influenced by the proximity of the Adriatic Sea, by the local topography and by the lake thermal capacity (Watzin et al., 2002).

The pluviometric regime is Mediterranean, with highest precipitation during November (ca. 144 mm) and the lowest in July (ca. 42 mm). The mean annual precipitation ranges from ca. 700 mm at the altitude of the lake to 1200 mm on the surrounding mountains ridges. The temperatures range between ca. 2 and 6 °C during winter and between 10 and 22 °C during summer. The mean annual temperature equals 11.5 °C (Popovska and Bonacci, 2007).

The wind regime is influenced by the morphology of the lake basin. Winds are characterized by a prevailing North provenience during winter, while during spring and summer, wind direction is mostly from South to South-East (Bordon, 2008; Hoffmann et al., 2012; Matzinger et al., 2006; Wagner et al., 2009).

2.3. Present day vegetation

LO is one of the largest water-reserve in the Balkans situated at the border between two biogeographical regions (Mediterranean and Alpine, Fig. 1), and an important site for studies on past evolution and speciation mechanisms connected to climatic and environmental changes (e.g. Albrecht et al., 2006; Föller et al., 2015; Stankovic, 1960; Wagner et al., 2008). Indeed, LO hosts a high number of relic and endemic species. Concerning the vegetation, Mediterranean and Balkan elements dominate, but several central European species are also widespread in the area. The vegetation is organized in altitudinal belts, developed from the lake level at 693 m a.s.l. to the top of the surrounding mountains at up to 2200 m a.s.l. (Matevski et al., 2011).

In riparian forests, willows (*Salix alba* L.) are dominant. Extrazonal elements of Mediterranean vegetation are present at lower elevations, while most forests are formed by deciduous elements. Below 1200 m a.s.l. deciduous and semi-deciduous oaks (*Quercus cerris* L., *Quercus frainetto* Ten., *Quercus petraea* (Matt.) Liebl., *Quercus pubescens* Willd., and *Quercus trojana* Webb) form mixed

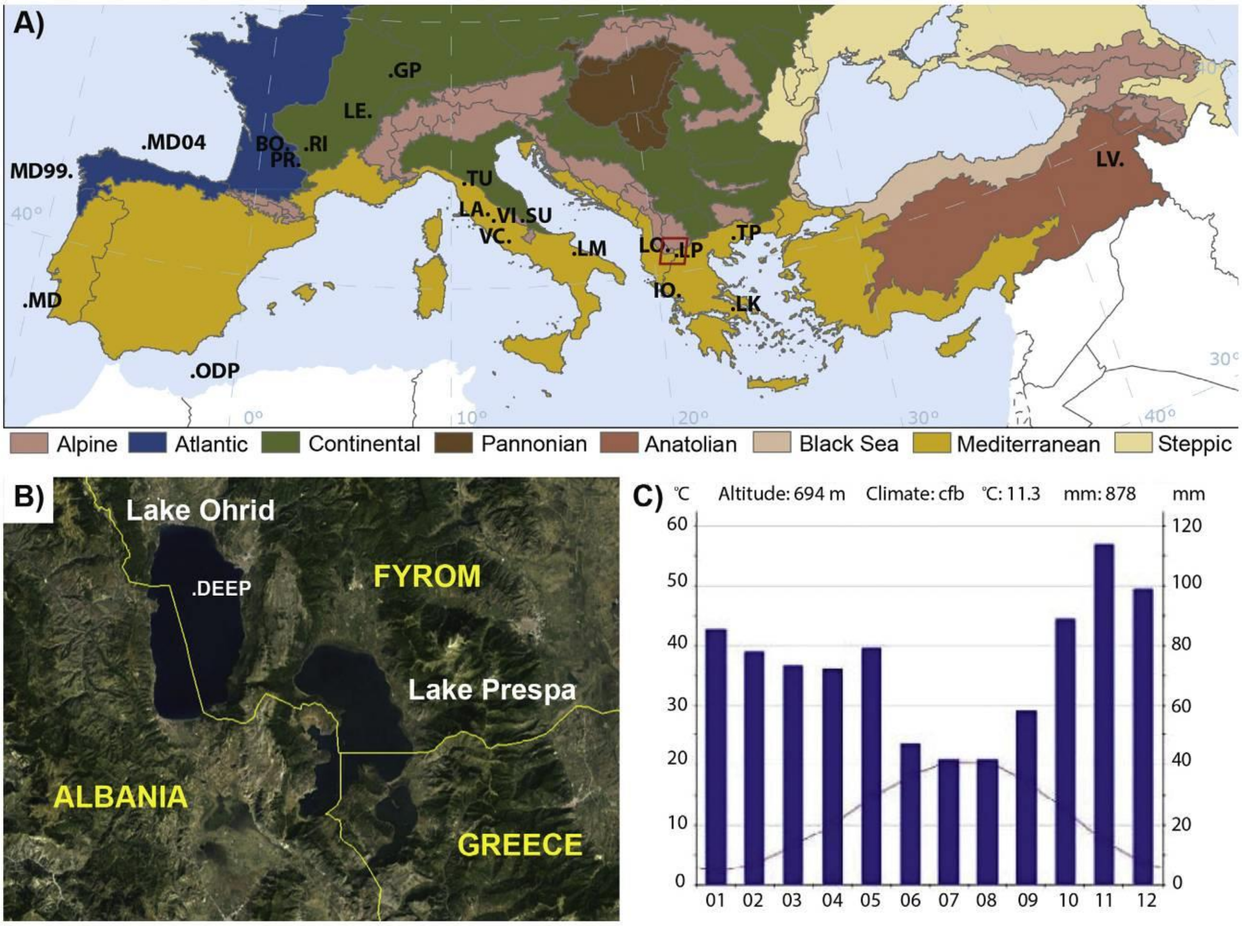

Fig. 1. A) Biogeographical regions of Mediterranean area (from European Environment Agency (EEA), 2016 modified) with the sites cited in this paper: MD99: MD99-2331 (Sánchez-Goñi et al., 2005); MD04: MD04-2845 (Sanchéz-Goñi et al., 2008); MD: MD95-2042 (Sánchez-Goñi et al., 1999; 2005); ODP: ODP997 (Martrat et al., 2014); PR-BO: Praclaux/Bouchet (Reille and de Beaulieu, 1990; Reille et al., 1998); RI: Ribains (de Beaulieu and Reille, 1992b; Kukla et al., 2002); LE: Les Echets (de Beaulieu and Reille, 1984); GP: La Grande Pile (de Beaulieu and Reille, 1992b; Woillard, 1978); TU: Tana che Urla (Regattieri et al., 2015); LA: Lagaccione (Magri, 1999); VI Lago di Vico (Magri and Sadori, 1999); VC: Valle di Castiglione (Follieri et al., 1988); SU: Sulmona (Regattieri et al., 2015, 2017); LM Lago Grande di Monticchio (Allen and Huntley, 2009; Brauer et al., 2007); LO: Lake Ohrid; LP: Lake Prespa (Panagiotopoulos et al., 2014); IO: Lake Ioannina (Frogley and Tzedakis, 1999; Tzedakis, 1994; Tzedakis et al., 2003); TP: Tenaghi Philippon (Milner et al, 2013; Tzedakis et al., 2006); LK: Kopais (Tzedakis, 1999; Okuda et al., 2001); LV: Lake Van (Pickarski et al., 2015a, b). B) Lake Ohrid and its surroundings (US Dept. of State Geographer © 2017 Google Image Landstat/Copernicus). C) thermopluviometric diagram of Struga metereological station (http://en.climate-data.org/location/29778/).

forests with hornbeams (*Carpinus orientalis* L., *Ostrya carpinifolia* Scop.). Mediterranean species such as *Pistacia terebinthus* L. and *Phillyrea latifolia* L. are present.

Between 1200 m a.s.l. and 1900 m a.s.l. mesophilous and montane species such as beeches, hornbeams, hazels and maples (*Fagus sylvatica* L., *Carpinus betulus* L., *Corylus colurna* L. and *Acer obtusatum* (*Acer opalus* subsp. *Obtusatum* (Waldst. & Kit. ex Willd.) Gams) are present, together with *Pinus leucodermis* Antoine, *Juniperus excelsa* M. Bieb., *Juniperus foetidissima* Willd. and *Aesculus hippocastanum* L. Above the treeline (1800 m a.s.l.), shrubby areas are dominated by dwarf junipers, and alpine grasslands are dominated by Poaceae. Scattered populations of Macedonian pine (*Pinus peuce* Griseb.) and of Bosnian pine (*Pinus heldreichii* H. Christ) are found at high elevation (Matevski et al., 2011; Panagiotopoulos et al., 2014; Sadori et al., 2016) and are considered to be Tertiary relicts. LO is also known for its rich local macrophytes flora that numbers more than 120 species. In the littoral zone, algae grow on the surface of the rocks and other hard surfaces. In the deeper water (5–15 m), the more common plants are *Potamogeton* spp., *Chara* spp., *Ceratophyllum* spp., *Myriophyllum* spp. and, closer to the shore, *Phragmites australis* (Cav.) Steud. In many areas, the colonial alga *Cladophora* spp. grows on moist surfaces (Avramoski et al., 2003).

3. Material and methods

The DEEP core was recovered in spring 2013 from the central part of the LO, at a water depth of 243 m (Fig. 1), under the umbrella of the Scientific Collaboration on Past Speciation Conditions in Lake Ohrid (SCOPSCO, Wagner et al., 2014) project of the International Scientific Continental Drilling Program (ICDP). From DEEP site, it was possible to obtain a 569 m long composite sequence (Wagner et al., 2017), covering at least the last 1.2 million years. A detailed description of the core recovery, correlation and sampling can be found in Wagner et al. (2014) and in Francke et al. (2016).

A comprehensive dataset, including lithological, sedimentological, tephrostratigraphical, bio/geochemical and stable isotope analyses has been obtained from the upper 247.8 m of the DEEP core, covering the last ca. 637 kyr, while palynology concerned the last

200 m, spanning the last 500 kyr. All the results obtained in the frame of the SCOPSCO project have been recently summarized by Wagner et al. (2017). The investigated sediment succession mainly consists of hemipelagic sediments with occasional intercalated tephra layers and mass wasting deposits, while the chronology of the DEEP site succession is based on eleven tephra layers correlated with wellknown radiometric ages of tephra coming form Italy and central Mediterranean further refined by tuning of biogeochemical proxy data against local summer insolation (Francke et al., 2016). For more detailed information about LO chronology, lithology and sediments analysis, the reader is referred to specific publications (e.g. Lacey et al., 2016; Leicher et al., 2016; Lindhorst et al., 2015; Wagner et al., 2014; Zanchetta et al., 2016).

Low-resolution (64 cm, corresponding to ca. 1600 years) pollen analyses of the upper 200 m of the DEEP core, covering the last 500 ka, have been performed by an international palynological team (Bertini et al., 2016; Sadori et al., 2016). The published pollen record shows alternations between non-forested and forested periods in conjunction with a progressive change from cooler and wetter to warmer and drier conditions during glacial and interglacial periods (Sadori et al., 2016).

3.1. Pollen analysis

A total of 143 sediment samples have been chemically processed and analysed for the present study, increasing spatial (16 cm) and temporal (400 years) resolution of the record. Based on the published age model, the new pollen data cover the time period between 128 and 70 ka. To better frame the curves, few pollen samples from Sadori et al. (2016) integrate the high-resolution one, providing a more complete diagram between 132.4 and 68 ka (Fig. 2, Table 1).

The palynological team involved in the SCOPSCO project has developed a standard protocol for chemical treatment of the samples and pollen identification, which were also used during the present study (Bertini et al., 2016; Sadori et al., 2016). For the estimation of pollen concentration *Lycopodium* spore tablets (Stockmarr, 1971) have been added to the sediment and chemical method slightly modified after Fægri and Iversen (1989), was used to extract pollen grains. For calculating percentages, the criteria of Berglund and Ralska-Jasiewiczowa (1986) have been used. Percentages of arboreal and non-arboreal taxa are generally calculated using terrestrial spermatophytes as the basis pollen sum. In this case, they have been calculated also excluding *Pinus* from the basis sum, due to its overwhelming presence in a large number of samples (Bertini et al., 2016; Sadori et al., 2016). Pine percentage was therefore calculated using the basis sum plus pines. For oak pollen, the distinction carried out by Smit (1973) was taken into account: *Quercus robur* type, including all deciduous oaks, *Quercus ilex* type including all the evergreen oaks minus *Quercus suber*, and *Quercus cerris* type, including semi-deciduous oaks and *Quercus suber*. Pollen diagrams (% and concentration) were drawn using Tilia software (Grimm, 2011). Visual inspection based on changes in Arboreal Pollen (AP) versus Non Arboreal Pollen (NAP), changes in

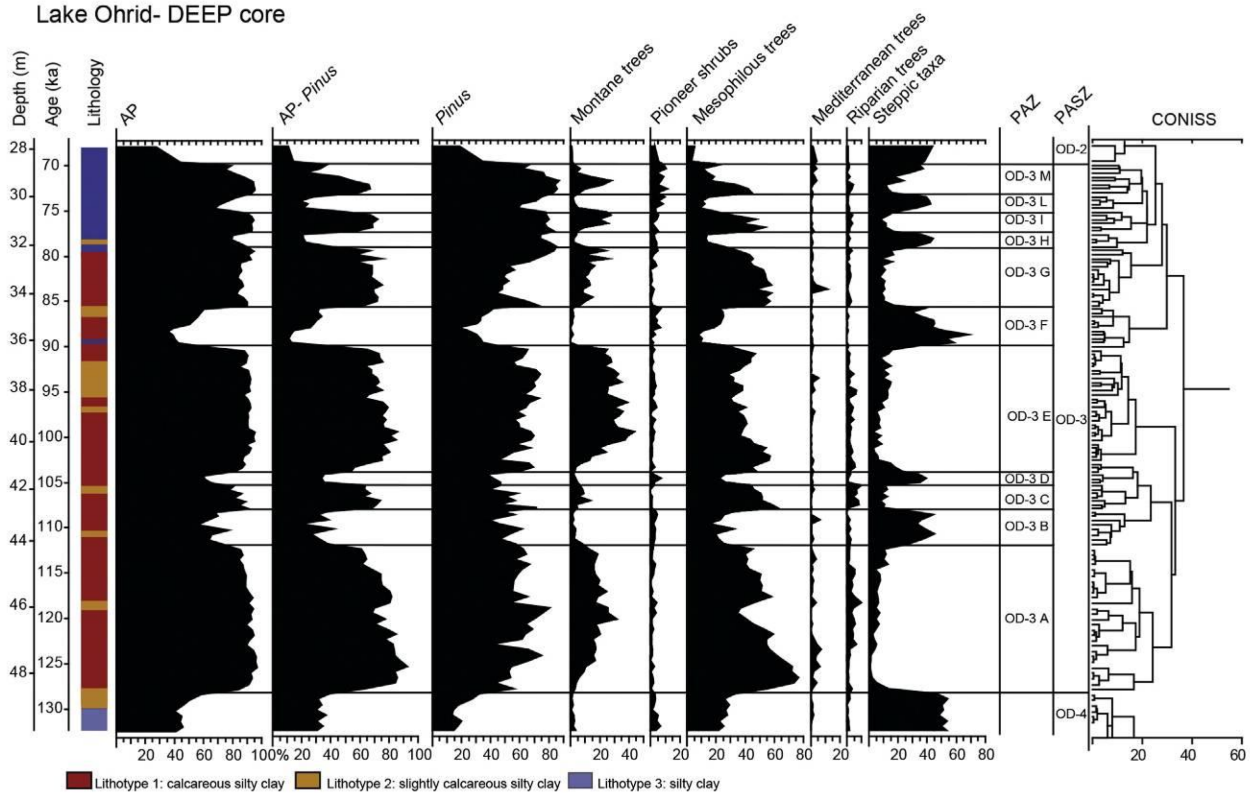

Fig. 2. Lake Ohrid (FYROM/Albania) - DEEP core - Pollen percentage diagram of selected taxa and ecological groups, against depth (m), age (ka), lithology (Francke et al., 2016) and CONISS. Montane trees (*Abies, Betula, Fagus, Ilex, Picea*); pioneer shrubs (*Ephedra distachya* type, *Ephedra fragilis* type, Ericaceae, *Hippophae, Juniperus* type); mesophilous trees (*Acer, Buxus, Carpinus betulus, Castanea, Celtis, Corylus, Fraxinus excelsior/oxycarpa, Ostrya/Carpinus orientalis, Hedera, Quercus robur* type, *Quercus cerris* type, *Tilia, Ulmus, Zelkova*); mediterranean trees (*Cistus, Fraxinus ornus, Olea, Phillyrea, Pistacia, Quercus ilex* type, *Rhamnus*); riparian trees (*Alnus, Populus, Salix, Tamarix*) and steppic taxa (Amaranthaceae, *Artemisia*). For zone description see Table 1.

Table 1
Lake Ohrid (FYROM/Albania) - DEEP core. Scheme of Pollen data. Pollen Assemblage Super Zones (OD-PASZ), Pollen Assemblage Zones (OD-PAZ).

PASZ/PAZ	Age (ka) Duration (ka) Depth (m)	VEGETATION AP excl. *Pinus* NAP pollen grains/g x10^3	AP (%) AP excl. *Pinus* (%)	MAIN FLORISTIC FEATURES CPT (Common Pollen Types) RPT (Rare Pollen Types)
OD-2	69.9–68.0 1.9 28.7–27.95	STEPPE AP: 3-20 NAP:5-16	27–43 11–14	CPT: *Artemisia*, Poaceae, Amaranthaceae, *Pinus*, *Q. robur* type. RPT: *Hippophae*, *Juniperus*.
OD-3M	73.4–69.9 3.5 30.0–28.7	MESOPHILOUS AND MONTANE AP: 3-18 NAP: 6-11	79–95 23–67	CPT: *Pinus*, *Abies*, Poaceae, *Artemisia*, *Q. cerris* type, *Q. robur* type. RPT: Amaranthaceae, *Juniperus* type, *Carpinus betulus*, Asteroideae.
OD-3L	75.4–73.4 2 30.8–30.0	STEPPE AP: 4-21 NAP: 10-20	76–93 19–60	CPT: *Pinus*, *Artemisia*, Poaceae. RPT: Amaranthaceae, Asteroideae, *Q. cerris* type, *Q. robur* type.
OD-3I	77.6–75.4 2.3 31.6–30.8	MESOPHILOUS AND MONTANE AP: 4-38 NAP: 7-18	90–95 52–72	CPT: *Pinus*, *Q. cerris* type, *Abies*, Poaceae. RPT: *Q. robur* type, *Carpinus betulus*, *Fagus*, *Ostrya/Carpinus orientalis*, *Artemisia*, Amaranthaceae, *Ulmus*, *Zelkova*.
OD-3H	78.8–77.6 1.6 32.0–31.6	STEPPE AP: 4-5 NAP: 13-15	85–92 20–40	CPT: *Pinus*, *Artemisia*, Poaceae. RPT: *Q. cerris* type, *Q. robur* type, Amaranthaceae, Asteroideae.
OD-3G	85.7–78.8 6.9 34.6–32.0	MESOPHILOUS AND MONTANE AP:10-46 NAP: 9-22	83–95 40–75	CPT: *Pinus*, *Q. robur* type, *Q. cerris* type, *Abies*, Poaceae. RPT: *Artemisia*, Amaranthaceae, *Q. ilex* type, *Carpinus betulus*, *Ostrya/Carpinus orientalis*, *Fagus*, *Tilia*.
OD-3F	89.8–85.7 4.3 36.2–34.6	STEPPE AP: 4-15 NAP: 18-30	35–70 11–32	CPT: *Artemisia*, *Pinus*, Amaranthaceae, Poaceae. RPT: *Q. robur* type, *Q. cerris* type, Asteroideae.
OD-3E	104–89.8 14.2 41.3–36.2	MESOPHILOUS AND MONTANE AP:7-62 NAP: 7-29	65–95 50–85	CPT: *Pinus*, *Q. robur* type, *Artemisia*. RPT: *Q. cerris* type, *Abies*, Poaceae, *Carpinus betulus*, Ranunculaceae, *Fagus*, *Ostrya/Carpinus orientalis*, Amaranthaceae.
OD-3D	105.2–104 1.2 41.8–41.3	STEPPE AP: 12-56 NAP: 22-32	60–67 35–56	CPT: *Pinus*, *Artemisia*, Poaceae, *Q. robur* type. RPT: *Q. cerris* type, Amaranthaceae, *Ostrya/Carpinus orientalis*, Ranuculaceae, *Juniperus* type.
OD-3C	108–105.2 2.6 42.9–41.8	MESOPHILOUS AND MONTANE AP: 45-74 NAP:22-35	77–86 63–67	CPT: *Pinus*, *Q. robur* type, *Q. cerris* type. RPT: *Abies*, Ranunculaceae, *Alnus*, *Ostrya/Carpinus orientalis*.
OD-3B	112.1–108 4 44.2–42.9	STEPPE AP: 7-49 NAP: 12-31	56–77 19–42	CPT: *Pinus*, *Artemisia*, Poaceae, *Q. cerris* type. RPT: *Q. robur* type, Amaranthaceae.
OD-3A	128–112.1 15.9 48.5–44.2	MESOPHILOUS, MONTANE AP: 30-102 NAP: 3-32	73–96 61–92	CPT: *Pinus*, *Abies*, *Q. robur* type, *Q. cerris* type, Poaceae, *Artemisia*. RPT: *Ostrya/Carpinus orientalis*, Ranunculaceae, *Carpinus betulus*, *Betula*, *Tilia*, Amaranthaceae, *Alnus*, *Q. ilex* type, *Ulmus*, *Zelkova*.
OD-4	131.6–128 3.6 49.5–48.5	STEPPE AP: 13-26 NAP: 17-49	40–60 30–40	CPT: *Artemisia*, Amaranthaceae, *Pinus*, *Q. cerris* type, *Q. robur* type. RPT: *Juniperus* type, Asteroideae.

the physiognomy of vegetation, and CONISS (included in TILIA software) were used to identify pollen zones (Figs. 2–5). For Pollen Assemblage Superzones (PASZ) denomination, the approach of Sadori et al. (2016) was used, following Tzedakis (1994). The present work mainly deals with the interval covered by the superzone PASZ OD-3 (128–69.9 ka), but includes also few samples of PASZ OD-2 and PASZ OD-4. In this paper, PASZ OD-3 was divided in eleven PAZ, Pollen Assemblage Zones (OD-3A to OD-3M), of which PAZ OD-3A, namely the Last Interglacial - LI, was divided into six Pollen Assemblage subZones, PZ (OD-3A1 to OD-3A6), Table 2.

4. Results and discussion

The data indicate a fairly good conservation of pollen and a significant taxonomic variety (ca. 95 different taxa). A mean pollen count of 628 terrestrial pollen grains has been obtained. Lower counts occurred in herbs-dominated samples. The total pollen concentration of terrestrial taxa (*Pinus* included) is between 13,000 and 295,000 pollen grains/g.

The pollen record is described in Tables 1 and 2, following pollen zonation used by Sadori et al. (2016). Results are presented in several pollen diagrams (Figs. 2–5) and compared with southern European pollen records (Fig. 6) and other proxies (Fig. 7). The LO record shows an alternation of periods characterized by forests and open vegetation, clearly resembling the well-known vegetation succession of other European pollen records (Fig. 6). The classic terminology originally used at La Grande Pile (GP, Woillard, 1978) is adopted to name the interstadial phases (Saint-Germain Ia, Ic, Saint-Germain II, Ognon I and II) and the stadial phases (Montaigu, Melisey I and II, stadial I and II) which follow the Eemian.

After the first comparison between long terrestrial and marine records (Tzedakis et al., 1997), the joined marine-pollen records from the Iberian margin (Fig. 1, Sánchez-Goñi et al., 1999, 2002, 2005, 2007, 2012) provided the basis to correlate the terrestrial records with the marine stratigraphy.

The direct correlation between the pollen and marine (benthic and planktonic oxygen isotope and SST) records from different European margin cores (Sánchez-Goñi et al., 2005; 2012) shows that the alternation of forest contractions (Mélisey I, Montaigu, Mélisey II, stadial I) and expansions (Eemian, St Germain Ia, St Germain Ib, St Germain II, Ognon I) during the MIS5 correspond to cooling and warming sea surface temperature (SST) events, indicating a pervasive coupling between the European temperature and eastern North Atlantic SST during the last climatic cycle at orbital and millennial time scales.

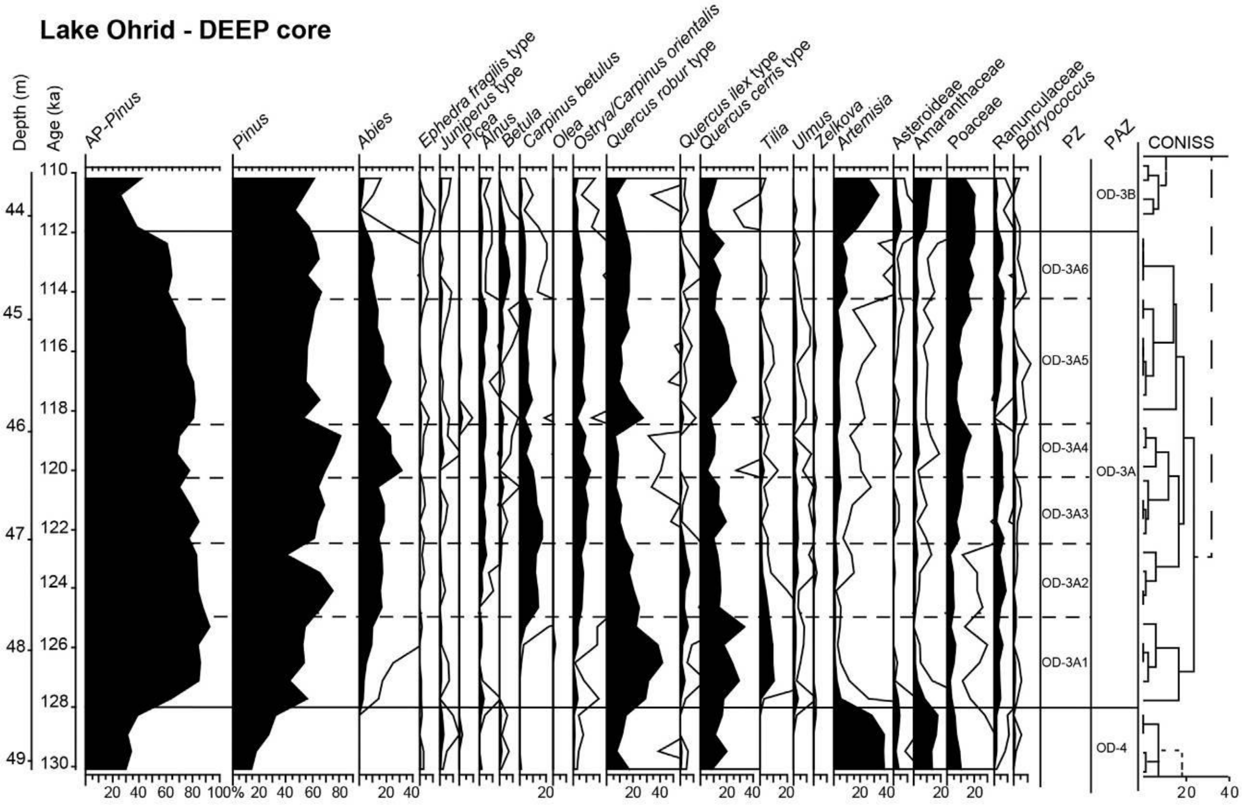

Fig. 3. Lake Ohrid (FYROM/Albania) - DEEP core. Eemian pollen percentage diagram, selected taxa. Curve magnification 5×.

4.1. Vegetational changes at Lake Ohrid in a South-European context

4.1.1. The glacial-interglacial transition (end of PASZ OD-4, 131.6–128 ka)

The first part of the time period investigated here corresponds to the PASZ OD-4 and to the final part of the penultimate glacial (Sadori et al., 2016). During this phase, the environment is characterized by open vegetation indicating cold and dry conditions with the prevalence of *Artemisia*, Amaranthaceae and Poaceae (Fig. 4 B). Herbaceous taxa concentration values have the highest values of the record during this period (ca 50 × 10^3 pollen grains/g, Fig. 5). At the end of this pollen zone, there is a noteworthy presence of mesophilous trees, with AP (*Pinus* included) over 30% (Fig. 2).

4.1.2. The Eemian interglacial (PAZ OD-3A, 128–112.1 ka)

The beginning of the Eemian in our record (PAZ OD-3A, Tables 1 and 2, Figs. 2–5) is dated to ca. 128 ka when AP percentage sharply increases, passing from 39 to 64%. Concentration data record the sharpest increase and the highest peak of AP (ca. 100 × 10^3 pollen grains/g, *Pinus* excluded) of the record (Fig. 5). This spread is mainly due to the expansion of *Quercus robur* type, *Quercus cerris* type and *Tilia* (Fig. 3), forming the bulk of mesophilous tree taxa and indicating rising temperature and precipitation. The highest mesophilous taxa percentages (almost 80%) were attained at ca. 127 ka. The period from 128 to 125 ka (OD-PZ 3A1, Table 2) corresponds to the so-called Eemian "climatic optimum". The increase of AP at the beginning of the LI is similar and almost synchronous (i.e. within the associated uncertainties of each record) with other Balkan sites. At Tenaghi Philippon (TP, Figs. 1 and 6), the Eemian reforestation is dated to 128 ka, with an increment of AP exceeding 80% (Milner et al., 2013, 2016). At Ioannina (IO, NW Greece, Fig. 1), the forested period began at ca. 127-126 ka, when AP increased over 50% (Tzedakis et al., 2003). The timing for the beginning of the Eemian observed at LO is also coherent on the wider regional scale. For example, at Lago Grande di Monticchio (LM, southern Italy, Figs. 1 and 6) Brauer et al. (2007) identified the start of the LI at ca. 127 ka, with AP reaching up to 80% (Fig. 6). At Lake Van, in the Near East (LV, eastern Turkey, Pickarski et al., 2015a; Fig. 1), the Eemian reforestation starts at 129.1 ka, with the deciduous oaks, *Ulmus*, *Juniperus* and *Betula* reaching the highest values between 128 and 127 ka. In the coupled marine-pollen record from the southern Iberian Margin (core MD95-2042, MD; Sánchez-Goñi et al., 1999, 2005, Figs. 1 and 6), it is clear that full interglacial conditions in the terrestrial realm occur at 126 ka, almost simultaneously with the highest Sea Surface Temperature (SST) recorded during marine substage 5e (Fig. 6). Noteworthy, these differences in the individual chronologies are negligible with respect to the uncertainty associated to each record, suggesting a rapid and synchronous response of southern Europe vegetation to increasing regional temperature.

From 128 to 125 ka (OD-3A1, Table 2) LO experienced also the most important spread of mediterranean taxa, mainly due to high percentages of *Quercus ilex* type (Figs. 2 and 3). Even if this spread is rather low (<10%), it may suggest increased seasonality, with persistence of rather favourable climate conditions for the mesophilous forest until 122.6 ka (OD-3A2, Table 2, Figs. 2 and 3). Enhanced seasonality of the precipitation (linked to higher

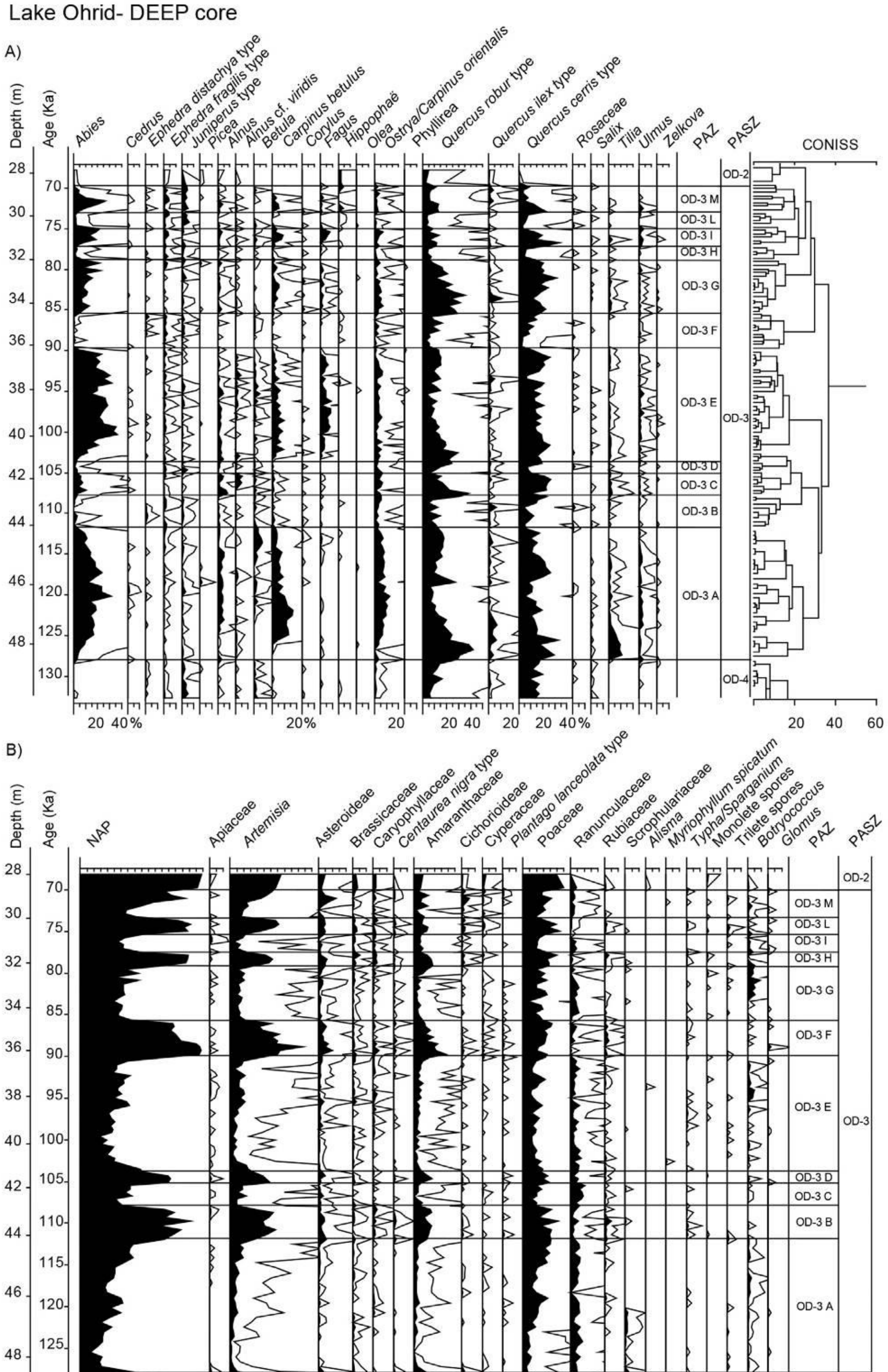

Fig. 4. Lake Ohrid (FYROM/Albania) - DEEP core. Pollen percentage diagram (selected taxa) of AP (A) and NAP (B). All curves are reported against age (ka). Depth (m) scale is drawn as well. Curve magnification 7×. *Pinus* curve is reported in Fig. 2.

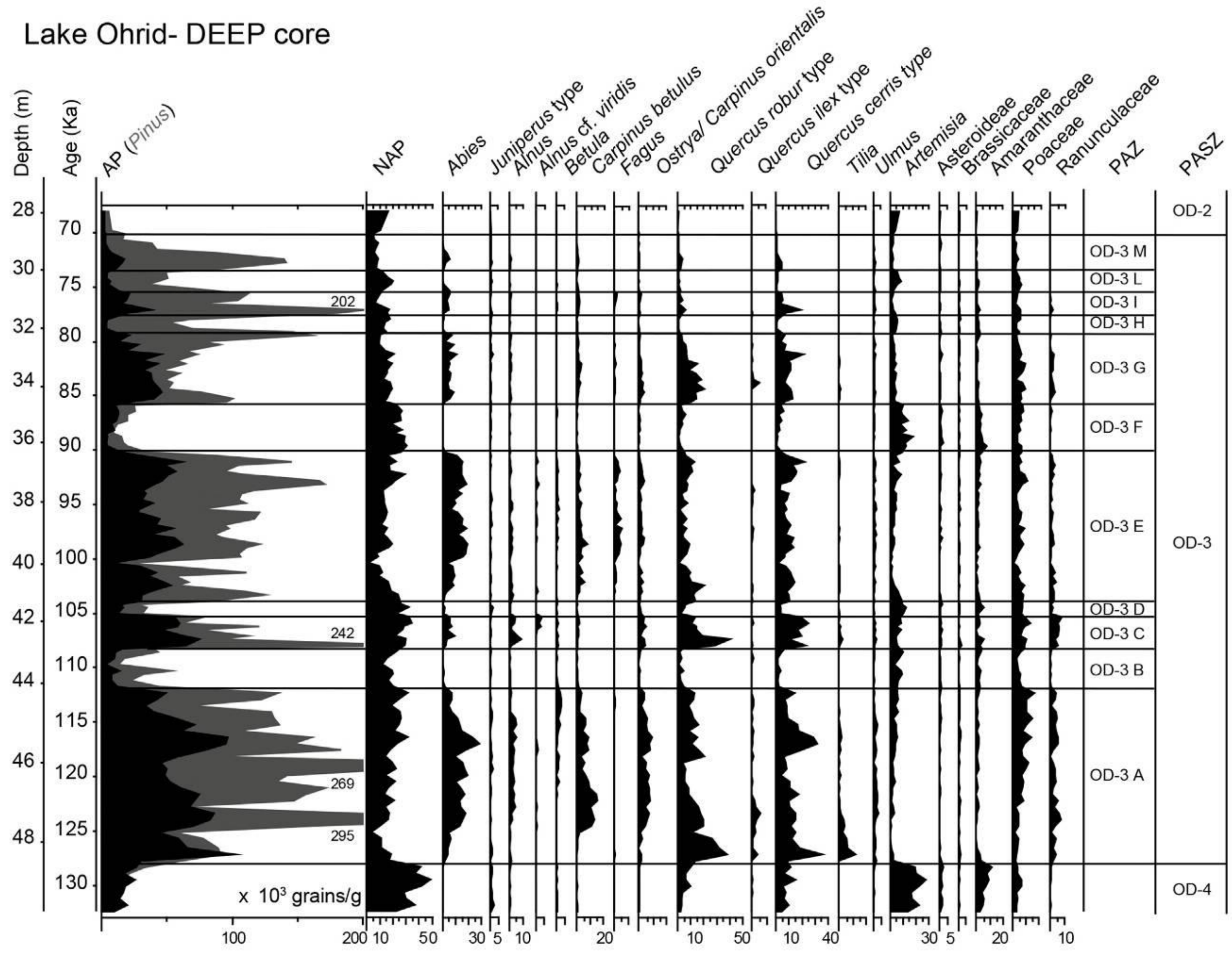

Fig. 5. Lake Ohrid (FYROM/Albania) - DEEP core. Pollen concentration diagram of selected taxa, against age (ka). Depth (m) scale is drawn as well.

percentage of mediterranean taxa) for the first part of the Eemian is also evident in the TP record and from the MD core (Milner et al., 2013; Sánchez-Goñi et al., 1999; 2007).

At LO, mesophilous taxa remain very high (i.e., above 70%) until ca. 125 ka (Fig. 2), when the second phase of the Eemian started (125–118.5 ka, OD-3A2 to OD-3A4).

From this period, although chronological uncertainties related to each record prevent a secure correlation of single events, LO and southern European vegetation experienced a series of short-term reductions in arboreal taxa.

At ca. 122 ka (first sample of OD-3A3), following a drop in *Pinus*, the LO percentage diagram shows a minimum in AP (Figs. 2, 3 and 6) matching a reduction in Mediterranean taxa (mainly *Quercus ilex* type) and a slight increase of *Carpinus betulus, Ostrya/Carpinus orientalis, Betula* and Poaceae. Concentration data evidence a general reduction of AP and confirms the increase of Poaceae (Fig. 5). Our data suggest a decrease of temperature accompanied by an increase in humidity. A similar trend was recorded in another core from LO (Bordon, 2008), situated closer to the lake shoreline than the DEEP core. The development of *Carpinus betulus* at ca. 122 ka, during the central phase of the Eemian, is not only observed at LO, but also in other southern European (beneath 50° N) sequences (Tzedakis et al., 2001 and references therein), while in northern Europe, *Pinus* and other coniferous, together with *Betula*, dominate (Müller and Kukla, 2004).

After a decrease in AP values at ca. 120.6 ka, the development of montane trees at LO (mainly composed of *Abies*, OD-3A4, Figs. 2 and 3) takes place at 120 ka, possibly indicating decreasing temperatures and wet conditions. Similarly, concentration values show an increase for *Abies* at 120 ka, but it seems already well established since at least 125 ka (Fig. 5), just after the climatic optimum for the mesophilous forest elements.

This cooling phase, with minor shift regarding the date, is also recorded in the other Mediterranean records. Indeed, at IO, around 122.6 ka, deciduous oaks, *Betula* and *Abies* increase, in combination with a decrease of *Carpinus betulus* and the disappearance of mediterranean taxa. After this episode, two other drops in temperature with increase of herbaceous values (around 120.4 ka and later at 118.1 ka) are recorded at IO (Frogley and Tzedakis, 1999). The same trend is observed at TP, after an increase in *Pinus*, *Betula* and *Alnus*, drops in arboreal taxa take place at 119 ka, and later at 116 ka and 114 ka (Milner et al., 2013). These short periods of forest reduction are also recorded at Lake Kopais (LK; Tzedakis, 1999, Fig. 1) and LM (Allen and Huntley, 2009; Brauer et al., 2007). In the latter record, similarly to LO, high percentages of *Abies* are found. At MD (Sánchez-Goñi et al., 1999), this period is characterized by a

Table 2
Lake Ohrid (FYROM/Albania) - DEEP core. Scheme of pollen data for PAZ OD-3A (Eemian), divided in Pollen Assemblage subZones (OD-PZ).

PZ	Age (ka) Duration (ka) Depth (m)	AP (%) AP excl. *Pinus* (%) *AP* (pollen grains/g x10^3) *NAP* (pollen grains/g x10^3)	MAIN FLORISTIC FEATURES CPT (Common Pollen Types) RPT (Rare Pollen Types)
OD-3A6	114.3–112.1 2.2 44.8–44.2	74–87 38–64 *12–49* *18–31*	CPT: *Pinus*, Poaceae, *Q. robur* type, *Q. cerris* type, *Artemisia*. RPT: *Abies*, Ranunculaceae, *Ostrya/Carpinus orientalis*, *Carpinus betulus*, *Betula*.
OD-3A5	118.5–114.3 4.2 46–44.8	88–94 68–82 *45–97* *14–32*	CPT: *Pinus*, *Abies*, *Q. cerris* type, *Q. robur* type, Poaceae. RPT: *Artemisia*, *Ostrya/Carpinus orientalis*, *Carpinus betulus*, Ranunculaceae, *Alnus*, Amaranthaceae, *Betula*, *Ulmus*, Botryococcus, *Tilia*.
OD-3A4	120.3–118.5 1.8 46.4–46	89–92 67–78 *52–48* *14–23*	CPT: *Pinus*, *Abies*, *Q. robur* type, Poaceae. RPT: *Ostrya/Carpinus orientalis*, *Q. cerris* type, *Carpinus betulus*, *Alnus*, *Juniperus* type, *Betula*.
OD-3A3	122.6–120.3 2.3 47.1–46.4	95–90 77–85 *60–75* *13–21*	CPT: *Pinus*, *Carpinus betulus*, *Q. cerris* type, *Abies*. RPT: *Q. robur* type, *Ostrya/Carpinus orientalis*, Poaceae, *Alnus*, Ranunculaceae, *Ulmus*, *Artemisia*.
OD-3A2	125–122.6 2.4 47.7–47.1	94–97 84–93 *43–86* *3–17*	CPT: *Pinus*, *Q. robur* type, *Abies*, *Carpinus betulus*, *Q. cerris* type. RPT: *Ostrya/Carpinus orientalis*, Poaceae, Ranunculaceae, *Q. ilex* type, *Tilia*, *Alnus*.
OD-3A1	128–125 3 48.5–47.7	59–94 39–86 *26–102* *11–41*	CPT: *Pinus*, *Q. robur* type, *Q. cerris* type, *Artemisia*. RPT: *Abies*, Amaranthaceae, *Tilia*, Ranunculaceae, Poaceae, *Q. ilex* type, *Ulmus*, Asteroideae, *Ostrya/Carpinus orientalis*, *Carpinus betulus*, *Betula*.

more oceanic weather, associated with a decrease in winter temperatures.

Before the end of the Eemian, at LO, arboreal taxa show a minimum (at 119.4 ka, Figs. 2 and 6) due to the decrease of mesophilous (mainly hornbeams and elms) and riparian trees. Deciduous and semi-deciduous oaks have a slight increase in concert with *Betula*, while the others montane taxa decrease. The decrease of forest biomass (Fig. 5) seems to be more prolonged, involving a minimum in AP concentration around 46×10^3 pollen grains/g from ca. 121 to 119 ka.

At ca. 118.5 ka (OD-3A5) interglacial conditions appear interrupted by a cold event marked by the decrease of deciduous *Quercus* both in percentages and in concentration (Fig. 5) and by the nearly complete disappearance of Mediterranean taxa. This cooling marks the beginning of the third climatic phase, between 118.5 and 112 ka, characterized by cooler and drier conditions.

At 118 ka, Bordon (2008)found an increase in coniferous forest, with the development of *Picea*. In the DEEP core, this taxon is almost absent during LI, but a peak of 2% occurs exactly at 118 ka (Fig. 3). This change suggests a major cooling, in fact *Picea* needs winter temperatures below -3 °C to develop (Huntley et al., 1989; Prentice and Helmisaari, 1991). The lower presence in LO record can be ascribed both to the central position of the core and to the scarce pollen productivity of *Picea* that makes it under-represented in pollen diagrams (Hicks, 1994).

At LV, around ca.118 ka develops an open vegetation in the same period with the increase of steppic taxa, while *Pinus*, deciduous oaks and *Carpinus betulus* decrease suggesting cooling and aridification, while from ca 114.2 ka to 112.4 ka, a temporary warming is recorded, with the re-expansion of *Pinus* and deciduous oaks (Pickarski et al., 2015a). At the same time, since ca. 114 ka, at LO a decrease of mesophilous and riparian trees matching an increase of Poaceae, is recorded (Figs. 2 and 4).

The end of the Eemian forest at LO is dated at ca. 112 ka, thus the Eemian forested phase has a length of ca. 16 ka. Since 112 ka, AP definitively decreases (from 63 to 32%, from 49×10^3 to 12×10^3 pollen grains/g, Figs. 3 and 5) and steppic taxa increase, indicating the re-establishment of cold and dry conditions. The timing and the vegetational trends for the end of the interglacial terrestrial phase are again coherent with other southern Europe sites (Fig. 6). At TP *Artemisia* and Amaranthaceae start to increase and AP decrease, reaching 30%, at ca. 112 ka. Then, at 111 ka, after a re-increase of *Pinus*, *Betula* and *Juniperus*, steppic taxa reach 60%, suggesting a new cold and dry phase (Milner et al., 2013). At IO, open vegetation increases between 112.3 and 111.8 ka, with a simultaneous short expansion of deciduous oaks (Tzedakis et al., 2003). At LM steppic taxa increase at ca 110 ka, while at LV the end of the Eemian is recorded at 111.5 ka (Pickarski et al., 2015a). In MD core, the last Eemian phase suggests a warming and drying trend on the basis of a slight increase in deciduous and evergreen oaks and *Cistus* as well as the decrease of Ericaceae (Sánchez-Goñi et al., 1999), although more recent interpretation suggest that precipitation towards the end of Eemian at 110 ka were higher with respect to the first part of the Eemian (Sánchez-Goñi et al., 2005).

The duration and the end of LI appear to be slightly different from site to site. This difference could be due to the chronology of single sites that, even if improved in recent years, can be still inaccurate. According to Turner (2000), the Eemian is shorter at north of the Alps and Pyrenees, while the long term conditions of LI are typical of southern Europe, where the forest persists until 112-110 ka, several millennia after the establishment of opening vegetation in northern Europe, where it is recorded at ca. 115 ka (Müller and Kukla, 2004; Tzedakis et al., 2003).

Within Eemian, *Zelkova* is the only extinct taxa found at LO, even if in very small and sparse amounts, similarly to what occurs at other southern Balkan sites (TP, NE Greece, Tzedakis, 1993 and Lake Kopais, LK, SE Greece, Okuda et al., 2001; Fig. 1). *Zelkova* is, on the contrary, widespread during the Eemian in Central Italy (Follieri et al., 1986, 1988; Bertini, 2010; Magri et al., 2017).

Our pollen results confirm the idea of an Eemian characterized

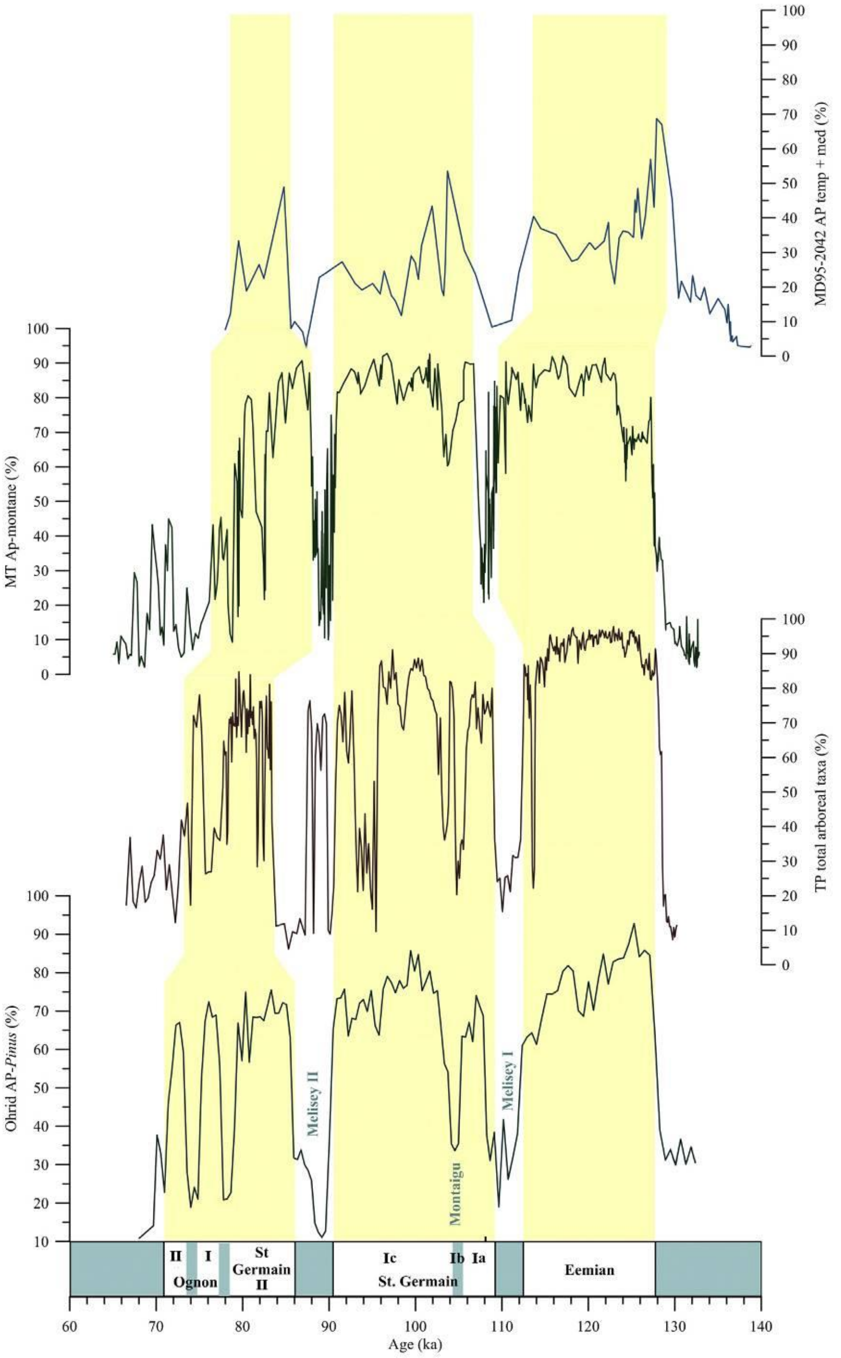

Fig. 6. Comparison of Lake Ohrid (LO) with other southern European pollen records. From bottom: AP (arboreal pollen) (*Pinus* excl.), LO, this study; total arboreal taxa from Tenaghi Philippon (TP, Milner et al., 2013, 2016); mesophilous and mediterranean woody taxa from Lago Grande di Monticchio (LM, Brauer et al., 2007); temperate and mediterranean arboreal taxa from the Iberian margin (MD95-2042, Sánchez-Goñi et al., 1999; 2007). Yellow shading indicates the three main forested period of the LIC, named after Woillard (1978). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

by the evolution of vegetation conditioned by climate changes. These results are also in line with the previous pollen studies from LO (core JO 2004; Bordon, 2008), from the wider Mediterranean area (Brewer et al., 2008; Sánchez-Goñi et al., 2005; Sirocko et al., 2005) and precise older ones (Litt et al., 1996).

4.1.3. *The Early Last Glacial (from PAZ OD-3B to PAZ OD-3M, 112.1–68 ka)*

After 112 ka, with the onset of the Early Last Glacial, the environment of LO started to change drastically into an open environment, with NAP peaking at 80% and concentration values reaching

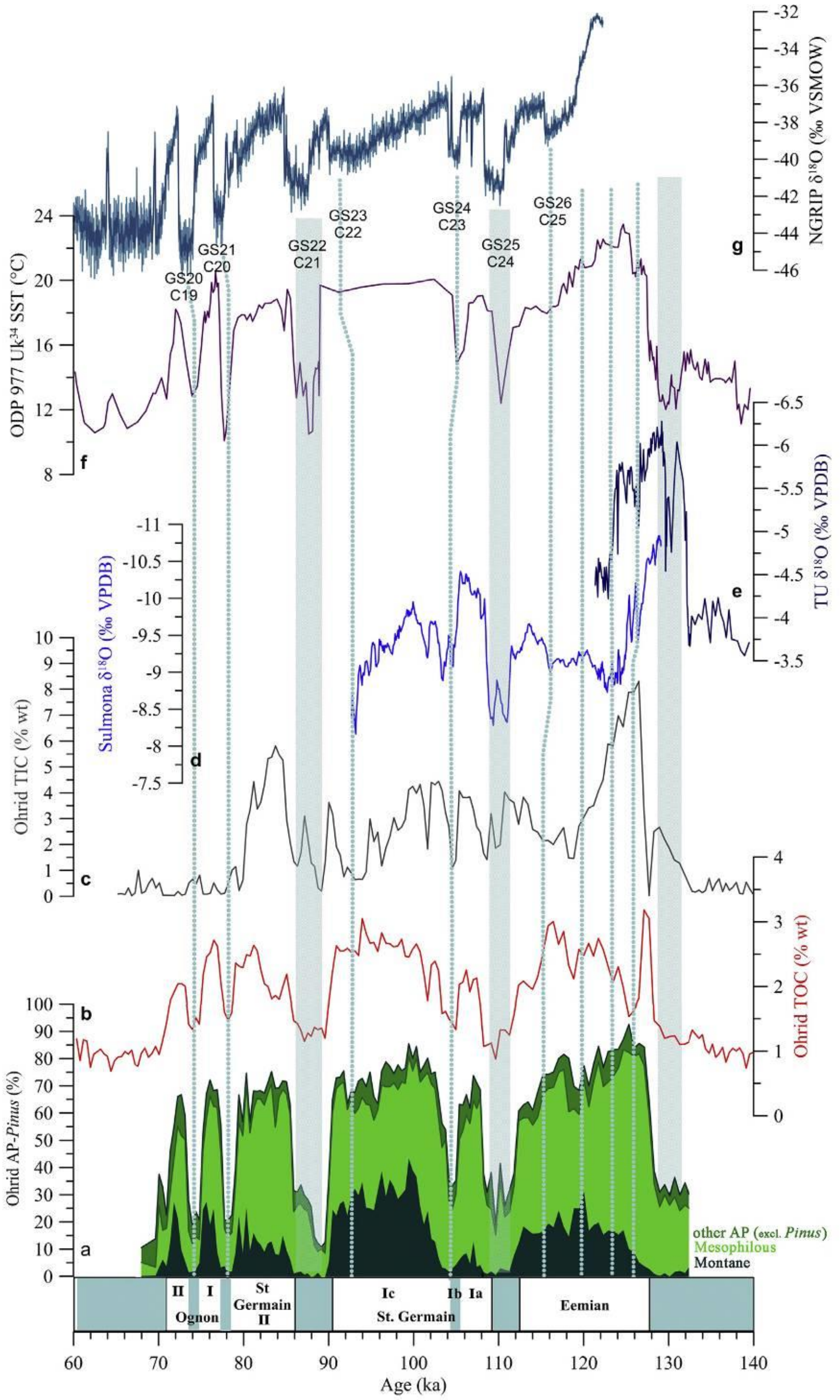

Fig. 7. Comparison of (a) montane, mesophilous and other AP (excl.*Pinus*) pollen curves from of Lake Ohrid (LO, present study) with other biogeochemical proxies from the lake: (b) TOC and (c) TIC (Francke et al., 2016), and with hydrological and climate proxies from the Mediterranean and the North Atlantic: (d) δ^{18}O record on endogenic lake calcite from the Sulmona Lake; (e) δ^{18}O speleothem record from Tana che Urla Cave, Central Italy (Regattieri et al., 2017, 2014 respectively); (f) Sea Surface Temperature (SST) from core ODP-977 (Western Mediterranean, Martrat et al., 2014); (g) Greenland δ^{18}O record (NGRIP, 2004). Numbers denote Greenland Stadials (GS), and the corresponding North Atlantic cold events (C events, after McManus et al., 1994). Dashed lines/intervals indicate the period of vegetation reduction corresponding to climate deterioration in the other curves.

25×10^3 pollen grains/g (Figs. 4B and 5). However, the LO record shows the persistence of many arboreal taxa (Figs. 2 and 4A), which confirms that the area played an important role as a refugium zone and experienced relatively wet conditions even during glacial/stadial phases (Bertini et al., 2016; Sadori et al., 2016). The Early Last Glacial period has been divided into eight pollen zones (Table 1). The first pollen zone (OD-3B, 112-108 ka, Figs. 2, 4 and 5) is equivalent to the Mélisey I stadial and represents the onset of a cold and arid climate all over southern Europe and the Near East.

Pollen zones OD-3C, D, E (108–89.8 ka Figs. 2, 4 and 5) are equivalent to interstadial St. Germain I. During this period (originally divided at GP in St. Germain Ia, Ib- Montaigu - and Ic), the main taxa are oaks, with deciduous ones dominating. They have a peak in concentration values at the beginning of St. Germain Ia of ca. 40×10^3 pollen grains/g (Figs. 4A and 5). *Abies* becomes dominant together with *Fagus*, whereas *Carpinus betulus* mainly occur in St. Germain Ic (Figs. 2 and 4A). *Fagus* increases after a drop of AP concentration recorded at 101 ka (Fig. 5) and reaches the highest percentage and concentration values (9% and 6×10^3 pollen grains/g, Figs. 4A and 5) of LIC at 97 ka. This pattern is similar to other mid altitude European records as Ribains and Les Echets in France (RI, de Beaulieu and Reille, 1984, 1992a; LE), suggesting a possible development of oceanic conditions, with cool summers and increased annual precipitations. Fig. 2 clearly shows that St. Germain Ic is the period characterized by the major development of mountain vegetation belt and a reduction of the mesophilous belt amplitude.

The St. Germain I interstadial is interrupted by a rapid cold oscillation (OD-3D, 105.2–104 ka), which can be regarded as analogous to GP Montaigu event (Woillard, 1978). It is characterized by the expansion of steppic taxa and the persistence of mesophilous trees (Figs. 2 and 4B; Tabs 1). In the LO record, this event is between ca. 104 and 105.2 ka. A similar vegetation patterns are recorded in other regions of the Balkans, with some differences during the cold and the last phases (Milner et al., 2016; Tzedakis, 1993; Tzedakis et al., 1997). An environment dominated by *Quercus* is present at GP (de Beaulieu and Reille, 1992b) and at LM (Allen et al., 1999; Brauer et al., 2007) in central Europe and at LV (Pickarski et al., 2015b) in the Near East. While in the Iberian Margin, at MD (Sánchez-Goñi et al., 1999), *Pinus* and deciduous oaks are present during the Montaigu event. Later, an increase in temperature and precipitation occurs, with the development of heathland and deciduous/Mediterranean forests.

Pollen zone OD-3F (89.8–85.7 ka, Figs. 2, 4 and 5) of LO is equivalent to stadial Mélisey II and turns out to be more rigid than Mélisey I. During this period steppic taxa rise in concentrations reaching the highest percentage values of the record at ca. 89 ka (Figs. 2, 4A and 5). Mélisey II is characterized also in other Balkan records (Bottema, 1974; Milner et al., 2016; Tzedakis, 1993, 1999) by a strong presence of steppic taxa and a reduction of arboreal taxa. At LM, *Pinus*, deciduous *Quercus*, *Abies*, *Fagus* and *Alnus* are still present during this stadial, although with very high amounts of steppic taxa (Allen et al., 1999; Brauer et al., 2007). After 88 ka pioneer trees increase, mainly with *Betula* and *Juniperus* type, preluding to the transition to the successive interstadial St. Germain II.

The second long forested period of LO record (OD-3G, 85.7–78.8 ka) is associated with St. Germain II and is followed by the equivalent of stadial I (OD-3H, 78.8–77.6 ka), Ognon I (OD-3I, 77.6–75.4 ka), stadial II (OD-3L, 75.4–73.4 ka) and Ognon II (OD-3M, 73.4–69.9 ka) of GP (Woillard, 1978). Three periods are characterized by warmer climatic conditions (OD-3G, I, M, Table 1, Figs. 2, 4 and 5) with AP reaching ca. 70% and two phases by colder ones (OD-3H, L, Table 1, Figs. 2, 4 and 5), with NAP reaching ca. 75%.

At LO, the three phases of forestation (OD-3G, I, M) are clearly distinct and dominated, besides *Pinus*, by mesophilous and montane trees indicating temperate and wet conditions. Pioneer shrubs (mainly *Juniperus* type) increase since the end of OD-3G. At 84 ka, during St. Germain II, there is a considerable drop in the percentages of *Pinus*, montane and mesophilous trees, recorded also in AP concentration values (from 45×10^3 to 31×10^3 pollen grains/g, Fig. 5), while Mediterranean trees have a peak of 15% and ca. 6×10^3 pollen grains/g, due to *Quercus ilex* type (Figs. 2, 4A and 5). *Artemisia* and Amaranthaceae slightly increase (Figs. 2 and 4 B). The alga *Botryococcus* has an increment after this event and reaches the highest values of the record (max. 10%, Fig. 4 B).

At LK (Tzedakis et al., 1997) the main taxa during St. Germain II are deciduous oaks, *Pinus* and *Juniperus*. At IO (Tzedakis, 1993), the vegetation composition is similar to that of LO, but *Carpinus betulus* and *Abies* seem to replace *Juniperus* in the final part. At TP deciduous *Quercus* and *Pinus* prevail and are accompanied by mesophilous and montane trees and *Juniperus* (Milner et al., 2016). At LV (Pickarski et al., 2015b), St. Germain II starts with the expansion of deciduous oaks. *Betula* and *Pistacia* cf. *atlantica* are also present, while *Pinus* rises during the second part of the interstadial.

The marine stratigraphy obtained at the Iberian margin ascribes St. Germain II, stadial I and Ognon I to MIS5a and stadial II and Ognon II to MIS4 (Sánchez-Goñi, 2007, 2013). A different attribution is provided by Milner et al. (2016) for TP, including in MIS 5a two forest phases (St. Germain II, Ognon I). At Lake Prespa, Panagiotopoulos et al. (2014) found two forest expansions in the interval dated from 81 to 71 ka, with the first one being more pronounced (higher AP percentages and the prevalence of oaks and *Abies*). These phases probably correspond to the Ognon interstadials. At Lagaccione and at Lago di Vico in central Italy, three forest oscillations subsequent to St. Germain I and locally named Etruria I, II, and III have been identified (Magri, 1999; Magri and Sadori, 1999). The first is the analogous of St. Germain II, while the latter two can be correlated to Ognon I and II that however seems to show a more marked forest expansion than that found at other southern European sites. de Beaulieu and Reille (1992b) had however questioned the existence of the "Ognons" at GP, at Les Echets (LE, Fig. 1, de Beaulieu and Reille, 1984), Ribains (RI, Fig. 1, de Beaulieu and Reille, 1992a) and Bouchet (BO, Reille and de Beaulieu, 1990; Reille et al., 1998) and their correlation with interstadials found in central Europe. Instead, at LM, Allen and Huntley (2009) ascribe the three forest phases occurring after St. Germain I (pollen zones 17a, 17c and 17e) to St. Germain II, while Brauer et al. (2007) ascribe to St. Germain II only the oldest of the three forest expansions.

Finally at the end of LO record, PASZ OD-2 (71-70 ka MIS4, Figs. 2, 4 and 5) indicates the transition to full glacial conditions, with steppic taxa being present at high percentages and concentrations, while the other ecological groups strongly decrease (Figs. 2 and 5).

4.2. Environmental changes at Lake Ohrid in a Mediterranean-North Atlantic context

The comparison of the pollen record with selected biogeochemical proxies from the LO sediments (Wagner et al., 2017 and references therein) helps to assess the relationships between vegetational and environmental changes (Fig. 7). Higher (lower) Total Organic Carbon (TOC) contents are representative for an enhanced (reduced) primary productivity in the epilimnion and a reduced (improved) decomposition of organic matter (OM) in the surface sediments of LO, based on the assumption that the organic matter is predominantly of aquatic origin (Francke et al., 2016). A strong primary productivity and reduced decomposition is explained by high spring and summer temperatures and enhanced nutrient supply from the catchment during warm and humid periods. As expected, the AP-*Pinus* and the TOC curves show very similar patterns, both for the general trends and for short-term climate oscillations, with maxima reflecting increasing temperatures and humidity. Slight differences in the amplitude can potentially be explained by a hampered OM preservation during times of high seasonality, as OM decomposition at Lake Ohrid predominately depends on winter mixing, and thus, on winter temperatures. The Total Inorganic Carbon (TIC) content in the sediments of LO is mainly due to the endogenic calcite, which is controlled by photosynthesis-induced precipitation of endogenic calcite in the epilimnion during spring and summer. Furthermore, endogenic calcite precipitation depends on the ions supply from the karstic limestones in the catchment, which is enhanced during warm and humid periods (Francke et al., 2016; Vogel et al., 2010). The comparison with the pollen record shows an overall similarity to the TIC record (Fig. 7). The three main periods can be easily recognized, although the second part of the Eemian and the St. Germain interstadials appear less expressed in TOC and TIC than in pollen. Interestingly, the TIC curve appears to resemble more closely the percentage of mesophilous trees compared to the montane taxa (Fig. 7).

We can now extend the comparison to other well-dated archives from the wider Mediterranean and the North Atlantic region in order to investigate how local climatic change is recorded in regional and extra-regional climatic patterns. The similarities among LO biogeochemical proxies and oxygen isotope records ($\delta^{18}O$) from speleothem and lacustrine endogenic calcite from Tana che Urla Cave (TU, Central Italy, Figs. 1 and 7, Regattieri et al., 2014) and extinct Sulmona Lake (SU, central Italy, Figs. 1 and 7, Regattieri et al., 2015, 2017) have already been observed by Zanchetta et al. (2016). In the central Mediterranean, speleothem and lake calcite $\delta^{18}O$ values are commonly related to local hydrology, with lower values being observed during wetter phases and higher values related to drier conditions (Bard et al., 2002; Drysdale et al., 2005, 2007, 2009; Giaccio et al., 2015a, 2015b; Regattieri et al., 2014, 2016a, 2017; Roberts et al., 2008; Zanchetta et al., 2007). This formed the basis to improve the chronology for MIS5 at LO via climatostratigraphic alignment (sensu Govin et al., 2015) of the TIC curve to the $\delta^{18}O$ records of SU and TU (Zanchetta et al., 2016). Comparison of the $\delta^{18}O$ records with the new LO high-resolution pollen record shows major similarities, suggesting that vegetational changes are concomitant to changes in hydrological activity also on the fine-scale, indicating a prompt response of vegetation to variations in Mediterranean rainfall amount (Fig. 7). Differences between isotope and pollen records regard only the earlier decrease in $\delta^{18}O$ observed at TU during the glacial/interglacial transition, that can be partly ascribed to changes in the isotopic composition of the sea related to ice melting (Marino et al., 2015). On the other hand, the earlier increase in the SU $\delta^{18}O$ values since 127 ka could be related to decreasing seasonality (Regattieri et al., 2017), and well agree with the reduction of Mediterranean elements apparent from the pollen record. During the Eemian, LO shows a series of low-amplitude oscillations, with minima in precipitation and mesophilous tree populations centered at ca. 126 ka, 122 ka, 119 ka and 114 ka highlighting a pervasive hydrological intra-interglacial variability (Fig. 7). This result is consistent with numerous speleothem, pollen and diatom records for widespread sites in central and southern Europe (e.g. Cheddadi et al., 1998; Couchoud et al., 2009; Milner et al., 2013; Regattieri et al., 2014, 2016b, 2017; Rioual et al., 2007). A low-amplitude instability during the LI has been detected also from oceanic proxies from the North Atlantic and the Mediterranean. Indeed, detailed faunal, isotopic and ice-rafted detritus (IRD) records have revealed the presence of a series of moderate surface water cooling events in the North Atlantic and the Mediterranean Sea (e.g. Jiménez-Amat and Zahn, 2015; Kandiano et al., 2014; Martrat et al., 2014; McManus et al., 1994; Mokeddem et al., 2014; Oppo et al., 2006). Drops in SST, associated water vapour advection, and shifts in atmospheric circulation patterns affect also the continental hydrology of the Mediterranean (Drysdale et al., 2005, 2007; Regattieri et al., 2014, 2017). Although a firm correlation of oceanic and terrestrial events is prevented by the chronological uncertainties associated to each record, the small contractions of arboreal vegetation observed at LO during the Eemian resemble fluctuations in Mediterranean SST from core ODP-977 from the Alboran Sea (Martrat et al., 2014, Fig. 1). Noteworthy, SST from this western portion of the Mediterranean Sea are highly correlated to those of the Portuguese margin (e.g. Drysdale et al., 2009; Martrat et al., 2007). Apart from these intra-interglacial events, of particular interest is the change occurring at ca. 115 ka. In fact, it can be related to the first stadial recorded in the Greenland record (GS26, NGRIP, 2004, Fig. 7) and to North Atlantic cold event C25 (McManus et al., 1994; Mokeddem et al., 2014). This event likely triggered the end of the forested Eemian phase in central and northern Europe, and coincides in Southern Europe with the beginning of the decrease in mesophilous trees, likely related to a permanent reduction in moisture availability. A similar pattern is also found in the LO record. Since the stadial Melisey I, corresponding to GS25 (and to event C24 in the North Atlantic), a strong coherence is found between the LO pollen and the NGRIP records. This event marks the end of the LI in Southern Europe (Sánchez-Goñiet al., 1999) and corresponds to the first IRD event reaching the mid-latitudes (Oppo et al., 2006). Since this point, the ice volume threshold triggering ice-sheet instability and the periodic large-scale perturbations of the Atlantic Meridional Overturning Circulation (AMOC) typical of glacial periods (Ganopolski and Rahmstorf, 2001) has been passed. The impact on the Mediterranean continental hydrology of these large-scale AMOC perturbations is well known (e.g. Drysdale et al., 2007; Regattieri et al., 2015), and indeed each C event, or Greenland stadial, is marked by significant reduction of arboreal vegetation at LO (Fig. 7). Interestingly, also the relative expression of these events is comparable between the ice and the pollen record, with major amplitude variations occurring during stadial corresponding to GS25, GS22, GS21 and GS20, centered according to our chronology at 110, 88, 78, 74 ka respectively. Additional events of contractions in the arboreal vegetation can be identified both in the pollen and in the hydrological records during the Early Last Glacial.

5. Concluding remarks

In this work, we present the high-resolution (400 yrs) pollen record from Lake Ohrid (southern Balkans), covering the LIC, equivalent to MIS5 (128–70 ka). The pollen diagram covers also the end of MIS 6 and the beginning of MIS 4 (from 132 to 68 ka).

The pollen record of LO is coherent with other bio-geochemical proxies obtained from the same core, with other southern European and Near Eastern pollen records (Figs. 1 and 6), and with hydrological records from the central Mediterranean (Fig. 7). They all indicate a prompt response of the vegetation to fluctuations in regional moisture availability and temperature changes. Both orbital-scale changes and millennial to centennial scale events are recorded.

The LIC record presents three main forested periods interspersed with shorter colder and drier periods, substantially following the classical scheme of the European pollen stratigraphy established by Woillard (1978) at GP. The first (Eemian), the second (St. Germain I), the third (St. Germain II) and the two successive minor (Ognon I and Ognon II) forested phases show high percentages of arboreal pollen. Dominant taxa are always mesophilous trees, while montane taxa become rather important during St. Germain I. Most arboreal taxa never disappear, even during stadials, indicating and confirming that the LO region has been a refugium during the glacial for mesophilous and montane taxa. Changes in ecological groups during the record indicate a clear organization in vegetational belts, similarly to the present-day condition, with mesophilous trees always prevailing and characterizing the zones.

At LO, a rapid increase in arboreal taxa and a corresponding decrease in herbaceous ones starting at ca. 130 ka, characterize the transition from glacial to interglacial conditions. The LI occurs after 128 ka, when AP exceeds 50%. It is characterized by an initial phase (128-125 ka) with increased temperature and precipitation (the climate optimum for mesophilous forests); a central phase (125–118.5 ka) characterized by slight cooling (*Carpinus betulus* expansion) and a latter phase (ca 118.5–112 ka), with decline in temperatures and precipitation (new increase of mesophilous with montane taxa) until the end of LI. Within the Eemian, several small-scale amplitude events with contractions of arboreal vegetation occur at 122, 119 and 114 ka and maybe ascribed to interglacial variability, in line with other hydrological and temperature records from the Mediterranean and the North Atlantic. This suggests that teleconnections between North Atlantic conditions and Mediterranean continental hydrology persisted also during period of low ice volume and were severe enough to impact the regional vegetation.

During the Early Glacial (112–73.4 ka), abrupt and significant cold and dryr events are clear in the Ohrid pollen and biogeochemical records. They closely mirror the succession of Greenland stadials and of North Atlantic cold events, triggered by ice-sheet instabilities (Ganopolski and Rahmstorf, 2001) and related to perturbations of the AMOC, SST and associated atmospheric patterns.

Overall, the new record provides new evidence for strong connections between ice sheets dynamics, North Atlantic conditions and hydrological patterns of the Ohrid region.

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CHAPTER 4:

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Pollen-based temperature and precipitation changes in the Ohrid Basin (western Balkans) between 160 and 70 ka

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Abstract. Our study aims to reconstruct climate changes that occurred at Lake Ohrid (south-western Balkan Peninsula), the oldest extant lake in Europe, between 160 and 70 ka (covering part of marine isotope stage 6, MIS 6; all of MIS 5; and the beginning of MIS 4). A multi-method approach, including the "Modern Analog Technique" and the "Weighted Averaging Partial Least-Squares Regression", is applied to the high-resolution pollen sequence of the DEEP site, collected from the central part of Lake Ohrid, to provide quantitative estimates of climate and bioclimate parameters. This allows us to document climatic change during the key periods of MIS 6 and MIS 5 in southern Europe, a region where accurate climate reconstructions are still lacking for this time interval.

Our results for the penultimate glacial show cold and dry conditions, while the onset of the "last interglacial" is characterized by wet and warm conditions, with temperatures higher than today (by ca. 2 °C). The Eemian also shows the well-known climatic tri-partition in the Balkans, with an initial pre-temperate phase of abrupt warming (128–121 ka), a central temperate phase with decreasing temperatures associated with wet conditions (121–118 ka), followed by a post-temperate phase of progressive change towards cold and dry conditions (118–112 ka).

After the Eemian, an alternation of four warm/wet periods with cold/dry ones, likely related to the succession of Greenland stadials and cold events known from the North Atlantic, occurred. The observed pattern is also consistent with hydrological and isotopic data from the central Mediterranean.

The Lake Ohrid climate reconstruction shows greater similarity with climate patterns inferred from northern European pollen records than with southern European ones, which is probably due to its intermediate position and the mountainous setting. However, this hypothesis needs further testing as very few climate reconstructions are available for southern Europe for this key time period.

1 Introduction

Since the Middle Pleistocene, the Quaternary is characterized by high-amplitude glacial–interglacial climate variability, occurring cyclically with a 100 ka (kiloanni) periodicity (e.g. Raymo et al., 1989; Tzedakis et al., 1997). The marine isotope stages MIS 6 (penultimate glacial) and MIS 5 (Last Interglacial Complex, LIC) are defined by marine oxygen isotope records ($\delta^{18}O$; Lisiecki and Raymo, 2005). MIS 6 is also named the penultimate glacial (Riss glaciation in the alpine area, Late Saale or Saalian Complex in northern and

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central Europe) and can be roughly dated from ca. 190 to ca. 130 ka, while MIS 5 lasts from ca. 130 to ca. 80 ka (Govin et al., 2015; Railsback et al., 2015, and references therein). The penultimate glacial is characterized by millennial-scale climate variability (Martrat et al., 2004) and ends by several abrupt events, which are probably related to the iceberg-rafted debris (IRD) deposition intervals in the north-east Atlantic (McManus et al., 1999). In contrast, the LIC includes the "last interglacial" (roughly equivalent to MIS 5e, or Eemian), followed by a period named "early last glacial" characterized by a succession of stadial (cold and dry conditions) and interstadial (warm and wet conditions) periods (MIS 5d to 5a). These stadials and interstadials correlate to glacial advances or retreats that are documented by ice-rafted debris in North Atlantic sediments (e.g. Bond events and Heinrich events: Bond et al., 1992; Bond and Lotti, 1995) and by changes in oxygen isotope composition in Greenland ice cores (Dansgaard–Oeschger cycles; Dansgaard et al., 1993). Equivalent to the marine isotope stages, the ice core records distinguish Greenland stadials (GS) and Greenland interstadials (GI) where short-lived cold episodes are associated with surface ocean cooling (C events). Across the LIC, seven such cold events (C19–25) have been documented (McManus et al., 1994; Oppo, 2006; Rasmussen et al., 2014).

The Eemian (127–110 ka; Turner 2002; Shackleton et al., 2003) is of particular interest with regard to orbital parameters inducing a strong seasonal forcing of insolation, contrasted vegetation changes (de Beaulieu and Reille, 1992; Zagwijn, 1996) and climatic conditions (Cheddadi et al., 1998; Sánchez-Goñi et al., 2012). Therefore, this period is also considered as a useful target for general circulation models (GCMs) data–model comparison (Kaspar et al., 2005; Otto-Bliesner et al., 2013). In the Northern Hemisphere, the Eemian was wetter (Fauquette et al., 1999; Guiot, 1990; Guiot et al., 1993; Klotz et al., 2003) and by up to 1–2 °C warmer in summer than the Holocene (Kaspar et al., 2005; Otto-Bliesner et al., 2013; Overpeck et al., 2006;), while sea level was ca. 6–9 m higher (e.g. Kopp et al., 2009). The Eemian thus allows us to study climate dynamics and ecosystem response in a warmer than present Northern Hemisphere without the influence of anthropogenic activity, thereby contributing to assessments of the future impact of the current anthropogenic climate change. Earlier studies of the Eemian considered it a stable, uninterrupted warm period (e.g. Guiot et al., 1993; McManus et al., 1994; Pons et al., 1992; Zagwijn, 1996) with climatic oscillations only recorded in the final part at the transition with the following glacial, i.e. the Weichselian of central and northern Europe, named early Würm in the alpine region (de Beaulieu and Reille, 1984, 1989; Field et al., 1994; Litt et al., 1996). However, more recent studies suggest that low-amplitude climatic fluctuations did occur during the Eemian (e.g. Brewer et al., 2008; Sanchéz-Goñi et al., 2005; Sirocko et al., 2005) and in NGRIP (North Greenland Ice Core Project) ice core isotope records (NGRIP Members, 2004). A pronounced short-lived climatic fluctuation, the intra-Eemian cold event, occurred around 122 ka (Maslin and Tzedakis, 1996). Climate change across the penultimate glacial and the Eemian is documented by numerous pollen records from marine and terrestrial archives (e.g. Govin et al., 2015; Kaspar et al., 2005; Otto-Bliesner et al., 2013). Some of these records have been used for the reconstruction of climatic parameters with a quantitative approach synthesized in Brewer et al. (2008). However, most of these have been carried out using pollen data from European sites located north of 45° N, while only few reconstructions were carried out in southern Europe. Two are based on pollen continental records, Lago Grande di Monticchio in southern Italy (Allen et al., 2000) and Ioannina in north-western Greece (Tzedakis, 1994) and two on marine pollen records, MD 99-2331 and MD 99-2042 on the Iberian margin (Sánchez-Goñi et al., 2005; Brewer et al., 2008). A first north–south comparison suggests that the two regions may have experienced a somewhat different climatic pattern during the Eemian (Brewer et al., 2008). While both regions experienced an early temperature optimum followed by a cooling trend, towards the end of the Eemian, temperatures and precipitation decreased more strongly in northern Europe compared to southern Europe (Brewer et al., 2008; Sánchez-Goñi, 2007, and references therein). Given that this comparison is based on 13 north European sites and on only 4 south European sites, there is a need to provide more reliable quantitative climate reconstructions in southern Europe for the penultimate glacial, for the Eemian and for the entire LIC in order to improve our understanding of the climate response to climate changes.

The Balkan Peninsula is unambiguously a key region at the confluence of central European and Mediterranean climate influences. The area is rich in extant Quaternary lakes and palaeolakes, with sediment records providing essential information on past vegetation and climate changes going back hundreds of thousands of years, such as Lake Ohrid (Albania and FYROM; e.g. Lézine et al., 2010; Sinopoli et al., 2018; Wagner et al., 2017), Lake Prespa (Albania, FYROM and Greece; Panagiotopoulos et al., 2014), Ioannina (west Greece; Tzedakis et al., 2003), Tenaghi Philippon (north-east Greece; Milner et al., 2016) and Kopais (south-east Greece; Tzedakis, 1999; Okuda et al., 2001). Despite the richness in long palaeoenvironmental archives, quantitative palaeoclimatic reconstructions have been rarely attempted or cover relatively short periods.

In this study, we use a multi-method approach to reconstruct climate parameters between the end of the penultimate glacial (160–128 ka) and the LIC (128–70 ka) inferred from the exceptionally long palynological record (569 m) of the Ohrid Basin in the western Balkans (Sadori et al., 2016). The palynological data have been acquired from a sediment core from the centre of the lake (DEEP site; Sinopoli et al., 2018). The MIS 6 to MIS 5 transition at Lake Ohrid has been the subject of accurate chronological alignments and synchronizations (Zanchetta et al., 2016) that yield an offset

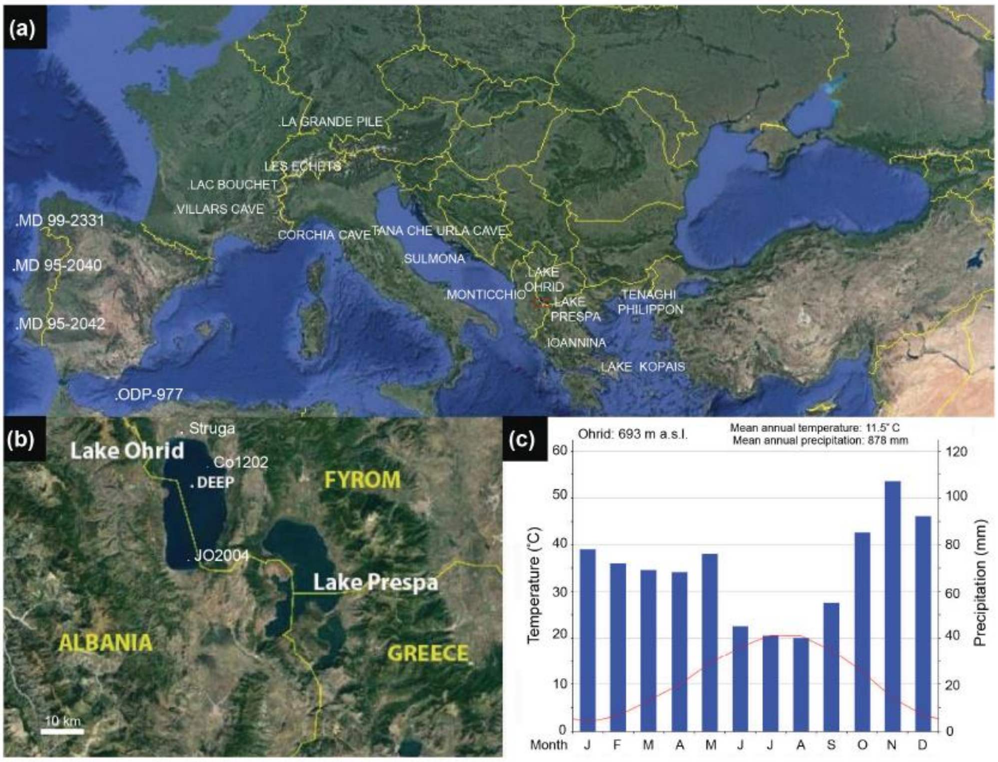

Figure 1. **(a)** Location map of the Mediterranean records cited in this paper. **(b)** Location map of Lake Ohrid and its surroundings (US Dept. of State Geographer© 2017 Google Image Landsat/Copernicus, Data SIO, NOAA, US Navy, NGA, GEBCO) **(c)**. Ombrothermic diagram of Struga meteorological station (http://en.climate-data.org/location/29778/, last access: 17 December 2018).

of 2 ka compared to other records (e.g. Govin et al., 2015; Railsback et al., 2015). The approach for paleoclimate reconstruction applied herein includes two methods frequently used in palaeoclimate reconstructions: the Modern Analog Technique (MAT; Guiot, 1990) and the weighted averaging partial least-squares regression (WAPLS; Ter Braak and Juggins, 1993). In order to test the reliability of our numerical approach, we compare the results to independent climate proxies from the Ohrid Basin such as biomarkers (Holtvoeth et al., 2017) and total inorganic carbon (TIC) concentrations, which largely represent authigenic calcite precipitation (Vogel et al., 2010; Francke et al., 2016). To discuss the climate signal at a more global scale, we compare our results to available pollen-based reconstructions from northern Europe and the Mediterranean, and to marine and terrestrial proxies from the Mediterranean and the Northern Hemisphere (e.g. De Abreu et al., 2003; Drysdale et al., 2005; NGRIP Members, 2004; Lisiecki and Raymo, 2005; Martrat et al., 2004; Regattieri et al., 2014, 2017; Sánchez-Goñi et al., 1999; Wang et al., 2010).

2 Site description

Lake Ohrid is located on the Balkan Peninsula at the border between the Former Yugoslav Republic of Macedonia (FYROM) and Albania (Fig. 1). It is probably the oldest lake in Europe, with an estimated age of > 1.2 Ma. The lake has a tectonic origin, as its catchment is located in a graben that formed during the Alpine orogenesis between ca. 10–2 Ma. Today, Lake Ohrid has a surface area of 360 km^2 (30 km long, 15 km wide, 693 m a.s.l.), an average depth of 164 m and a maximum depth of 293 m. The basin is bordered to the west by the Jablanica mountains (1514 m a.s.l.) and to the east by the Galičica mountains (2265 m a.s.l.). The latter separate the watersheds of Lake Ohrid and the adjacent Lake Prespa (849 m a.s.l.), which is located ca. 10 km to the east, although the two lakes are connected via a karst aquifer system. Apart from inflow from Lake Prespa, Lake Ohrid is supplied with water from surface run-off via small streams, rivers and by direct precipitation. Modern climate in the Ohrid region is Mediterranean with continental influences. The thermal capacity of the lake as well as its proximity to the Adriatic Sea and the local topography affects the local climate. The mean annual temperature recorded in the Ohrid region averages 11.5 °C; temperatures range between ca. 2 and 6 °C in winter (minimum in January) and between 10 and 22 °C in summer (maximum in July). The morphology of the catchment also affects the wind regime, with northerly winds prevailing during winter and south-southeasterly winds during spring and summer. The pluviometric regime is Mediterranean, with an average annual precipitation of 878 mm (Fig. 1).

Lake Ohrid has a rich macrophytic flora (more than 124 species) distributed into different zones dominated by *Lemna trisulca* L., *Phragmites australis* (Cav.) Trin. ex Steud., *Potamogeton* L., Characeae, *Ceratophyllum* L., *Myriophyllum* L. and the colonial alga *Cladophora* spp. The present vegetation around Lake Ohrid belongs to the sub-mediterranean type, in which mediterranean and Balkan elements dominate together with central European ones. The vegetation is sequenced in altitudinal belts, starting from lake level (693 m a.s.l.) to the top of the mountains (ca. 2200 m a.s.l.). Riparian forest (dominated by *Salix alba* L.), with elements of mediterranean vegetation (*Fraxinus ornus* L., *Pistacia terebinthus* L. and *Phyllirea latifolia* L.), is present from the altitude of the lake level to lower elevations together with *Buxus sempervirens* L., *Quercus trojana* Webb, *Carpinus orientalis* L. and *Ostrya carpinifolia* Scop. Otherwise, forests are characterized by mixed deciduous elements and are mainly composed of *Quercus cerris* L., *Q. frainetto* Ten., *Q. petraea* (Matt.) Liebl., *Q. pubescens* Willd. up to 1600 m a.s.l., followed by montane and mesophilous forests (from 1600 to 1800 m a.s.l.) dominated by *Fagus sylvatica* L. in association with *Carpinus betulus* L., *Corylus colurna* L. and *Acer obtusatum* (*Acer opalus subsp. obtusatum* (Waldst. & Kit. ex Willd.) Gams). *Abies alba* Mill. and *A. borisii-regis* Matt. mixed forests grow below 1900 m a.s.l. at the upper limit of the forested area, while sub-alpine grassland and shrubland with *Juniperus excelsa* (subsp. *polycarpos* (K. Koch) Takhtajan) are found above the treeline in mountains situated at south-east of the lake. Towards the east, *Pinus peuce* Griseb., is present at high elevation, associated with *Pteridium aquilinum* (L.) Kuhnor, *Vaccinium myrtillus* L. Sparse population of *Pinus* species considered to be Tertiary relics are present in the wider area.

3 Materials and methods

3.1 Pollen data from the DEEP core

A drilling campaign within the scope of the International Continental Scientific Drilling Program (ICDP) was carried out as part of the project Scientific Collaboration On Past Speciation Conditions in Lake Ohrid (SCOPSCO) in 2013. Six parallel cores were recovered from the depocentre of the lake at 243 m water depth (DEEP site). A composite sequence representing an overall sediment depth of 569 spanning at least the last 1.2 million years has been obtained (Wagner et al., 2017). According to the age model, the uppermost 247.8 m of the DEEP core cover the last 637 ka (Francke et al., 2016).

Palynological data has been published for the upper 200 m of the DEEP pollen record, covering the last 500 ka, with a time resolution of ca. 1600 years (Bertini et al., 2016; Sadori et al., 2016, 2018). Results have shown an alternation of forested and non-forested periods that are ascribed to five glacial–interglacial cycles. The study presented herein is based on "higher-resolution" pollen data summarized in Fig. 2 (one sample every ca. 400 years; Sinopoli et al., 2018, in the following named "high-resolution").

3.2 Quantitative reconstruction of temperature and precipitation

We adopted two different methods in order to improve the error assessment of our approach (e.g. Klotz et al., 2003; Kühl et al., 2010; Peyron et al., 2005, 2011, 2013). It has been demonstrated by several studies that reconstructions based on just one method can have limitations, depending on the time interval and on the methods chosen (Birks et al., 2010; Brewer et al., 2008). Here, we have selected the Best Analogs Approach or Modern Analog Technique (MAT; Guiot, 1990) and the Weighted Average Partial Least-Squares Regression (WAPLS; Ter Braak and Juggins, 1993), two classical methods already used to reconstruct climate changes in the Mediterranean during the Holocene and other time periods (e.g. Brewer et al., 2008; Mauri et al., 2015; Peyron et al., 2011, 2013). Both methods are based on the assumption that climate change strongly influences the distribution and composition of vegetation as every plant species tolerates distinct ranges of temperature and humidity. The MAT is based on the comparison between fossil pollen assemblages and modern ones. The MAT determines the degree of dissimilarity (in terms of taxa abundance and composition) between modern pollen data (associated with known climatic parameters) and the fossil data for which the climatic parameters are to be estimated. For each fossil pollen assemblage, a number of modern pollen assemblages are selected (based on a chord distance calculation) as the closest ones or "analogues". The number of analogues used may affect the quality of the reconstructions. In the present paper, the most robust reconstructions are obtained using six analogues. This is the optimal number of analogues (determined using the lowest root-mean-square error of prediction) in order to minimize the chances of falsely determining two modern samples to be analogues or considering two analogous samples not to be analogues. The method uses the present-day climate data associated with the selected modern analogues to infer the past climate values (Guiot, 1990). In contrast to the MAT, the WAPLS method is a transfer function, which uses a real statistical calibration between climate parameters and modern pollen data. The method is based on unimodal relationships between pollen percentages and climate. In WAPLS, several components are calculated based on weighted averaging al-

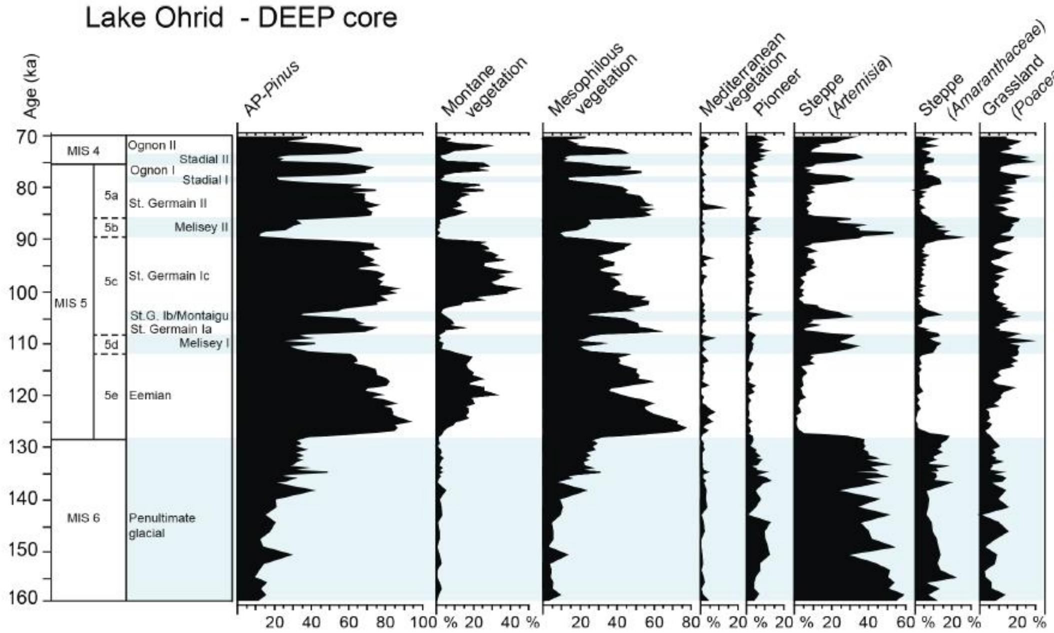

Figure 2. Lake Ohrid (FYROM and Albania) – DEEP core – Pollen percentage diagram of selected taxa and ecological groups against age (ka). Montane vegetation: Abies, Betula, Fagus, Ilex, Picea; mesophilous vegetation: *Acer*, *Buxus*, *Carpinus betulus*, *Castanea*, *Celtis*, *Corylus*, *Fraxinus excelsior/oxycarpa*, *Ostrya/Carpinus orientalis*, *Hedera*, *Quercus robur* type, *Quercus cerris* type, *Tilia*, *Ulmus*, *Zelkova*; Mediterranean vegetation: *Cistus*, *Fraxinus ornus*, *Olea*, *Phillyrea*, *Pistacia*, *Quercus ilex* type, *Rhamnus*; steppe: *Artemisia*, Amaranthaceae, Chicoriodeae and Asteroideae; and grassland: *Poaceae* and *Cyperaceae*. Data from Sadori et al. (2016) and Sinopoli et al. (2018).

gorithms that successively explain more variance in the data; this means that taxa, which better define a climate parameter, are weighted more than the other ones (Ter Braak and van Dam, 1989). A cross-validation has been performed to determine the right number of components (Ter Braak and Juggins, 1993). For both methods, we have used a modern pollen dataset containing more than 3088 samples from European and Mediterranean regions (Peyron et al., 2013). From this dataset, we have excluded those pollen samples collected in warm to hot steppes in order to improve the climate reconstruction during steppic phases (Tarasov et al., 1998). Moreover, *Pinus* has been excluded due to its overwhelming presence in the DEEP record that potentially masks climatically controlled environmental signals from other taxa. The differences between the two methods probably depend on the lack of present-day European analogues for some glacial vegetation formations.

Five climate parameters have been reconstructed for the DEEP pollen record excluding *Pinus* (Fig. 3; for the reconstruction with *Pinus* see Fig. S1 in the Supplement) with each method: (1) the mean temperature of the coldest month (MTCO), (2) the mean temperature of the warmest month (MTWA), (3) the mean annual temperature (TANN), (4) the mean annual precipitation (PANN) and (5) the growing degree days above 5 °C (GDD5) (Peyron et al., 1998). The analysis was carried out with the software package R, a system for statistical computation and graphics (R Foundation, https://www.r-project.org/, last access: 17 December 2018) by using the package "rioja" (Juggins, 2016). Error bars have been calculated but are not shown in the figure for graphic clarity. They are available in the Supplement (Fig. S2). Figure S3 indicates the reliability of the analogues selected by reporting the squared-chord distance between the first and the last analogue for a chosen climate parameter (TANN) calculated by the MAT method. The first (last) analogue corresponds to the closest analogue with the low (high) chord distance.

4 Results

Previous low-resolution data show that MIS 6 was characterized by a prevalence of *Artemisia*, Amaranthaceae and Asteroideae since 160 ka (Sadori et al., 2016). During the LIC, high-resolution data provide evidence for forested periods (interglacial and interstadials) alternating with periods of a more open environment (stadials). The pollen analysis revealed that the surroundings of Lake Ohrid during the Eemian were characterized by mesophilous communities prevailing on montane ones (Fig. 2). Forests were mainly featured by expansion of *Quercus robur* and *Q. cerris* types together with *Pinus* and *Abies* (Sinopoli et al., 2018). Trees never completely disappear, being also recorded during sta-

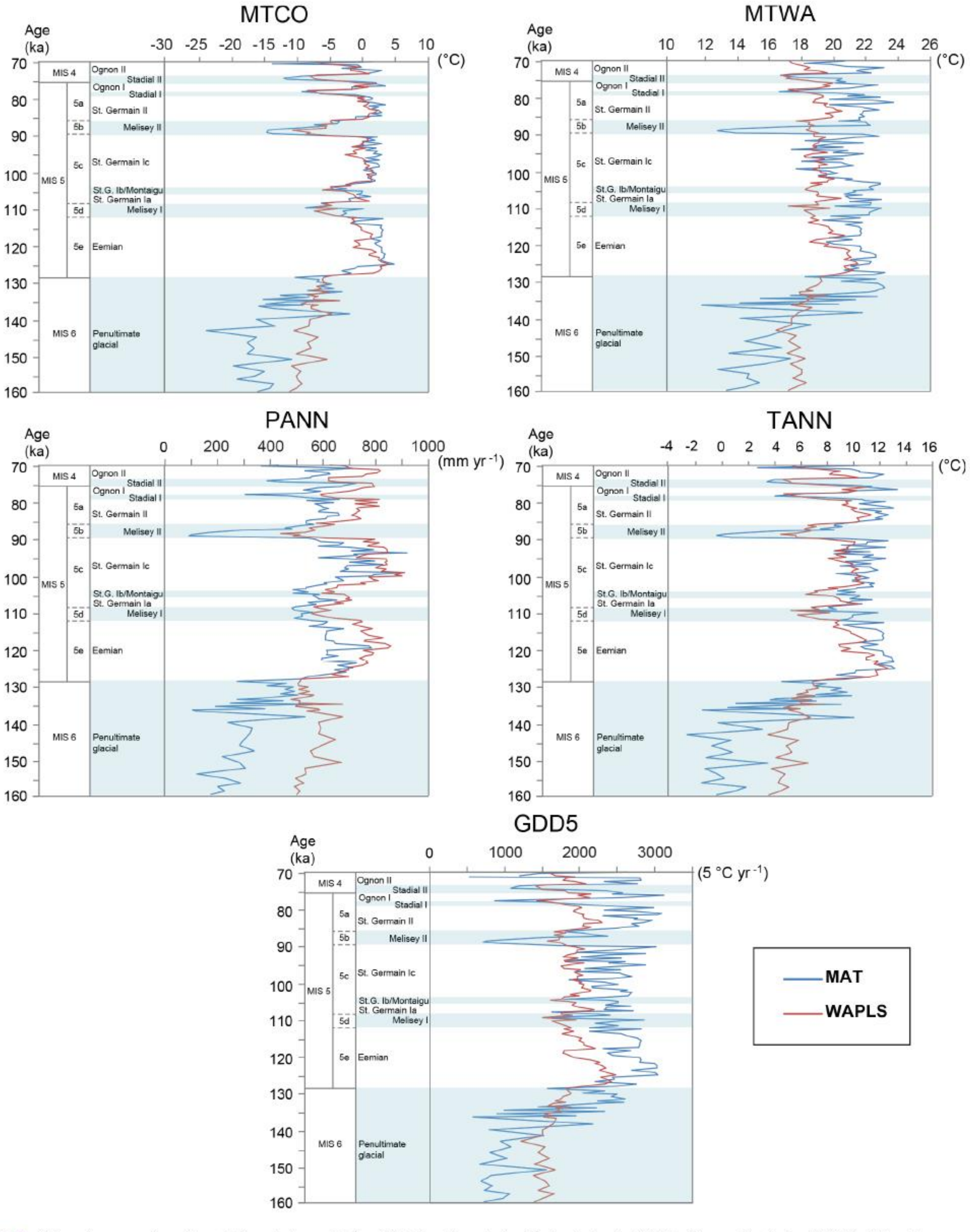

Figure 3. Climate reconstruction inferred from Lake Ohrid pollen data (Sadori et al., 2016; Sinopoli et al., 2018). Climate parameters obtained with the MAT method (blue line) and the WAPLS method (red line): MTCO (mean temperature of the coldest month), MTWA (mean temperature of the warmest month), PANN (mean annual precipitation), TANN (mean annual temperature) and GDD5 (growing degrees days over 5 °C). Climate parameter values are plotted against age (ka); they are not expressed in anomalies (past climate value minus the modern measured value). Blue shading indicates cold periods (penultimate glacial and early last glacial stadials).

dial periods, albeit at low percentages. Here we adopt the terminology used by Woillard (1978) for La Grande Pile pollen record to enhance comparability (see Table 1). We are aware that the marine stratigraphy does not always precisely match the terrestrial one (e.g. Sánchez-Goñi et al., 2007).

Our climate reconstruction suggests cold and dry conditions during MIS 6 and, in MIS 5, an alternation of warm and wet conditions during the Eemian and St. Germain I and II interstadials with cooler and dryer ones occurring during stadials (Fig. 3).

4.1 The late part of the penultimate glacial (MIS 6, 160–128 ka)

The second part of MIS 6 was very cold and dry (Fig. 3) as suggested by the results from both MAT and WAPLS. This portion of the glacial period can be divided into a first part, between 160 and 143 ka, which is characterized by cold and dry climate conditions (mean annual temperature below 6 °C and annual precipitation mainly between 350 and 600 mm yr^{-1}), and a second part, lasting from 143 to 128 ka, when several short-term high-amplitude oscillations are reconstructed, especially from 140 to 135 ka. These abrupt changes involve all the climate parameters. These oscillations represent significant shifts in mean annual temperature (TANN) and precipitation (PANN), ranging from 2.7 to 10 °C and from 120 to 600 mm yr^{-1}, respectively. The GDD5 (growing degrees days over 5 °C, annual accumulated temperature over 5 °C) pattern is strongly linked to the MTWA (mean temperature of the warmest month) pattern. The pronounced peak in temperature around 138 ka is probably linked to the high percentages of mesophilous taxa; however, this increase seems overestimated with the MAT. Notably, this oscillation and also the other lower-amplitude oscillations between 143 and 128 ka are more marked in the reconstruction inferred from the MAT (Fig. 3). These values are probably overestimated as the MAT is more sensitive than WAPLS and other methods such as a PDF (probability density function; Brewer et al., 2008; Kühl et al., 2010). Brewer et al. (2008) demonstrated that a wider spread of estimates is found during colder periods and that the analogue methods seem to give a larger variability in time than the other methods, especially during the cold periods.

4.2 The Last Interglacial Complex, LIC (MIS 5, 128–70ka)

4.2.1 The last interglacial (128–112 ka) or Eemian

The transition to the last interglacial, dated at 128 ka, is marked by a rapid rise in temperature and in precipitation, being very close to modern values. The so-called thermal maximum of the Eemian, occurring at Lake Ohrid between 128 and 121 ka, is characterized by TANN between 10 and 12 °C, the highest of the investigated period, 2 °C warmer than the present day (Figs. 3, 5, 6). Winter temperatures were also warmer than today, while summer temperatures were close to modern values and precipitation 100 mm lower than present day (Figs. 3, 5). A cool event is suggested between 121 and 118 ka, while precipitation reaches the highest values of the Eemian at around 119.4 ka. After this cool phase, during the last part of the last interglacial (118–112 ka), we reconstruct a progressive cooling and a decrease in precipitation until the end of the Eemian at 112 ka.

4.2.2 The early last glacial (112–70 ka)

The early last glacial (Table 1) is characterized by an alternation of short cold and dry periods with longer warm and wet ones.

- Warm and wet interstadial periods: St. Germain I (108–90.2 ka), St. Germain II (85.7–78.8), Ognon I (77.6–75 ka), Ognon II (73.4–69.9 ka).
- Cool and dry stadial periods: Melisey I (112–108 ka), Montaigu (105.2–104 ka), Melisey II (90.2–85.7 ka), stadial I (78.8–77.6 ka), stadial II (75–73.4 ka).

Interstadials: warm and wet conditions

The first interstadial following the Eemian (Fig. 3) corresponds to the St. Germain I (108–90.2 ka) that can be divided (Table 1) into three parts, two of which, St. Germain Ia (108–105.2 ka) and St. Germain Ic (104–90.2 ka), are warm and wet, while the other, Melisey II (105.2–104 ka), is cold and dry. During St. Germain Ia, both TANN and PANN increase suggesting that the St. Germain I was warm and wet, but still to a lower extent than the Eemian. In contrast, the St. Germain Ic appears to be wetter and overall warmer than St. Germain Ia (Fig. 3). The precipitation increases strongly and reaches values between ca. 600 and 900 mm yr^{-1}, which is the wettest period between 160 and 70 ka. A pronounced dry event is centred at 95.3 ka. The second interstadial (85.7–78.8 ka) corresponding to St. Germain II is characterized by temperate conditions comparable to those of St. Germain Ic (104–90.2 ka) even if it seems drier. The following two interstadials corresponding to the Ognon I and II (77.6–75 and 73.4–69.9 ka) show climate conditions comparable to those occurring during the second interstadial (Fig. 3).

Stadials: cold and dry conditions

The temperate conditions of the last interglacial are interrupted by a first cooling event corresponding to the stadial Melisey I (112–108 ka) characterized by cold and dry conditions (Fig. 3). A second abrupt event is recorded between 105.2 and 104 ka, namely during the Montaigu cooling (St. Germain Ib) that divides the St. Germain I into two "interstadials". During this event, precipitation reaches values similar to those of the previous stadial (Melisey I). Temperature and precipitation follow the same pattern with a strong

Table 1. Correlation of nomenclature defined by Woillard (1978) for La Grande Pile (NE France) with common terrestrial nomenclature and the marine isotope stages (MIS; Lisiecki and Raymo, 2005). This is just a scheme and a precise correspondence between MIS 5 substages and the terrestrial phases defined by Woillard (1978) is not yet precisely established.

Marine stratigraphy		**Common name**	**La Grande Pile**	**Lake Ohrid limit (yrs ka)**
MIS 4		Early last glacial	Ognon II	73.4–69.9
			Stadial II	75–73.4
MIS 5	5a		Ognon I	77.6–75
			Stadial I	78.8–77.6
			St. Germain II	85.7–78.8
	5b		Melisey II	90.2–85.7
	5c		St. Germain Ic	104–90.2
			St. Germain Ib (Montaigu event)	105.2–104
			St. Germain Ia	108–105.2
	5d		Melisey I	112–108
	5e	Last interglacial	Eemian	128–112
MIS 6		Riss glaciation		160–128

decrease at 104.6 ka. Melisey II (90.2–85.7 ka) appears as the coldest and driest event of the early last glacial (Fig. 3), with a strong temperature and precipitation decrease evidenced by both methods. As during the end of MIS 6, the cooling reconstructed with the MAT is probably overestimated given that the analogue method provides a large variability during the cold periods. However, the climate was certainly very cold during Melisey II, particularly in winter as illustrated by the WAPLS. Precipitation reaches extremely low values, dropping to ca. 100 mm yr^{-1}, which is even lower than in MIS 6 but here too the drying seems overestimated with the MAT for the same reasons as temperatures. The following two stadials (78.8–77.6 and 75–73.4 ka) should indicate a pattern very similar to Melisey II, with an abrupt decrease in temperature and precipitation followed by a likewise abrupt increase at the end of each phase (Fig. 3).

5 Discussion

5.1 Differences between MAT and WAPLS and reliability of the methods

The temperature reconstructions from both methods are reasonably coherent (trends and values) during the interglacial and interstadials, but a wider spread of estimates is found during colder periods (Fig. 3) for which the analogues method suggests higher-amplitude oscillations and lower values than those inferred by the transfer function (Fig. 3). More precisely, during ca. 160–143 ka, both methods produce low-amplitude oscillations in temperatures, but the values determined by MAT appear to be around 4 °C lower than those determined by WAPLS. Even if the precipitation curves produced by both methods show the same trend, reconstructed values by MAT are roughly 300 mm lower than those resulting from WAPLS. After 143 ka, the differences between the two methods are more pronounced (Fig. 3). It is worth mentioning that WAPLS precipitation values are inside the error bars (Fig. S1). Discrepancies between the methods may be related to several factors that either depend on the method itself or on the composition of past pollen assemblages. As mentioned in Sect. 3.2 modern analogues methods are very sensitive to minor variations in the pollen assemblages, especially during glacial periods (Brewer et al., 2008). Similar discrepancies associated with MAT also occur in the reconstruction of La Grande Pile; strong cold and dry oscillations are evidenced (and probably overestimated) after the Eemian thermal optimum by Brewer et al. (2008). MAT is frequently used to reconstruct the climate of the Late Glacial and Holocene (e.g. Mauri et al., 2015; Peyron et al., 2005) but, as demonstrated by Guiot et al. (1993), ambiguous outcomes may occur particularly for past glacial and cold intervals (stadials). The major problem appears to be the lack of modern analogues or only limited similarity with past glacial vegetation (Guiot et al., 1993; Peyron et al., 1998). Indeed, as reported in several studies (Guiot, 1987; Guiot et al., 1993; Klotz et al., 2003), glacial steppe vegetation dominated by high percentages of Amaranthaceae (as at Lake Ohrid, Fig. 2) has no present-day analogue in Europe. For this reason, we have used modern samples from cold steppe principally from the Tibetan Plateau and from Russia as "potential" analogues for glacial periods (Peyron et al., 1998, 2005). Squared-chord distance has been used to determine the degree of dissimilarity (Fig. S1), revealing that our reconstruction can be judged reliable and without a no-analogs situation occurring. The differences between the two methods for cool/cold periods may also be ascribed to the quasi-continuous presence of arboreal taxa in steppic assemblages. During the period between 143 and 128 ka, the major oscillations are probably overestimated and likely linked to the presence of arboreal mesophilous (temperate) taxa in steppic pollen assemblages. Mesophilous taxa amount to 10 %–30 %, with a prevalence of deciduous and semi-deciduous oaks, while pioneer shrubs are between 5 % and 10 %, with prevalence of ***Juniperus*** (Fig. 2). This discrepancy attests to the specific local hydroclimatic features of the Ohrid Basin and its fundamental role as a refugium for many arboreal taxa. Considering the very high sensitivity of the MAT, WAPLS seems to be a better method to reconstruct the climatic changes during cold events in refuge areas.

5.2 Climate changes at Lake Ohrid: comparison with independent proxies and other climate reconstructions

Our data are in agreement with climate signals depicted in geochemical data from the DEEP site (Francke et al., 2016; Wagner et al., 2017) and other Lake Ohrid cores (core JO2004 from the south of the lake; Bordon, 2008; core Co1202 from the north-east; Holtvoeth et al., 2017; see Fig. 1; Vogel et al., 2010). When comparing our results to the Eemian climate reconstruction of JO2004 (Bordon, 2008), the trends are similar, while some differences in temperature and precipitation values should be pointed out. They probably result from differences in pollen assemblages due to the different positions of the analysed cores. Core JO2004 was retrieved from the southern part of the lake, closer to the lake shoreline. Therefore, its pollen assemblages show increased values of local taxa and of those not dispersed over long distances; in contrast, these taxa are found in lower abundance or not at all in the central part of the basin from where the DEEP core was retrieved. Due to the central position of the DEEP and the morphology of the territory around the lake (vegetation organized in altitudinal belts) we assume that our climate reconstruction integrates the palynological signal of the surrounding mountain ranges and, consequently, our data accounts for a regional and not a local climate reconstruction. In Fig. 4, the temperature and precipitation (PANN and TANN) signals are compared to the TIC and the total organic carbon (TOC) records from the DEEP core and to the TIC and TetraEther indeX of archaeal lipids (TEX_{86}) from core Co1202. For more information about these proxies see Francke et al. (2016), Vogel et al. (2010), Holtvoeth et al. (2017) and references therein. All proxies reported in Fig. 4 are used as indicators for environmental and climatic change. Concerning proxies from the DEEP core, PANN and TANN resemble TIC and TOC. TIC concentrations and precipitation of mainly authigenic carbonate is controlled by water temperature and productivity, but also by ion concentrations in the lake, which depend on precipitation and the activity of the karst aquifer system (Vogel et al., 2010; Francke et al., 2016). Minima in TOC that correspond to minima in TANN indicate that these minima are the result of restricted productivity combined with increased decomposition of organic matter due to the prolonged winter season and enhanced mixing of the water column (Francke et al., 2016). However, TOC reflects autochthonous and allochthonous organic matter input, i.e. supply of biomass from both the lake as well as the surrounding land (Francke et al., 2016; Holtvoeth et al., 2017; Zanchetta et al., 2018). The productivity of the terrestrial vegetation and supply of terrestrial organic matter to the lake seem to be largely controlled by precipitation rather than temperature; thus, explaining similarities with the PANN record. While TIC and TOC may co-vary at times they are not generally causally related. During MIS 6, TIC is mostly very low, suggesting cold and dry climate conditions (Francke at al., 2016), in agreement with the pollen-inferred mean annual temperature and precipitation (Fig. 4). At the transition toward MIS 5, TIC and TEX_{86} values increase together, indicating a warming and augmentation of humidity, consistent with the increase in PANN and TANN inferred from pollen. The distinct high-amplitude fluctuations inferred from pollen during the final part of MIS 6 could at least partly be due to lake-level changes as the water table during this period was generally on the rise (Lindhorst et al., 2010; Holtvoeth et al., 2017; Wagner et al., 2017). As mentioned before, the (modern) lake basin and parts of the lake floor show a pronounced terraced morphology. The relatively rapid flooding of extended, nearly horizontal surfaces, in particular at the northern and southern ends of the lake, may thus have diminished sizeable parts of (flat) terrestrial habitat in short periods of time. The impact of lake-level change on the low-lying terrestrial habitats could be clearly seen in the biomarker and pollen records of core Co1202 (Holtvoeth et al., 2017). While localized processes are likely averaged out by the longer-distance transport of material towards the distal DEEP site, a basin-wide effect of lake-level change and the associated distribution of low-lying biomes in the north, northeast and south of the basin might have to be considered in order to explain the observed fluctuations in the PANN and TANN records of the DEEP core between 136 and 130 ka precipitation-controlled lake-level change may have affected the surface area of low-lying terrestrial habitats on terrace surfaces before the temperature threshold for the precipitation of authigenic carbonate (TIC) was crossed, leading to the 2000 or 3000 years offset in the beginning of the high-amplitude fluctuations in pollen-derived PANN and TANN records and the rise in TIC.

The beginning of the last interglacial is almost synchronous as indicated by the records of TIC (DEEP), carbonate and TEX_{86} (Co1202, Fig. 4). However, according to the TIC and TEX_{86} records of Co1202, the thermal maximum, characterized by stable conditions, occurs between 126.5 and 124 ka in contrast to our reconstructed temperature that increases earlier at 127 ka. This slight discrepancy is probably due to differences in the chronology established independently for the two cores. An explanation for the delay of TIC values takes into account the time needed for the dissolution of calcite from the surrounding rocks and/or dissolution of endogenic calcite after deposition (see Francke et al., 2016). At long timescales, calcite precipitation occurs during periods of high precipitation such as interglacials and interstadials when supply of calcium and carbonate ions from calcite dissolution into the lake increases, and/or elevated temperature and high evaporation occur. Biogenic calcite formation is hampered during dry and cold periods (glacial and stadials) due to decreased precipitation and associated nutrient supply to reduced terrestrial calcite dissolution and inflow of dissolved carbonate from the karst system (Lézine et al., 2010). Soon after the "thermal maximum" (128–121 ka) TIC values decrease together with mean annual temperature; by contrast, at the same time precipitation rises. The low TIC content can be explained by lower water temperature, which hampers calcite precipitation. Slight progressive drying occurs from 121 ka until the end of the Eemian at 112 ka. This trend corroborates the climate reconstruction based on core JO2004 (Bordon, 2008) and confirms the assumption that the Last Interglacial was not a uniform wet and warm phase in western Europe (e.g. Cheddadi et al., 1998; Guiot et al., 1993; Klotz et al., 2004; Kühl and Litt, 2003; Rousseau et al., 2006; Sánchez-Goñi et al., 2005) and that successive cool and dry events occur at ca. 110 and 105 ka.

5.3 Comparison with European climate reconstructions inferred from pollen records

Lake Ohrid's chronology is well established for MIS 5 due to the high number of tephra layers (Francke et al., 2016; Leicher et al., 2016), in particular for the transition between the Riss glaciation and the Eemian, for which a further correlation with geochemical and pollen data from Lake Ohrid and other proxies from Mediterranean sequences was carried out by Zanchetta et al. (2016). For other European pollen records such chronological constraints are not available and thus the chronologies are probably less precise. Keeping in mind the existing chronological uncertainties, a comparison of precipitation and temperature anomalies is carried out, with the values inferred from three other long pollen records (Fig. 5) spanning the interval between 140 and 70 ka: Les Echets, Le Bouchet and La Grande Pile (Fig. 1). Lake Ohrid, despite being considered as "a southern site", shows past climate trends similar to the French records (Fig. 5). This similarity is probably due to its high elevation, causing enhanced precipitation relative to the rest of southern Europe and making it similar to regions directly subjected to the North Atlantic circulation. In order to discuss Lake Ohrid's climate record more in depth on a European scale, a further comparison is shown in Fig. 6. Here, Lake Ohrid climate anomalies are plotted with the ones estimated by Brewer et al. (2008) for southern and central-northern European sites, using a pollen-inferred multi-method approach that takes into account the various sources of errors in paleoclimate reconstructions. The investigated interval is, in this case, limited to the period 135–105 ka, which includes the whole Eemian (ca. MIS 5e–d according to Sánchez-Goñi, 2007). During the final part of MIS 6 (Figs. 3, 6), climate seems to have been particularly harsh at Lake Ohrid, with highly reduced precipitation compared to other European sites (Brewer et al., 2008) or to the present. However, the precipitation anomaly values are comparable to those of the French sites (Fig. 5). For the latter, we have to consider that the same methods have been applied, which could have resulted in the more consistent values. There are opposite trends, difficult to interpret, in the anomalies at the end of MIS 6 in the considered records. La Grande Pile, Les Echets and Le Bouchet reconstructions show a "thermal maximum", the so-called climate optimum, from 127 to 118 ka followed by an abrupt cooling around 117 ka (Fig. 6 and Brewer et al., 2008). The signal reconstructed for northern Europe is different from the French sites; Brewer et al. (2008) had identified a climate tri-partition during the Eemian, already evidenced by Tzedakis (2007, and references therein): early optimum, followed by slight cooling, followed by a sharp drop in temperatures and precipitation. This set of changes appears to be restricted to the north, with a very different set of changes in the south. In southern Europe, the Eemian climate appears to have remained warm with stable conditions over a long period between 126 and 105 ka (Fig. 6). Lake Ohrid is located

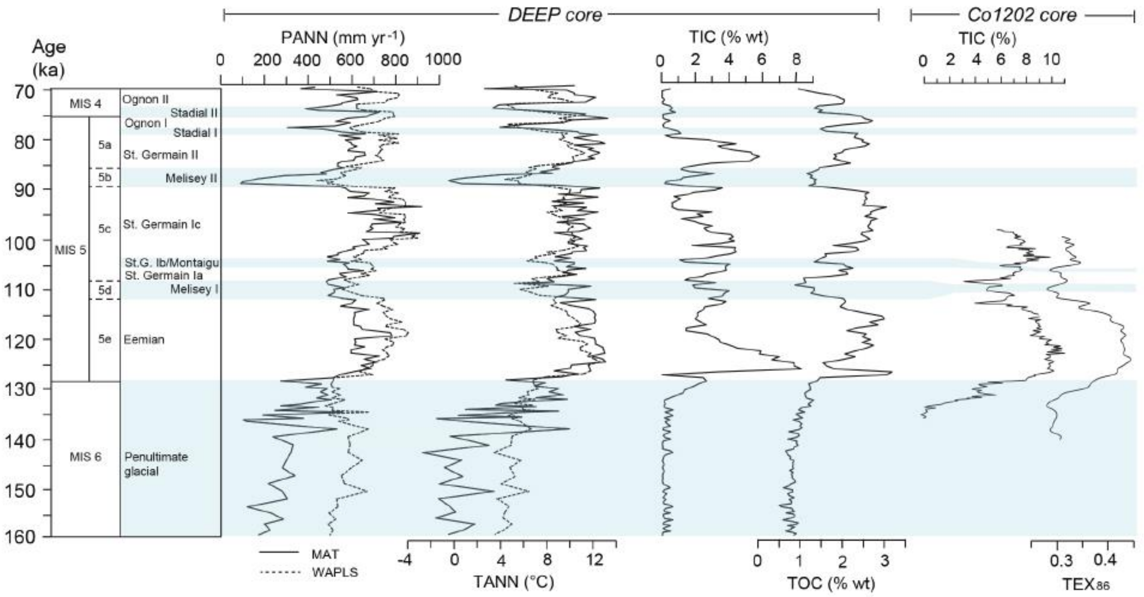

Figure 4. Lake Ohrid: comparison between DEEP core annual temperature (TANN), precipitations (PANN) and TIC (Francke et al., 2016) with TIC and TEX_{86} (Co1202 core; Holtvoeth et al., 2017). Blue shading indicates cold periods (penultimate glacial and early last glacial stadials).

in a central position on the Balkans Peninsula, at the confluence of central European and Mediterranean climates. The Lake Ohrid climate reconstruction also shows a climate optimum in the early part of the Eemian and then a progressive cooling without a sharp drop in temperatures and precipitation (Fig. 6); this suggests an intermediate climate signal, more similar to the French sites (Fig. 5) than to the northern or southern European ones (Fig. 6). Brewer et al. (2008) show that climate changes during this period were heterogeneous, with greater winter warming in the centre and north-east of Europe than in the west and north-west. Other studies of the spatial distribution of temperature changes during this period have shown similar trends in temperature, with the largest positive anomalies in central and northern Europe, and negative anomalies in south-eastern Europe (Kaspar et al., 2005; Turney and Jones, 2010; Otto-Bliesner et al., 2013). Furthermore, one remaining question is whether the climate of this period was very close to modern values or warmer and wetter than the present day as suggested by existing studies (Guiot et al., 1989). The time series of anomalies presented here (Fig. 5) suggest a positive anomaly of 1 to 2 °C for the Ohrid Basin, strongly depending on the method used. Melisey I is the first cooling event, with a significant reduction in temperatures and precipitation, although less pronounced than at the French sites (Fig. 5). At Lake Ohrid, a surprising positive anomaly in the middle of Melisey I is suggested and is potentially due to the persistence of trees during stadials, highlighting the important role of the Ohrid Basin as a refugium for arboreal taxa. According to several studies carried out in central and northern Europe (Guiot et al., 1993; Klotz et al., 2004; Rioual et al., 2001), the Melisey I event is characterized by an abrupt decline in temperatures first, followed by increasing continental conditions, with a subsequent decline in winter temperatures and an increase in summer temperatures. Other pollen records from Lake Ohrid also strongly suggest that climatic conditions remained favourable to grow mesophilous taxa (Bordon, 2008; Holtvoeth et al., 2017; Lézine et al., 2010). St. Germain Ia (Figs. 3 and 5) is drier than St. Germain Ic at Lake Ohrid, with the latter showing annual precipitation up to ca. 400 $\text{mm}\,\text{yr}^{-1}$ higher than during the former. The values are consistent with the data obtained by Klotz et al. (2004) for central Europe, more specifically in the northern Alpine foreland. The same trend is also recorded in the French sites presented here (Fig. 5). Melisey II appears as the most extreme stadial of the LIC, coinciding with the maximum extension of ice sheets during the Early Weichselian. However, the cooling reconstructed at Ohrid is probably overestimated with the MAT for the same reasons as during MIS 6. If we consider the WAPLS reconstruction, the anomalies estimated at Ohrid during Melisey II are 2 °C higher than for the French sites (Figs. 3 and 5). During St. Germain II, temperature and precipitation values for Lake Ohrid are similar to those of St. Germain Ia (Figs. 3 and 5). This pattern is corroborated by other studies for the North Atlantic, using marine $\delta^{18}\text{O}$ data (Keigwin et al., 1994), for North Europe (e.g. Guiot et al., 1989) and for the Iberian margin (Sánchez-Goñi et al., 2000). At the end of the interstadial, a trend towards low

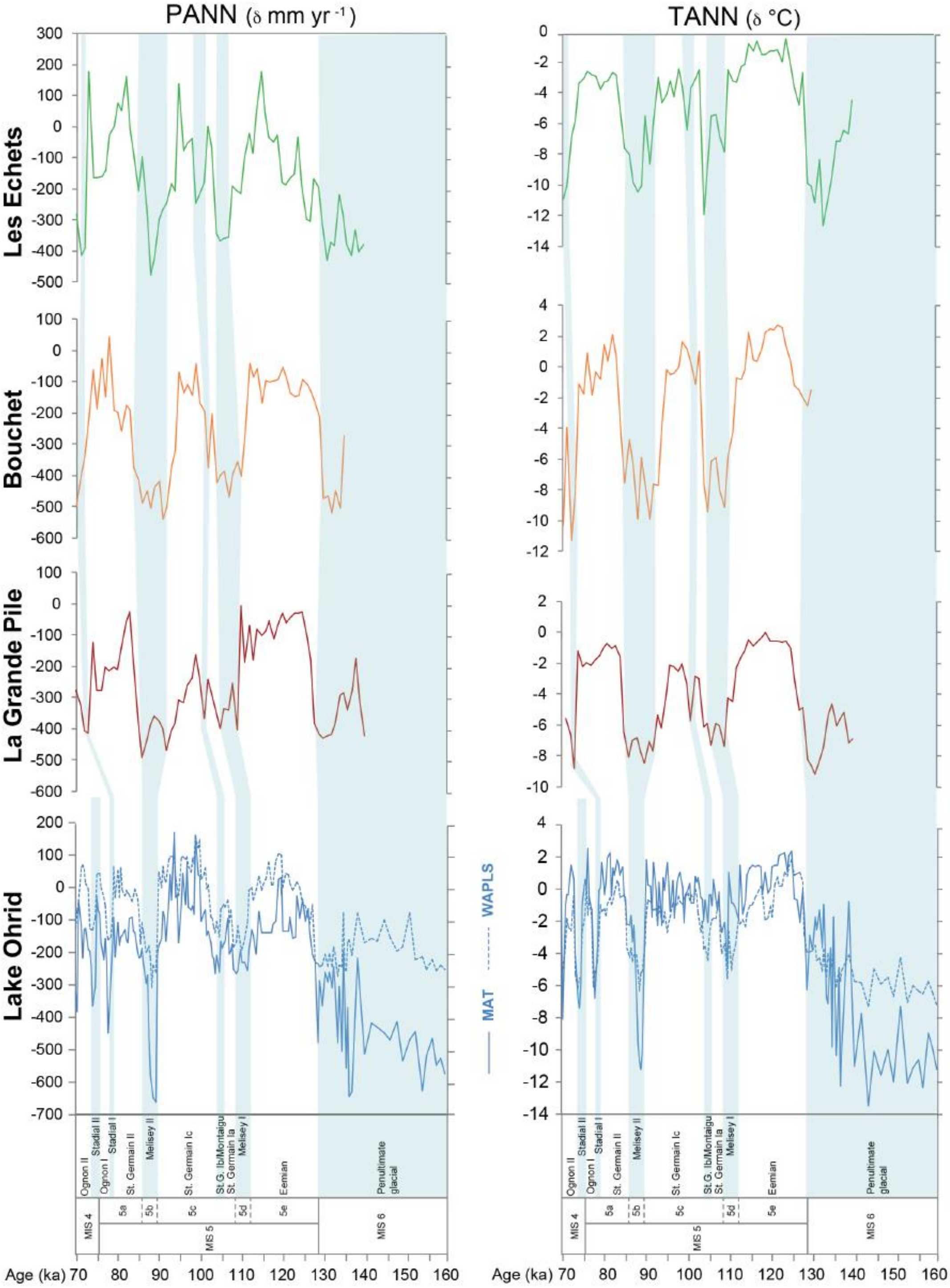

Figure 5. Comparison between Lake Ohrid climate parameters with available climate reconstructions: Les Echets (265 m a.s.l.), Le Bouchet (1200 m a.s.l.) and La Grande Pile (330 m a.s.l.) from Guiot et al. (1989, 1990, 1993). TANN (mean annual temperature) and PANN (mean annual precipitation) are plotted against age (ka). Values represent anomalies (past climate value minus the modern measured value). Blue shading indicates cold periods (penultimate glacial and early last glacial stadials).

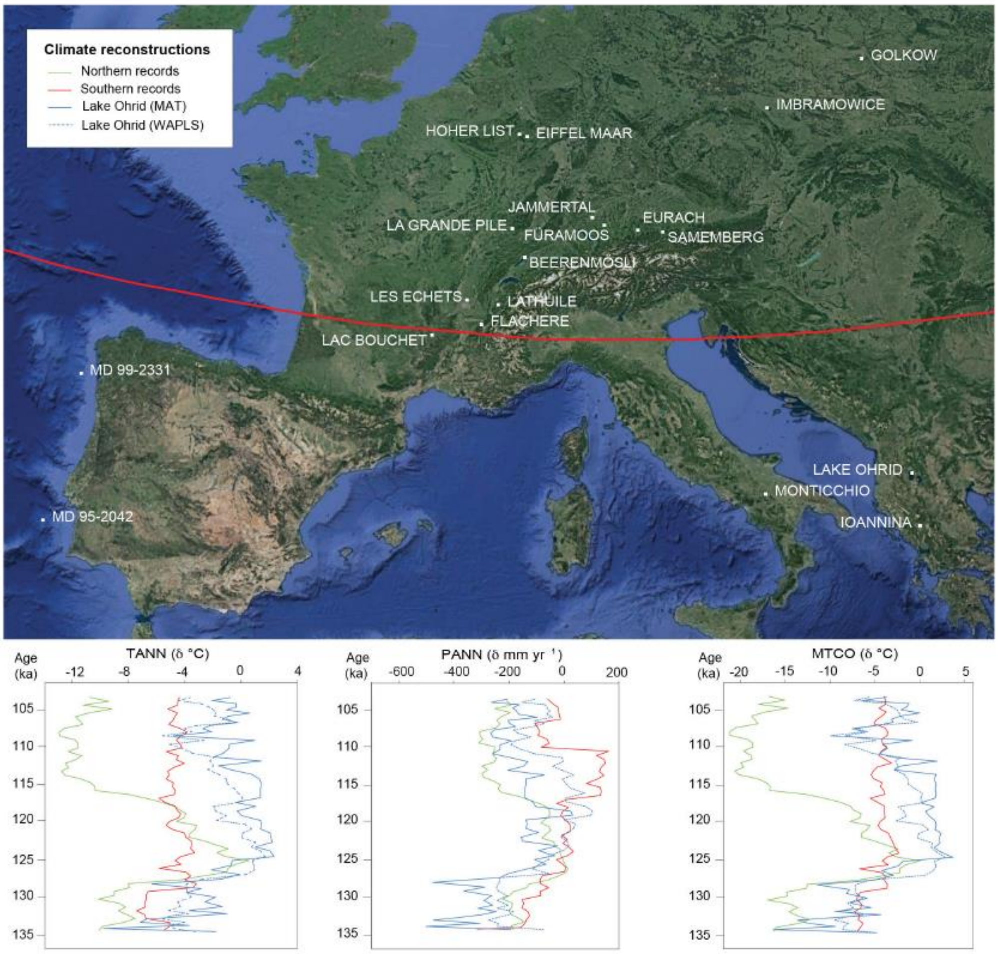

Figure 6. Comparison between the Lake Ohrid climate reconstruction and the climate reconstruction performed by Brewer et al. (2008) for north and south Europe; TANN (mean annual temperature), PREC (mean annual precipitation) and MTCO (mean temperature of the coldest month) are plotted against chronology (ka). Values represent anomalies (past climate value minus the modern measured value).

temperatures and an increase in precipitation is recorded at Lake Ohrid, in agreement with the climate reconstruction of Guiot et al. (1989) for the French pollen records (Fig. 5). The most striking feature of Lake Ohrid, recorded at the top of the studied sequence, is the presence of two interstadials following St. Germain II, namely Ognon I and Ognon II. These interstadials are visible, even if less marked in other eastern Mediterranean records (Tenaghi Philippon; Müller et al., 2011; Lake Van: Pickarski et al., 2015) and could be correlated with the Dansgaard–Oeschger events DO 19 and 20 (Dansgaard et al., 1993).

5.4 Comparison with other European and North Atlantic proxy records

In order to discuss the Ohrid climate signal at a wider scale, Fig. 7 shows the correlation of the reconstructed climate parameters with marine and continental proxies from Mediterranean and North Atlantic regions (Fig. 1).

In speleothem and lake sediment records, $\delta^{18}O$ is mostly seen as an indicator of the "amount of precipitation", lower (higher) values are related to increasing (decreasing) humidity (Bard et al., 2002; Drysdale et al., 2005, 2009; Regattieri et al., 2014; Zanchetta et al., 2007, 2016). The Ohrid precipitation trend shows similarities with the oxygen isotope records reported in Fig. 7, suggesting a generally good agreement with the variations in Mediterranean rainfall detected in Italy in speleothems from Antro del Corchia and Tana che Urla (Drysdale et al., 2005; Regattieri et al., 2014) and in the lake record of Sulmona (Regattieri et al., 2017). According to Drysdale et al. (2009), there is a break in the decrease in $\delta^{18}O$ in continental and marine values prior to the beginning of the Eemian at ca. 129 ka, which can be related to Heinrich event 11 (H11; Shackleton et al., 2003). During this event,

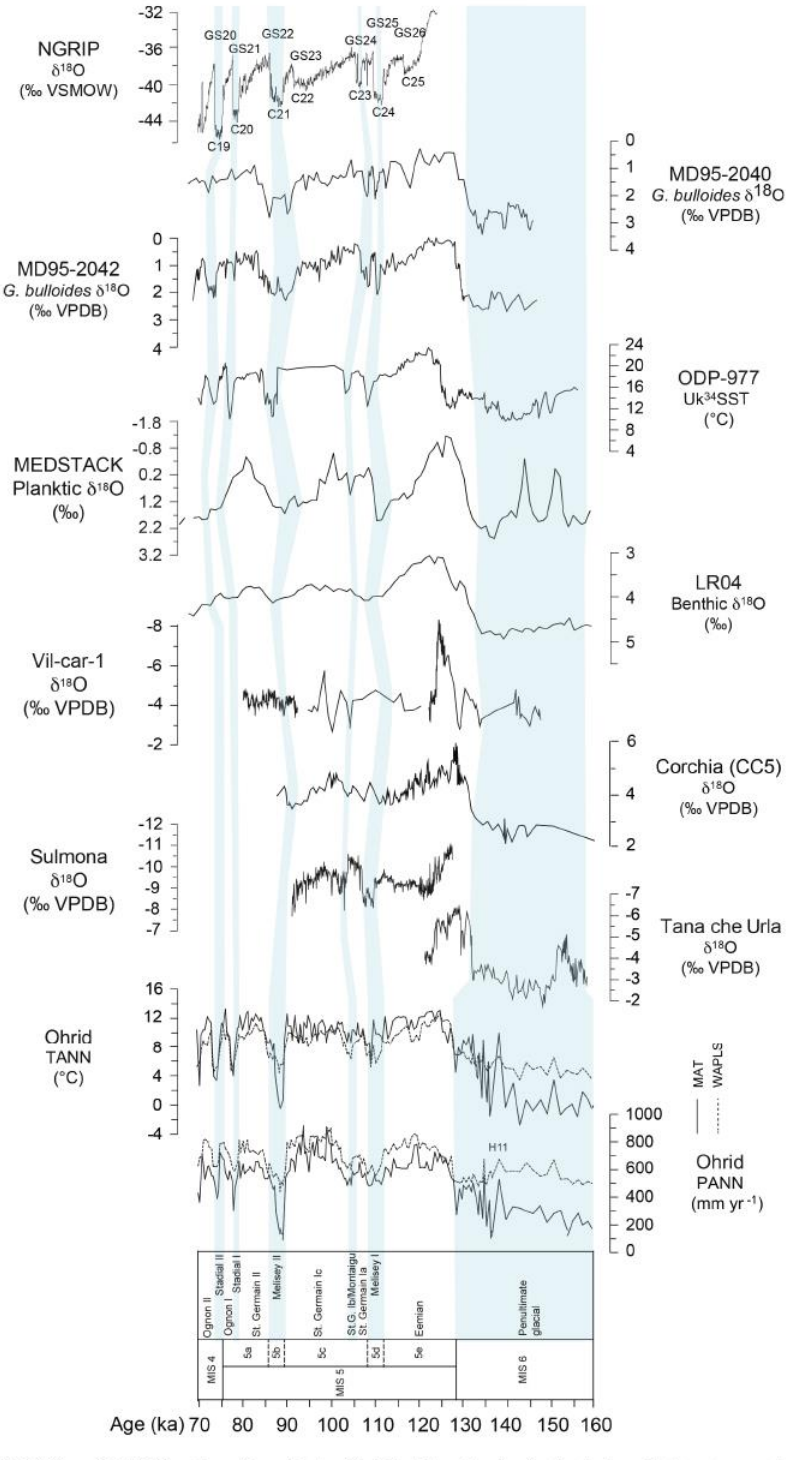

Figure 7. Comparison of TANN and PANN values from Lake Ohrid with other hydrological and climate proxies from the Mediterranean and the North Atlantic: $\delta^{18}O$ speleothem record from Tana che Urla cave and $\delta^{18}O$ of endogenic calcite from Sulmona lake (Regattieri et al., 2017 and 2014, respectively); $\delta^{18}O$ speleothem record from Corchia cave (CC5, Drysdale et al., 2005); $\delta^{18}O$ benthic from LR04 stack (Lisiecki and Raymo, 2005); planktic $\delta^{18}O$ from MEDSTACK data (Wang et al., 2010); sea surface temperature (SST) from core ODP-977 (Western Mediterranean; Martrat et al., 2004); planktic $\delta^{18}O$ from Iberian margin (MD95-2042; Sánchez Goñi et al., 1999; Sánchez Goñi et al., 2005); planktic $\delta^{18}O$ from Iberian margin (MD95-2040, De Abreu et al., 2003); Greenland $\delta^{18}O$ record (NGRIP Members, 2004). Numbers denote Greenland stadials (GS) corresponding to North Atlantic cold events (C events; after McManus et al., 1994). Blue shading indicates cold periods (penultimate glacial and early last glacial stadials).

the North Atlantic thermohaline circulation and the North Atlantic deep-water formation shut down with a consequent phase of cooler and drier conditions for mid-latitude western Europe (Genty et al., 2003). At Lake Ohrid (Fig. 7), H11 is clearly detected for the first time in a climate reconstruction, and in the TIC records of the DEEP core and Co1202 core (Figs. 4, 7).

Important changes during the LI have also been detected, besides at Lake Ohrid, in the alkenone-based sea surface temperature (SST) reconstruction of the ODP-977 sediment core (Alboran Basin; Martrat et al., 2004) in δ^{18}O records of the Iberian margin (MD95-2042 and MD95-2040; Sánchez Goñi et al., 1999, 2005; De Abreu et al., 2003) and from Greenland (Fig. 7), in line with other studies on speleothems and on Mediterranean and North Atlantic marine records (e.g. De Abreu et al., 2003; Demény et al., 2017; Drysdale et al., 2009; Lisiecki and Raymo, 2005; Martrat et al., 2007, 2014; McManus, et al., 1994; Mokeddem et al., 2014; NGRIP Members, 2004; Oppo et al., 2006; Sánchez Goñi et al., 1999, 2005; Wang et al., 2010). Based on the ODP-977 alkenone data (Martrat et al., 2004, 2014), warm SSTs occurred during interstadial periods, while cold SSTs persisted during stadials Melisey I and II. SST changes are associated with large shifts in mean annual air temperature and moisture content as reflected in vegetation changes inferred from pollen analysis in European and Mediterranean records (Martrat et al., 2004; Tzedakis et al., 2003). The connection between Lake Ohrid and the North Atlantic (Fig. 7) is also highlighted by the evidence of the Melisey I stadial, which corresponds to the North Atlantic event C24 (and to GS25), the Montaigu event, corresponding to C23 (and GS24), and the Melisey II stadial, which corresponds to C21 (and GS22). Besides this event, the final part of MIS 5 at the transition to MIS 4 at Lake Ohrid is characterized by a series of abrupt climate changes (Ognon I and II phases) composed of two interstadials and two stadials. The latter correspond to the North Atlantic cold events C20 (GS21) and C19 (GS20) (Fig. 7). A similar pattern can be depicted in the SST record of ODP-977 (Fig. 7) with two abrupt warming events, preceded by a strong cooling after a long period of stability (Martrat et al., 2014).

6 Conclusions

We provide a quantitative reconstruction of climate parameters based on the pollen record from Lake Ohrid (DEEP site), using two complementary approaches for the period between 160 and 70 ka. This period covers the last part of the penultimate glaciation, equivalent to MIS 6 (160–128 ka), and the Last Interglacial Complex (LIC, 128–70 ka), equivalent to MIS 5, as well as the first part of MIS 4.

Our results for the LIC show an alternation of warm and wet periods (128–112, 108–90.2, 85.7–78.8, 77.6–75 and 73.4–70 ka) with cold and dry ones (112–108, 105.2–104, 90.2–85.7, 78.8–77.6 and 75–73.4 ka) attributable to the well-known succession of climatic events occurring during MIS 6 and 5.

With regard to the last interglacial, our results provide evidence that the Eemian was not as stable, confirming existing studies. The climate reconstruction led to distinguish three periods: a climatic optimum (128–121 ka), followed by progressive cooling in conjunction with an increase in precipitation (121–118 ka), and, finally, a period characterized by a decrease in both temperatures and precipitation (118–112 ka).

The early last glacial (from 112 to 70 ka) is characterized by a succession of cold and warm periods (stadials and interstadials) in which cold ones show an increase in seasonality and dry conditions. This climatic trend can be correlated to the succession of Greenland stadials and of North Atlantic cold events (Dansgaard et al., 1993; GRIP Members, 1993), illustrating the teleconnections between the North Atlantic realm and the Mediterranean region. The same succession of cold and dry events at Lake Ohrid is also coherent with hydrological and isotopic data from the central Mediterranean.

At a wider scale, our results showed a great similarity between Lake Ohrid and climate reconstructions of French and central European records rather than the stacked curve of four southern European records. Lake Ohrid shows intermediate features between these two areas; our curves are in line with those of other southern European climate proxies (e.g. central Italian speleothems). Future climate reconstructions and independent proxies are needed for the southern Mediterranean to resolve the complex regional expressions of past climate changes.

Data availability. Pollen data from the first 500 ka years of the sequence (Sadori et al., 2016) are available through the online database PANGAEA at https://doi.org/10.1594/PANGAEA.892362 (Sadori et al., 2018). Higher resolution pollen data (Sinopoli et al., 2018) and climate reconstruction data (this paper) are not public yet as they will be part of further elaborations by authors of this article.

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Author contributions. The paper was written by GS, LS (all sections) and OP (Sects. 3, 4, 5, 6) with substantial contributions from BW, AF, JH (Sects. 1, 2, 5, 6) and AM (Sects. 1, 4, 5, 6). Data analysis was carried out by GS with the supervision of OP. Data management and the elaboration of figures and diagrams have been provided by GS and AM.

Competing interests. The authors declare that they have no conflict of interest.

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CHAPTER 5:

CONCLUSIONS:

This thesis is focused on the palaeonvironmental and climatic changes occurred during the period between 130 and 70 ka (including the whole Last Interglacial Complex), with the aims to investigate the long-term climate variability, on the basis of high resolution pollen data from Lake Ohrid sediments (Albania/F.Y.R.O.M. border). Lake Ohrid is the oldest extant lake in Europe and one of most ancient in the world. The climate reconstruction obtained from pollen data is based on a wider interval, 160-70 ka.

The pollen analysis of the uppermost 200 m of DEEP core sequence, covering the last 500 ka, have been investigated with a resolution of 1.6 ka and revealed an alternation between forested and open environment periods reflecting the glacial-interglacial cycles of the marine isotope stratigraphy (last 12-13 only pro parte Marine Isotope Stages) and a progressive change from cooler and wetter interglacial conditions (before 288 ka) to warmer and drier ones towards the end (last 130 ka). This change suggest a shift towards Mediterranean climate, indeed from MIS 9, Mediterranean taxa become a stable presence.

Besides the continuous and overrepresented presence of *Pinus*, the main ecological groups at Lake Ohrid during interglacials (forested phases) are mesophilous taxa, while during glacials (open environment phases), steppic taxa prevail together with a good persistence of trees. Changes in ecological groups indicate a clear organization in vegetational belts similar to the present environment, while the presence of arboreal plants nearby Lake Ohrid during glacial periods, suggests that the lake probably had a role on moisture supply by favoring the existence of refugia for arboreal plants.

The preliminary results from DEEP long sequence have raised several issues that only with the improvement of analyses through high-resolution studies was possible to corroborate.

The high-resolution (400 yr) pollen analysis of LIC, not only confirmed the hypothesis of the presence of plant refugia around Lake Ohrid, but provided also new data from a key period for discussion on future climate.

The model age for the entire Lake Ohrid sequence is based on the use of tephrostratigraphic information, cyclostratigraphy, and orbital parameters. A correct chronology for the Last Interglacial Complex and in particular for the transition between MIS 6 and MIS 5 was possible thanks also to data from this thesis, by comparing pollen data from the same period with other proxies coming from DEEP sequence. A good correlation between Lake Ohrid environmental changes and other terrestrial/marine records from a wider region was established. This makes Lake Ohrid important as it can be of help to improve the time control for other records for which such chronological constrains are not available.

Pollen results revealed that the penultimate glacial (high-resolution palynological study is still in progress) was characterized by low pollen concentration values and dominant herbaceous plants, with a shift from grassland dominated environment (Poaceae and Cyperaceae) to a steppe dominated one with prevalence of *Artemisia*, Chenopodiaceae and Asteroideae in the last part (since 160 ka). Climate reconstruction for this last part of the glacial (160-128 ka) detected a series of climatic abrupt changes, probably ascribable to the climate variability occurring at the end of the glacial periods. This interpretation is in line with other proxies from the same lake and from European, North Atlantic and Greenland records.

Concerning the Last Interglacial Complex, pollen analysis from DEEP core have made possible to complete the knowledge about vegetational and climate change successions at Lake Ohrid, respect to previous studies on the same basin (JO2004 core, Bordon, 2008 PhD thesis), becoming a new reference record for MIS 5 in southern Europe. Indeed, considering the investigation on climate reconstruction, as mentioned in the introductive paragraph, only one record located in southern Europe (45° lat. N) has been investigated (Lago Grande di Monticchio. Allen et al., 2000).

The LIC includes, besides the Eemian, the succession of stadials (Melisey I and II, stadial I and II) and interstadials (St. Germain I and II, Ognon I and II) of the Early Last Glacial phase. This alternation between cold and drier period and warmer and wetter ones at Lake Ohrid is reflected by the vegetation with an interspersed succession between open environment, characterized by prevalence of steppic taxa and persistence of arboreal ones and forested periods, characterized by mesophilous trees (montane taxa become rather important during St. Germain I) and corroborated by quantitatively-based climate reconstructions.

Lake Ohrid pollen record results and climatic information inferred from it are coherent with other bio-geochemical proxies obtained from the same core, with other European and Near Eastern pollen records, and with hydrological records from the central Mediterranean. They all indicate a prompt response of the vegetation to fluctuations in moisture availability and temperature changes. At a wider scale the several vegetation contractions together with colder and drier events that occur during the Early Glacial are correlated to the succession of cold events and glacial advances/retreats detected in the northern Atlantic Ocean and in the Greenland ice core records, associated to the North Atlantic Meridional Overturning Circulation and atmospheric patterns. This suggests that both orbital-scale changes and millennial to centennial scale events are recorded at Lake Ohrid.

Furthermore the continuous presence at Lake Ohrid of most arboreal taxa during stadials support the presence of refugia areas for mesophilous and in minor part for montane taxa in the nearby region during the glacial and LIC stadials.

Concerning the Last Interglacial, a rapid increase in arboreal taxa characterizes the transition from glacial to interglacial conditions. The Eemian forested phase occurs after 128 ka, when AP exceeds 50 %, more or less coinciding with other European and Mediterranean records.

Pollen analysis and climate reconstructions based on Lake Ohrid sediments identified three key-phases for the Last Interglacial with a slight different timing: an initial phase (between 128 and 125/121 ka) with a rapid increase in temperature and precipitation (the climate optimum for mesophilous forests), a central phase (between 125/121 and 118.5/118 ka) characterized by a slight cooling and increase in precipitations (*Carpinus betulus* expansion), and a latter phase (between 118.5/118 and 112 ka), with a decline both in temperatures and precipitation (new increase of mesophilous with montane taxa).

The chronological difference is related to the data used for the interpretation: developments of vegetation are detected by pollen; inferred climate parameters probably better define climate changes inducing changes in vegetation.

My results evidenced once more that Eemian was not a stable period, but that it was characterized by several climate oscillations especially towards the final part (since 125 ka). This change maybe ascribed to interglacial variability, in line with other hydrological and temperature records from the Mediterranean and the North Atlantic, suggesting the persistence of teleconnections between the two regions also during the period of low ice volume.

The end of the Eemian forest at Lake Ohrid is dated at 112 ka, in line with the other southern European records. Indeed the Eemian duration was shorter at north of the Alps and Pyrenees, while at the South, long term conditions occurred. Forest persisted until 112-110 ka, for several millennia after the establishment of opening vegetation in northern Europe, recorded at ca. 115 ka.

Instead, the climate tripartition observed at Lake Ohrid is consistent with northern European records (i.e. La Grande Pile), while as reported by studies based on climate reconstruction of southern Europe record (Iberian Margin, Lago Grande di Monticchio and Ioannina), in the south temperatures remain quite stables.

Climate reconstruction inferred by pollen data from this thesis has revealed that despite Lake Ohrid is situated in southern Europe, at the border with Mediterranean area, it records also the general features of northern Europe sequences. Anyway the scarce availability of information for southern Europe requires an implementation of studies based on climate quantification.

In conclusion, on the basis of general and high-resolution data from DEEP core, Lake Ohrid can be considered a key site for the comprehension of climate changes during glacial/interglacial cycles. By comparing DEEP record with other European and Near Eastern pollen sequences and with benthic and planktic isotope data, similarities and matches were noted, revealing a good response of the lake to fluctuations in climate providing furthermore new evidence for LIC and Eemian climate and for the connections between ice sheets dynamics, North Atlantic conditions and hydrological patterns of Mediterranean region.

Perspectives:

The comparison of reconstructed climatic data from the Last Interglacial Complex with climate models was not carried out yet. Anyway, I hope that in the future it will be possible to develop also this aspect, also in consideration of the importance to plan scheduled actions in defense of the environment and human life in view of global warming.

APPENDIX:

PUBLICATIONS:

ARTICLES:

- Bertini A., Sadori L., Combourieu-Nebout N., Donders T.H., Kouli K., Koutsodendris A., Joannin S., MasiA., Mercuri A.M., Panagiotopoulos K., Peyron O., **Sinopoli G.**,Torri P., Wagner B., 2016. All together now: an international palynological team documents vegetation and climate changes during the last 500 kyr at Lake Ohrid (SE Europe). Alpine and Mediterranean Quaternary, in print (in Scopus).
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ABSTRACTS:

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