Referee #1

This paper presents a significant body of new information on Lake Ohrid and its environmental history. I strongly support publication of this work. I look forward to a more careful discussion of iron in these sediments (Fe, Siderite variability) as part of the paleomagnetic chronostratigraphy and potential for early Fe sediment diagenesis.

In order to meet the comment of referee #1, we included in chapter 4.3.2 "Environmental history - Long-term changes" some sentences with respect to the presence of Fe-sulfides, which is discussed in more detail in the recent paper of Just et al. (2016).

".... Conversely, drier and warmer conditions after ca. 320 ka likely reduced mixing of the water column during the interglacials, which would lead to anoxic bottom waters and a better preservation of organic matter. Just et al. (2016) proposed a decrease in sulfide availability, either by lower sulfate concentration in lake water or ceased upward migrating fluids, changing the geochemical regime in Lake Ohrid. Such conditions are indicated by a shift from predominant glacial formation of Fe-sulfides to siderite around 320 ka, when higher Fe concentrations and limited sulphur content of sediments may have prevented the formation of greigite (Fig. 4; Just et al., 2016)."

Referee #2

The MS presents a synthesis of initial results of the SCOPSCO deep drilling of Lake Ohrid project, previously published in a series of papers in Biogeosciences. It brings together information from the four main aims of the project (age and origin of lake; seismotectonic history; volcanic activity and climate change; biodiversity and endemism) and compares results from different types evidence and approaches. As such, the whole is greater than the sum of its parts and the study is of great value to the scientific community. The text is well-written and organized and the figures of excellent quality. I have one substantive comment and one minor quibble.

1. A potentially important conclusion emerging from several strands of evidence is a long-term trend from cooler and wetter to drier and warmer glacials and interglacials, starting at ~300 ka. However, closer examination reveals that the trends between different types of evidence are not always congruous.

Water depths estimated from seismic data suggest a decrease in lake levels from 300 ka, but the trend is reversed from MIS 4 to today, with water depths increasing. The authors suggest (p. 17, l. 22) that this is in broad agreement with regional vegetation trends inferred from pollen analysis, but this not entirely accurate: the pollen data show that the two driest periods were the penultimate (MIS 6) and last glacial (MIS 4-2). This is mainly based on the large expansions of Artemisia during these intervals, vis-à-vis very low values in earlier glacials (incidentally, a feature that has not been observed in other long pollen sequences).

The claim that pollen data and inferred water depths show parallel trends is repeated on p. 20, but, again, if water depths increase from MIS 4, then there is divergence between the two over this interval. The pollen data suggest that in addition to glacials, a drying trend is also observed in interglacials. This is mainly based on the reduction of montane tree values in MIS 5 and MIS 1 (especially the almost complete disappearance of Picea; though Fagus increases somewhat from MIS 5c onwards) (Sadori et al., 2016). On the other hand, Mediterranean taxa percentages don't show any trend apart from a brief maximum at the MIS 4/3 boundary (which is unexpected), so it might be more useful to show the montane taxa in Fig. 4.

The drying trend theme is picked up again on p. 21, with the oxygen isotopic evidence. More specifically, a trend towards higher interglacial d18O in endogenic calcite after 300 ka is invoked, but close inspection shows that it is only MIS 5 that shows that; Holocene values are not that different from earlier interglacials. Interestingly, the d18O record from siderite shows lowest values in the penultimate and last glacials. This is interpreted (p. 21, 30-31) as evidence for lower evaporation during glacials, which is reasonable. However, it is also interpreted as a "higher influence of winter precipitation (increased seasonality), which supports the interpretation of the palynological record". This, in fact, appears at odds with the high Artemisia expansions.

In conclusion, while the inference of a drying trend is potentially a very interesting and exciting observation, I would suggest that a more nuanced interpretation is needed, as close inspection reveals a more complicated picture amongst the different lines of evidence.

We completely agree with the referee that the inference of a drying trend with cooler and wetter to drier and warmer glacials and interglacials starting at ~300 ka is a very general statement and a more nuanced discussion with respect to the individual lines of evidence will help provide the nuance. A very detailed look at each proxy including comparisons is available in the individual papers, particularly in Lacey et al. (2016) and Sadori et al. (2016). As this new paper here is designed as an overview paper, we kept the discussion more general, but added relevant information to emphasize differences more clearly. In order to meet the comment we modified also the respective sentence in the abstract.
" The multi-proxy dataset covering these 637 kyr indicates long-term variability. Some of the proxies show a general trend from cooler and wetter to drier and warmer glacial and interglacial periods around 300 ka."

- We stated already in the text that the hydro-acoustic data do not allow us to infer detailed and timely well-constrained lake level or climate changes due to tectonic activity and chronological uncertainties. This is evident as the new reconstruction supposes lowest lake level during MIS 5, whereas hydro-acoustic and sediment core data in Lindhorst et al. (2010) infer lowest lake level during early MIS 6. We added the following sentences (chapter 4.3.2 "Environmental history - Long-term changes") to point out the differences between the two reconstructions:
" The lake level curve from north-eastern Lake Ohrid is only partly in phase with the minimum lake level curve based on the new hydro-acoustic reconstruction (Figs 2 and 4). Whereas the terraces in the northeastern basin provide relatively precise water depths, the reconstruction based on hydro-acoustic information (Fig. 2) can provide only minimum water depths and is certainly biased by subsidence."

- We modified the respective sentences to changes in pollen community in chapter 4.3.2 "Environmental history - Long-term changes"). Following the suggestion of the reviewer, we replaced Mediterranean taxa in Fig. 4 montane taxa and added relevant information in this chapter.
We also figured out that there was an error in the drawing of the Mediterranean taxa and the pioneers curve. We will submit a corrigendum to the Sadori et al. (2016) paper. As the short peak of Mediterranean taxa at the MIS 4/3 boundary resulted from the error in the drawing and this curve is not so significant for a site such Ohrid, we removed this curve from Fig. 4 and used the corrected drawing (new Fig. 4).

- We do not agree with the comment that only MIS 5 shows a drying trend. Lacey et al. (2016) show a comparison figure of average ∂^{18}O values, which clearly shows MIS 5 and 1 have the highest average baseline of the last 640 ka. Also, when calcite data or "warm periods" (rather than inter glacials senso stricto) are considered, there is a clear drying trend through from 300 ka after the transition to lower $\partial^{18}O$ in MIS 9. The isotope data thus support the very general lake level reconstruction based on the hydro-acoustic data with lowest lake levels during MIS 6 or 5. We agree with referee #2, however, that the sentence "higher influence of winter precipitation (increased seasonality), which supports the interpretation of the palynological record" needs to be removed, as the two proxies do not show an unequivocal pattern of seasonality, thus confirming the need for a more nuanced interpretation and discussion.

- We added some sentences to the higher late MIS 6 climate variability, which matches well with the record from Lake Ioannina.
"... It thus seems that the outlet was active most of the time and climate driven lake-level change may have existed only for relatively short periods or has been compensated at least partly by tectonic activity. Significant variations in TOC and isotope data during early MIS 6 imply a higher variability of the climate compared to the latter period of MIS 6 (Fig. 4). These observations correspond well with palynological studies from the Ioannina basin, where distinct vegetation changes between 185-155 ka indicate a high climate variability, whereas a greater abundance of steppe taxa and other herbaceous elements, combined with lower tree pollen percentages, during the latter MIS 6 after 155 ka indicate that the landscape was predominantly open in character and more stable (Roucoux et al., 2011)."

2. Referencing appears somewhat idiosyncratic at times, with an overall tendency to cite recent works. Thus, on p. 23 the attribution for the work on D/O and Heinrich events of the last glacial should include the original papers by Bond et al. (1992, 1993, Nature) and Dansgaard et al. (1993 Nature), while for older glacials McManus et al. (1999, Science), Raymo et al. (1998, Nature) and Barker et al. (2011, Science), probably deserve a mention. On the same page, (l. 12-13), important papers on the impact of HE and D/O events include Shackleton et al. (2000 Paleoceanography), Roucoux et al. (2001, QR), Margari et al. (2010 Nature Geoscience).

While the need to limit the overall number of references in a work of this wide scope is understandable, the paucity of references on the body of work on the environmental impacts of North Atlantic millennial-scale variability in the Balkans seems to be an oversight (e.g. Tzedakis et al., 2002, Science, 2004, Geology; Margari et al., 2009 QSR; Müller et al., 2011 QSR; Roucoux et al., 2011 JQS; Fletcher et al., 2013 QSR). Finally, on the fascinating topic of the reservoir vs cradle function of Lake Ohrid, it might be worth recalling that that local buffering from extreme environmental effects in refugial areas may have not only led to reduced extinction rates, but also allowed lineage divergence to proceed, and thus refugia may have acted both as 'museums' for the conservation of diversity and as 'cradles' for the production of new diversity (Tzedakis et al., 2002 Science; Tzedakis, 2011 J. of Biogeogr.).

We tried to keep the number of references reasonable and therefore did not include important papers, which also deserve to be cited in the text. Following the suggestion of referee #2, we added all relevant papers and information.

p. 14, l. 5 References for Lake Ioannina?

Lindhorst et al. (2015) refer to Tzedakis (1994). We added this reference in the text.

MPT: At several places mention is made of the 'end of the MPT'. Could this be more specific?

For the MPT, we now refer in the text to the period between 1250 and 700 ka according to Clark et al. (2006).

In sum, this is an extremely useful work and I am happy to recommend publication, subject to minor revision, which is needed to address the issues raised above.

We added the acknowledgements and included our thanks to both reviewers.

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The environmental and evolutionary history of Lake Ohrid (FYROM/Albania): Interim results from the SCOPSCO deep drilling project

Bernd Wagner[1], Thomas Wilke[2], Alexander Francke[1], Christian Albrecht[2], Henrike Baumgarten[3], Adele Bertini[4], Nathalie Combourieu-Nebout[5], Aleksandra Cvetkoska[6], Michele D´Addabbo[7], Timme H. Donders[6], Kirstin Föller[2], Biagio Giaccio[8], Andon Grazhdani[9], Torsten Hauffe[2], Jens Holtvoeth[10], Sebastien Joannin[11], ~~Eci~~Elena Jovanovska[2], Janna Just[1], Katerina Kouli[12], Andreas Koutsodendris[13], Sebastian Krastel[14], Jack H. Lacey[15,16], Niklas Leicher[1], Melanie J. Leng[15,16], Zlatko Levkov[17], Katja Lindhorst[14], Alessia Masi[18], Anna M. Mercuri[19], Sebastien Nomade[20], Norbert Nowaczyk[21], Konstantinos Panagiotopoulos[1], Odile Peyron[11], Jane M. Reed[22], Eleonora Regattieri[1,8], Laura Sadori[18], Leonardo Sagnotti[23], Björn Stelbrink[2], Roberto Sulpizio[7,24], Slavica Tofilovska[17], Paola Torri[19], Hendrik Vogel[25], Thomas Wagner[26], Friederike Wagner-Cremer[6], George A. Wolff[27], Thomas Wonik[3], Giovanni Zanchetta[28], Xiaosen S. Zhang[29]

[1] Institute of Geology and Mineralogy, University of Cologne, Cologne, Germany

[2] Department of Animal Ecology & Systematics, Justus Liebig University Giessen, Giessen, Germany

[3] Leibniz Institute for Applied Geophysics (LIAG), Hannover, Germany

[4] Dipartimento di Scienze della Terra, Università di Firenze, Firenze, Italy

[5] CNRS UMR 7194, Muséum National d'Histoire Naturelle, Institut de Paléontologie Humaine, Paris, France

[6] Palaeoecology, Department of Physical Geography, Utrecht University, Utrecht, The Netherlands

[7] Dipartimento di Scienze della Terra e Geoambientali, University of Bari, Bari, Italy

[8] Istituto di Geologia Ambientale e Geoingegneria – CNR, Rome, Italy

[9] Faculty of Geology and Mineralogy, University of Tirana, Albania

[10] School of Chemistry, University of Bristol, Bristol, U.K.

[11] CNRS UMR 5554, Institut des Sciences de l'Evolution de Montpellier, Université de Montpellier, Montpellier, France

[12] Faculty of Geology and Geoenvironment, National and Kapodistrian University of Athens, Athens, Greece

[13] Paleoenvironmental Dynamics Group, Institute of Earth Sciences, Heidelberg University, Heidelberg, Germany

[14] Institute of Geosciences, Christian-Albrechts-Universität zu Kiel, Kiel, Germany

[15] Centre for Environmental Geochemistry, School of Geography, University of Nottingham, Nottingham, UK

[16] NERC Isotope Geosciences Facilities, British Geological Survey, Keyworth, Nottingham, UK

[17] University Ss Cyril and Methodius, Institute of Biology, Skopje, Macedonia

[18] Dipartimento di Biologia Ambientale, Università di Roma "La Sapienza", Rome, Italy

[19] Dipartimento di Scienze della Vita, Laboratorio di Palinologia e Paleobotanica, Università di Modena e Reggio Emilia, Modena, Italy

[20] Laboratoire des Sciences du Climat et de l'Environnement, UMR 8212, CEA/CNRS/UVSQ et Université Paris-Saclay 91198 Gif-Sur-Yvette, France

[21] Helmholtz Centre Potsdam, GFZ German Research Centre for Geosciences, Potsdam, Germany

[22] Geography, School of Environmental Sciences, University of Hull, Hull, UK

[23] Istituto Nazionale di Geofisica e Vulcanologia, Rome, Italy

[24] IDPA-CNR, via M. Bianco 9, Milan, Italy

[25] Institute of Geological Sciences & Oeschger Centre for Climate Change Research, University of Bern, Bern, Switzerland

[26] The Lyell Centre, Heriot-Watt University, Edinburgh, UK

[27] Department of Earth, Ocean and Ecological Sciences, School of Environmental Sciences, University of Liverpool, Liverpool, UK

[28] Dipartimento di Scienze della Terra, University of Pisa, Pisa, Italy

[29] Institute of Loess Plateau, Shanxi University, Taiyuan, China

Correspondence to: B. Wagner (wagnerb@uni-koeln.de)

Abstract

This study reviews and synthesises existing information generated within the SCOPSCO (“(‘Scientific Collaboration on Past Speciation Conditions in Lake Ohrid”)Ohrid’) deep drilling project. The four main aims of the project are to infer (i) the age and origin of Lake Ohrid (Former Yugoslav Republic of Macedonia/Republic of Albania), (ii) its regional seismotectonic history, (iii) volcanic activity and climate change in the central northern Mediterranean region, and (iv) the drivers of biodiversity and endemism.influence of major geological events on the evolution of its endemic species. The Ohrid basin formed by transtension during the Miocene, opened during the Pliocene and Pleistocene, and the lake established *de novo* in the still relatively narrow valley between 1.9 and 1.3 Myr ago. The lake history is recorded in a 584 m long sediment sequence, which was recovered within the framework of the International Continental Scientific Drilling Program (ICDP) from the central part (DEEP site) of the lake in spring 2013. To date, 5054 tephra and crypto-tephra horizons have been found in the upper 460 m of this sequence. Tephrochronology and tuning biogeochemical proxy data to orbital parameters revealed that the upper 247.8 m represent the last 637 kyr. The multi-proxy dataset covering these 637 kyr indicates long-term variability, with. Some proxies show a change from generally cooler and wetter to drier and warmer glacial and interglacial periods around 300 ka. Short-term environmental change caused, for example, by tephra deposition or the climatic impact of millennial-scale Dansgaard-Oeschger and Heinrich events are superimposed on the long-term trends. Evolutionary studies on the

extant fauna indicate that Lake Ohrid was not a refugial area for regional freshwater animals. This differs from the surrounding catchment, where the mountainous setting with relatively high water availability provided a ~~refugial area~~refuge for temperate and montane trees during the relatively cold and dry glacial periods. Although Lake Ohrid experienced significant environmental change over the last 637 kyr, preliminary molecular data from extant microgastropod species do not indicate significant changes in diversification rate during this period. The reasons for this constant rate remain largely unknown, but a possible lack of environmentally induced extinction events in Lake Ohrid and/or the high resilience of the ecosystems may have played a role.

1 Introduction

Systematic limnological studies started in the early 20th century and were first carried out in Europe, for example, at Lake Geneva (e.g., Forel, 1901), a number of lakes in Germany (e.g., Thienemann, 1918), and at Lake Ohrid on the Balkan Peninsula (reviewed in Stanković, 1960). These initial studies focused on hydrological data, such as temperature, dissolved oxygen and bottom morphology, and on biological data, such as the distribution and ecology of lake biota. Analytical and technological advances in the following decades facilitated a more comprehensive understanding of the interactions between catchment dynamics, hydrology, and the living world of lakes. This led to the establishment of new institutions, such as the Hydrobiological Institute at Lake Ohrid in 1935 (Stanković, 1960).

Besides analyses in extant lakes, early scientists were also interested in studying past changes in lake systems, and paleolimnology, a sub-discipline of limnology, was established in the 1920s. This field started with the collection of sediment cores from lakes to interpret stratigraphic data on plant and animal fossils as a record of the lake's history (National Research Council, 1996). Particularly with the establishment of radiometric dating methods in the 1950s and 1960s, paleolimnological studies developed into a powerful tool for long- and short-term reconstructions of the climatic and environmental history of lakes and their catchments.

One of the most important developments in paleolimnological work has been the formation of a multi-national continental drilling program – the International Continental Scientific Drilling Program (ICDP). The ‘Potsdam Conference’, conducted in 1993, defined the scientific and management needs for the ICDP and declared Lake Ohrid, Europe’s oldest freshwater lake, as an ICDP target site.

One of the most outstanding characteristics of Lake Ohrid, besides its presumed old age, is its high degree of endemic biodiversity. With more than 300 described eukaryotic endemic taxa (Föller et al., 2015), Lake Ohrid belongs to the most biodiverse ancient lakes, i.e., lakes that have continuously existed for >100 kyr (Albrecht and Wilke, 2008). If its surface area is taken into account, it may have the highest endemic biodiversity amongst all lakes worldwide. Though Lake Ohrid has long been considered to be of Tertiary age, estimates vary considerably, between ca. 2 and 10 Ma (reviewed in Albrecht and Wilke, 2008). Likewise, its limnological origin remains poorly understood, and hypotheses ~~vary between~~include paleogeographical ~~connection~~connections to former marine or brackish water systems~~, or~~ and a *de novo* formation from springs and/or rivers (see also Albrecht and Wilke, 2008 for further information and references therein).

The unique characteristics of Lake Ohrid, together with the lack of knowledge regarding its origin, precise age, and limnological/biological evolution, provided the main motivation to establish an international scientific deep drilling project. Its continuous existence over a long timescale together with an extraordinary degree of endemic biodiversity made Lake Ohrid an ideal ‘natural laboratory’ to study the links between geological and biological evolution and to unravel the driving forces of speciation, leading to the interdisciplinary project ‘Scientific Collaboration on Past Speciation Conditions in Lake Ohrid’ (SCOPSCO). The four major aims of the SCOPSCO project are to (i) obtain more information on the age and origin of Lake Ohrid, (ii) unravel the regional seismotectonic history including effects of major earthquakes and associated mass-wasting events, (iii) obtain a continuous record containing information on Quaternary volcanic activity and climate change in the central northern Mediterranean region, and (iv) evaluate the influence of major geological events on biotic evolution and the generation of the observed extraordinary degree of endemic biodiversity (Wagner et al., 2014). Based on several site surveys and studies conducted between 2004 and

2011, an ICDP drilling campaign at Lake Ohrid was carried out in spring 2013 using the ‘Deep Lake Drilling System’ (DLDS) from the ‘Drilling, Observation and Sampling of the Earths Continental Crust’ (DOSECC) consortium. In total, more than 2100 m of sediments were recovered from four drill sites, with a maximum penetration of 569 m below lake floor (blf) at the main drill site (DEEP) in the central part of Lake Ohrid (Fig. 1).

Subsampling and analyses are ongoing, but initial, detailed results of geological and biological investigations of the upper 247.8 m (637 ka) of the DEEP sediment sequence and newer results from biological studies on the extant fauna of Lake Ohrid were recently published in a special issue in the journal 'Biogeosciences' ~~("~~(‘Integrated perspectives on biological and geological dynamics in ancient Lake ~~Ohrid",~~Ohrid’, edited by Wagner et al.). The aim of this paper is to review and synthesise the results of the 14 individual papers of this special issue and to complement them with information from former and new studies in order to provide a comprehensive overview on progress towards achieving the four main aims defined for SCOPSCO.

2 Site information

Lake Ohrid is a transboundary lake shared between the Former Yugoslav Republic of Macedonia (FYROM) and the Republic of Albania (Fig. 1). The lake is located at 693.5 m above sea level (a.s.l.) and has a maximum length of 30.4 km (N~~-~~–S), a maximum width of 14.7 km (W~~-~~–E), a surface area of 358 km^2, and a tub-shaped bathymetry with a maximum water depth of 293 m, a mean water depth of ~151 m, and a total volume of 50.7 km^3 (Fig. 1; Popovska and Bonacci, 2007; Lindhorst et al., 2012). Water loss occurs by evaporation (13.0 $m^3\ s^{-1}$) and by the artificially controlled surface outflow in the northern part of the lake, River Crni Drim, which flows into the Adriatic Sea. Outflow rates vary between 22.0 $m^3\ s^{-1}$ (Popovska and Bonacci, 2007) and 24.9 $m^3\ s^{-1}$ (Matzinger et al., 2006 and references therein), depending on seasonal and long-term variations in water level of up to ~1.5 m between 1950 and 2000 (Popovska and Bonacci, 2007). The total water loss can be averaged to ~36.5 $m^3\ s^{-1}$ and is balanced by water input from ~~direct precipitation, rivers, as well as~~ surface and sublacustrine springs, direct precipitation, as well as rivers. Published data of the annual precipitation in the watershed of Lake Ohrid vary between 698.3 and 1194.0 mm yr^{-1}, with higher precipitation at higher altitudes and an average of 907 mm yr^{-1} (Popovska and Bonacci, 2007). The average monthly rainfall is highest in winter, with a maximum in November and December, and lowest between June and September. The lake level, however, is highest in June due to snowmelt input and lowest in October and November, before the start of autumn rainfall (Popovska and Bonacci, 2007). The seasonal and long-term variations in water budget allow only an approximation of the water input from the various sources. Direct precipitation and river inflows (45%) as well as surface and sublacustrine karst springs (55%) contribute to the overall water input (Matzinger et al., 2006). The River Sateska, which was previously a direct tributary of the Crni Drim, was artificially diverted into Lake Ohrid in 1962 and is today the largest surface river inflow with a contribution of ~15% of the total inflow of Lake Ohrid (Matzinger et al., 2006; Poposka and Bonnacci, 2007). The karst springs are located primarily along the eastern shoreline of the lake (Fig. 1) and karst waters originate in almost equal proportions from mountain range precipitation and via outflow from Lake Prespa, located ~10 km to the east and ~155 m higher in altitude (Matzinger et al., 2006). Calculating the ratio between the volume of Lake Ohrid (50.7 km^3) and its outflow (~23.5 m^3 s^{-1}) results in a theoretical water residence time of ~70 years (Matzinger et al., 2006; Popovska and Bonacci, 2007). This theoretical residence time is reduced to ~45 years, when evaporation is taken into account and calculated with the total water output or input (~36.5 m^3 s^{-1}). However, the real water residence time is probably much higher, as sporadic mixing intervals or incomplete mixing, variations in wind stress, or kinetic effects of inflow water entering may affect the lake's hydrology (Ambrosetti et al., 2003). For example, Lago Maggiore in Italy was classified as a holo-oligomictic lake prior to 1970, when the upper 150–200 m of the water column mixed every winter and complete mixing occurred irregularly every few years (Ambrosetti et al., 2003). This is similar to Lake Ohrid today (Matzinger et al., 2006) and the real residence time at Lago Maggiore is higher by a factor of 3 to 4 than the theoretical residence time (Ambrosetti et al., 2003).

Physical and chemical characteristics of Lake Ohrid have been provided in several publications and annual reports (e.g., Watzin et al., 2002; Matzinger et al., 2006; Jordanoski et al., 2004, 2005; Naumoski et al., 2007; Schneider et al., 2014). Average total phosphorous (TP) concentrations of <10 mg m^{-3} and Secchi depths ranging between 7 and 16 m characterise the pelagic zone of Lake Ohrid as oligotrophic. These oligotrophic conditions explain why bottom water oxygen concentrations of above 4 mg L^{-1} are recorded even in years without complete overturn (Matzinger et al., 2006). The surface water temperature varies between ~25°C in summer and ~7°C in winter, while bottom water temperatures are ~6°C throughout the year. The boundary between epilimnion and hypolimnion is between 30 and 50 m, depending on the season. The pH decreases from 8.6–8.9 in surface waters to 7.9–8.4 in bottom waters. The specific conductivity is around 200 µS cm^{-1} in surface waters, around 150 µS cm^{-1} at 50–200 m water depth and increases again in deeper waters. The concentration of Si is lowest in the trophogenic surface waters, where it is taken up by diatoms, and increases gradually to <2 mg L^{-1} in bottom waters (Stanković, 1960). The littoral part of the lake exhibits a slightly higher trophic state (Schneider et al., 2014). These meso- to slightly eutrophic conditions in relatively shallow waters might be due to a direct input of nutrients from the catchment, higher temperatures, and increasing anthropogenic pollution over the last several decades (Kostoski et al., 2010; Schneider et al., 2014). The macrophytic flora in the littoral part of Lake Ohrid can be subdivided into different belts, with *Chara* species in water depths between 3 and 30 m, *Potamogeton* species in shallow waters, and a discontinuous belt of *Phragmites australis* along the shore (Albrecht and Wilke, 2008; Imeri et al., 2010).

The vegetation in the catchment of Lake Ohrid can be categorized along altitudinal belts (cf., Filipovski et al., 1996; Matevski et al., 2011). Grasslands and agricultural land are encountered in the littoral zone and the lowlands surrounding the lake, followed by forests 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*) up to 1600 m a.s.l. Mesophilous/montane species such as *Fagus sylvatica*, *Carpinus betulus*, *Corylus colurna*, *Acer obtusatum*, and *Abies borisii-regis* dominate at higher altitudes up to 1800 m a.s.l. Due to intense grazing, the timberline is between 1600 and 1900 m a.s.l. Reforestation is now slowly replacing the existing alpine pasture lands and grasslands at and above this altitude (Matevski et al., 2011). Sparse populations of several *Pinus* species, considered to be Tertiary relics, are located in the wider region of Lake Ohrid (Sadori et al., 2016). Em et al. (1985) considered the Ohrid-Prespa region to be a refugial area with remains of vegetation of other species (e.g., *Pinus heldreichii*, *Quercus trojana*, *Juniperus excelsa*, *Aesculus hippocastanum*, *Genista radiata*).

The highest mountains in the Lake Ohrid watershed, which encompasses 1002 km^2 *sensu stricto* and 2393 km^2 including the Lake Prespa catchment, reach 1532 m a.s.l. in the Mocra Mountains to the west, and 2288 m a.s.l. in the Galičica Mountains to the east of the lake. The average altitude of the Lake Ohrid watershed is 1109 m a.s.l. About 12% of its watershed is located at an altitude above 1500 m a.s.l. (Popovska and Bonacci, 2007). Intensely karstified Triassic limestones and Devonian siliciclastic bedrock dominate in the southeastern, eastern, and northwestern catchment (e.g., Wagner et al., 2009; Lindhorst et al., 2015). Ultramafic metamorphic and magmatic rocks including ophiolites of Jurassic and Cretaceous age crop out in the west. The plains at the northern, northeastern, and southern lake shore are covered by Quaternary sediments.

3 Material and methods

3.1 Field work

3.1.1 Seismic and hydro-acoustic surveys

Seismic and hydro-acoustic surveys were carried out on Lake Ohrid between 2004 and 2009. Parametric sediment echosounder profiles span >900 km in length and were collected at operating frequencies between 6 and 12 kHz (SES-96 light in 2004 and SES 2000 compact in 2007 and 2008, Innomar Co.). These frequencies allowed up to 60 m of penetration into the sediments at a vertical resolution of ~20 cm. Over 500 km of profiles were collected by multichannel seismic surveys using a Mini GI Air Gun (0.2 L in 2007 and 0.1 L in 2008) and a 16-channel 100 m long streamer. The Mini GI Air Gun operated at frequencies between 150 and 500 Hz and allowed a maximum penetration of several hundred metres at a vertical resolution of ~2 m. A multibeam survey in 2009, using an ELAC Seabeam 1180 sonar system, was used to acquire detailed bathymetric information of the lake floor below ~20 m water depth. More detailed information on the technical specifications of the seismic and hydro-acoustic systems, their settings, the location of the individual profiles, and the operational logistics can be found in Wagner et al. (2014) and Lindhorst et al. (2015).

3.1.2 Coring and onsite analyses

Several gravity and piston coring campaigns were carried out from local research vessels or small floating platforms (UWITEC Co.) on Lake Ohrid between 2004 and 2011. Whereas surface sediments collected by gravity corer throughout the basin were used to reconstruct the recent settings and the most recent history of Lake Ohrid (e.g., Matzinger et al., 2007; Wagner et al., 2008a; Vogel et al., 2010c), piston cores with a maximum penetration of ~15 m blf were collected from the lateral parts of the lake, where the water depth did not exceed 150 m (e.g., Wagner et al., 2008b, 2009; Belmecheri et al., 2009; Vogel et al., 2010a, 2010b). These piston cores enabled a reconstruction of the environmental, climatic, and tephrostratigraphic history of the lake back to ~140 ka and provided fossil records of pollen (Wagner et al., 2009), molluscan faunas (Albrecht et al., 2010)), and diatom floras (Reed et al., 2010).

Based on the site surveys, five primary target sites in Lake Ohrid were proposed for the SCOPSCO ICDP project. One of these sites, Lini (Co1262; Fig. 1), was cored in 2011 using a UWITEC platform and piston corer at 260 m water depth. Although the Co1262 sediment sequence reached only 10.08 m blf, this is the most complete Holocene sequence retrieved to date. Studies on the core material contributed to a better understanding of the tectonic activity (Wagner et al., 2012) and the Late Glacial to Holocene environmental history of the region (Lacey et al., 2015; Zhang et al., 2016).

The remaining four sites were cored in spring 2013 using the DLDS (Wagner et al., 2014; Francke et al., 2016). At the main site, the DEEP site in the central part of the Lake Ohrid basin, six holes (5045-1A to 5045-1F) were drilled with a maximum depth of ~569 m blf (Fig. 1) and an average distance of ~40 m between the individual holes (for details see Francke et al., 2016). In total, ~1500 m of sediment cores were recovered, cut into up to 1 m long segments, and stored in a reefer at 4°C before being shipped to the University of Cologne, Germany, for further processing.

Onsite analyses during the 2013 deep drilling campaign included borehole logging, core scanning for magnetic susceptibility, and sedimentological and palaeobiological core catcher analyses. Borehole logging was carried out with various probes at all four drill sites. The logging tools comprised magnetic susceptibility (MS), dipmeter, resistivity, borehole televiewer, spectral gamma ray (SGR), and sonic. While SGR was run through the drill pipe in order to prevent caving of sediments into the drill hole, all other tools were run in 40–50 m long open-hole sections, except for the uppermost 30 m blf, which were kept open with drill pipes to allow re-entry of other probes. Details of the borehole logging tools, logging speed, and vertical resolution are given in Baumgarten et al. (2015). Check shots were recorded for hole 5045-1C, allowing a very good seismic-to-core correlation for the DEEP-site.

In order to determine volume-specific MS on the sediment cores and to carry out preliminary core correlation, all cores were scanned onsite at a resolution of 2 cm with a Bartington MS2C loop sensor (10 cm internal diameter) mounted on a multi sensor core logger (MSCL, Geotek, UK). Smear slide analyses of core catcher material (~3 m resolution) from holes 5045-1B and 5045-1C were used for onsite diatom analyses (Wagner et al., 2014).

3.1.3 Biological sampling

Biological field sampling within the SCOPSCO project focused on the collection of living invertebrates from the lake and its surroundings in order to conduct phylogenetic and metacommunity analyses. The collection methods for gastropods followed those described in Hauffe et al. (2011) and Schreiber et al. (2012), and included hand collecting, snorkeling, sieving, and dredging from small boats or the research vessel of the Hydrobiological Institute Ohrid. Samples were preserved in 80% ethanol for subsequent analyses.

In order to improve the interpretation of changes in sedimentary lipid biomarker composition, samples from main modern terrestrial organic matter pools, i.e., soils and leaf litter, as well as macroalgae and macrophytes (*Characeae* spp., *Cladophora* spp., *Potamogeton* spp., *Phragmites* spp.) were collected from the eastern and southern realm of the Ohrid Basin (for details see Holtvoeth et al., 2016). All samples were oven-dried shortly after collection (70°C, 48 hours) and kept frozen prior to biomarker analysis.

3.2 Laboratory work

The geological work carried out on the gravity and piston cores from the site surveys and on the cores obtained during the ICDP drilling campaign comprises a broad suite of ~~different~~ analytical methods. It includes lithological description after core opening, measurement of the geophysical properties, and granulometric, geochemical, mineralogical, and rock-magnetic analyses. These analyses are carried out on whole core sections, on split core surfaces, and on discrete samples (cf., Wilke et al., 2016) and are described in detail in several individual publications (Matzinger et al., 2007; Wagner et al., 2008a, 2008b, 2009, 2012; Belmecheri et al., 2009, 2010; Holtvoeth et al., 2010, 2016; Leng et al., 2010; Lindhorst et al., 2010; Matter et al., 2010; Vogel et al., 2010a, 2010b; Lacey et al., 2015, 2016; Francke et al., 2016; Just et al., 2016; Leicher et al., 2016). Dating of the sediment successions was mainly based on radiocarbon dating ~~and~~as well as tephrostratigraphic and tephrochronological work. Tuning of sediment proxies to orbital parameters, such as summer insolation and winter season length, or to other records has only been carried out on the sediment sequence from the DEEP site (Baumgarten et al., 2015; Francke et al., 2016; Zanchetta et al., 2016). Optical and geochemical information was used for a correlation of the DEEP core sequences and led to a composite profile of 584 meters composite depth (mcd) (Francke et al., 2016 and unpublished data). Some of the sediment sequences were also studied for their fossil diatom, pollen, ostracod, or mollusc compositions. The sample preparation for the micro- and macrofossil analyses and the determination of the taxa are described in detail in the individual publications (Belmecheri et al., 2009, 2010; Wagner et al., 2009, 2014; Albrecht et al., 2010; Reed et al., 2010; Cvetkoska et al., 2016; Sadori et al., 2016; Zhang et al., 2016).

Information on interspecific relationships between Ohrid endemics and Balkan species, and on the drivers of speciation processes and community changes was derived from extant taxa by conducting molecular phylogenetic, lineage-through-time plot, and diversification-rate analyses (for details see Föller et al., 2015 and references therein), as well as modeling of community assembly processes (see Hauffe et al., 2016).

4 Results and discussion

4.1 Age and origin

4.1.1 Age

At the start of the SCOPSCO project, the age and origin of Lake Ohrid were poorly constrained. Previous geological and biological age estimates varied from 2 to 10 Ma (summarised in Albrecht and Wilke, 2008). Our new results allow for more precise age estimation. Based on SGR from borehole logging, MS from core logging, and total inorganic carbon (TIC) analyses on core catcher samples from the DEEP site, and by comparing these data with global climate records, such as the benthic isotope stack LR04 (Lisiecki and Raymo, 2005), a minimum age of 1.2 Ma has been proposed for the permanent lake phase of Lake Ohrid (Wagner et al., 2014). This minimum age is supported by the results from more detailed studies of the uppermost 247.8 mcd of the DEEP site sequence, which cover the last 637 kyr, according to an age model derived from tephrochronology and tuning of bio-geochemical proxy data to orbital parameters (Francke et al., 2016). The high-resolution data allow a better understanding of proxy variation over time and show that high TIC characterises interglacial periods and very low TIC represents glacial periods, as previously inferred from studies on core catcher material (Wagner et al., 2014). Indeed, a prominent TIC maximum at ~368 m blf in the core catcher samples from the DEEP site was presumed to represent the Marine Isotope Stage (MIS) 31 at 1.081~~-~~–1.062 Ma (Wagner et al., 2014), which is regarded as one of the warmest interglacials ~~at the onset of~~during the Mid Pleistocene Transition (MPT; e.g., Melles et al., 2012) between 1250 and 700 ka (Clark et al., 2006). The lithology of the DEEP site sediment sequence indicates that lacustrine, hemi-pelagic sediments comprise the upper ~430 m blf, whereas littoral and fluvial sediments dominate below (Wagner et al., 2014). The transition from fluvial or littoral facies to hemi-pelagic sediments most likely indicates the onset of full lacustrine conditions in Lake Ohrid. Five TIC maxima below the presumed MIS 31 maximum and above the fluvial or littoral facies (cf., Wagner et al., 2014) could represent five additional interglacials, which would place the onset of hemi-pelagic sedimentation within MIS 41 and refines the minimum age of Lake Ohrid to ca. 1.3 Ma.

An age estimation for the onset of lacustrine sedimentation in the Lake Ohrid basin has been derived from comparing seismic and chronological information from core Co1202 recovered in the north-eastern part of the lake (Fig. 1). Tracking seismic reflectors from this coring location (~2 km from the DEEP site) to the central part of the lake allowed for the transfer of chronological information of the core into the basin centre (Lindhorst et al., 2015). In addition, the strength of the reflectors was correlated with chronological information and glacial/interglacial cycles derived from pollen analyses at Lake Ioannina, (Tzedakis, 1994), 200 km to the South of Lake Ohrid. Based on this information, an average sedimentation rate of 0.43 mm yr^{-1} was calculated for the last 450 kyr in the basin centre (Lindhorst et al., 2015). Using this sedimentation rate for the maximum sediment fill of ~800 m blf observed in the basin centre, resulted in an age of 1.9 Ma for the onset of sedimentation (Lindhorst et al., 2015). At the DEEP site a somewhat lower average sedimentation rate of 0.39 mm yr^{-1} can be calculated for the upper 247.8 mcd or for the last 637 kyr (Francke et al., 2016). Sediment compaction with increasing sediment depth (cf. Baumgarten et al., 2015) may have caused further lowering of the calculated sediment accumulation rate downward and also would lead to older ages compared to those based on a constant sedimentation rate of 0.43 mm yr^{-1}. However, lacustrine, hemi-pelagic sediments only form the upper ~430 m blf of sediments at the DEEP site, which represents only half of the maximum sediment fill equivalent to ~800 m blf. As the underlying littoral and fluvial sediments most likely have significantly higher sedimentation rates, the extrapolated age of 1.9 Ma for the onset of hemi-pelagic sedimentation can be regarded as a tentative maximum age, assuming there were no major phases of erosion and/or non-deposition.

Overall, based on this new geological information, the minimum and maximum age of Lake Ohrid can be restricted to ca. 1.3 and 1.9 Ma, respectively. More precise age estimation will be obtained by ongoing tephrostratigraphic work and paleomagnetic analyses, which may reveal the existence of major reversals in the Earth's magnetic field, such as the Jaramillo (1.075-0.991 Ma), Cobb Mountain (1.1938-1.1858 Ma), or Olduvai (1.968-1.781 Ma) subchrons (Nowaczyk et al., 2013 and references therein).

These estimates of 1.3-–1.9 Ma correspond well to evolutionary data for endemic Lake Ohrid species obtained prior to the drilling campaign. Based on genetic information from extant endemic species and molecular-clock analyses, the onset of intralacustrine speciation in various groups of Lake Ohrid endemics (= “(=‘ancient lake species flocks”)flocks’) started between 1.4 Ma for the limpet genus *Acroloxus* (Albrecht et al., 2006) and 2.0 Ma for the endemic *Salmo trutta* trout complex (Sušnik et al., 2006) and the *Dina* leech flock (Trajanovski et al., 2010). Assuming that the origin of Lake Ohrid predates the onset of intralacustrine speciation events, the latter authors suggested that the minimum age of Lake Ohrid is approximately 2.0 Ma. However, they were not able to explain why the species flocks investigated differed in their time of origination and why some of the flocks were as young as 1.3 Ma. A potential explanation is now provided by the initial results of the SCOPSCO deep drilling campaign, which indicate that persisting lacustrine conditions with pelagic or hemi-pelagic sedimentation established between 1.9 Ma and 1.3 Ma ago. The period of lake establishment and persisting lacustrine conditions may have comprised up to several hundred thousand years, which in turn might have given rise to most species flocks in Lake Ohrid.

4.1.2 Origin

There is a broad consensus that the 40 km long and N-S-trending Ohrid graben basin developed as part of the Alpine orogeny during a transtensional phase in the Late Miocene, followed by an extensional phase since the Pliocene (e.g., Cvijić 1911; Aliaj et al., 2001; Dumurdzanov et al., 2004; Reicherter et al., 2011; Lindhorst et al., 2015). There is little consensus on the limnological origin of the lake itself, however. Albrecht and Wilke (2008) summarized four related hypotheses. Three of these hypotheses favour an origin as part of a marine ingression or a brackish-water lake system during the Miocene: the Mesohellenic Trough hypothesis, the Tethys hypothesis, and the Lake Pannon hypothesis. A fourth hypothesis favourspostulates a *de novo* origin, i.e., that Lake Ohrid formed in a dry polje fed by springs during the Pliocene or Pleistocene. The latter is supported, in part, by the known existence of substantial active karst aquifers (Matzinger et al., 2006) and the seismic data, which indicate that Lake Ohrid formed in a relatively narrow and elongated valley (Lindhorst et al., 2015). Moreover, sediments at the base of the DEEP site sequence are formed by gravel, which is overlain by alternating peat layers, sand horizons, and fine-grained sediments, and contain a relatively shallow, obligate fresh water diatom flora (Wagner et al., 2014). These sediments indicate very dynamic environments, ranging from fluvial to slack water conditions, with varying shallow water conditions, and support, in combination with the presumed Pleistocene age of Lake Ohrid, the *de novo* hypothesis of lake formation.

4.2 Sediment architecture and basin development

In addition to information on the formation of the Ohrid basin, the hydro-acoustic data sets from Lake Ohrid can also provide knowledge on mass transport deposits (MTDs) and on long-term lake level change.

The evaluation of the seismic and hydro-acoustic data sets indicated that MTDs are only observed during the last ca. 340 ka in Lake Ohrid (Lindhorst et al., 2016). Older MTDs are not covered by the seismic profiles or may be masked by multiple reflections below 250~~-~~–300 m sediment depth in the central part of the basin. Five major MTDs are detected during MIS 9, 7, and 6. Since ca. 80 ka, the number of MTDs increased, however this is accompanied by a trend of decreasing MTD volume. Due to the restricted vertical resolution of the seismic data sets, the age control of the MTDs is relatively imprecise. Nevertheless, it seems that the occurrence of MTDs is not driven by or a response to glacial/interglacial cyclicity, as they occur during glacials, interglacials, and their respective transitions. Although MTDs are detected throughout the entire basin (Lindhorst et al., 2016), they cluster along the major faults in the southeastern and northwestern part of the basin and are probably the result of fault activity and major earthquakes (Lindhorst et al., 2012; Wagner et al., 2012). ~~No indications for these MTDs are found in the drill cores of the DEEP site.~~ Hence, MTDs in the Ohrid basin apparently have a rather limited spatial extent and are not accompanied by basin-wide suspension clouds or turbidites. MTDs with a maximum thickness of <3 cm are observed in the DEEP site record, with clusters in MIS 8, late MIS 6, and MIS 2 (Francke et al., 2016). The thickness of these MTDs is significantly below the vertical resolution of the seismic data.

The hydro-acoustic data can also provide information about the tectonic history of the basin with respect to lake-level fluctuations. The minimum water depth can be estimated from measuring the depth difference of individual reflectors between their largest depth in the basins and the minimal depth of occurrence at the lake margins. The minimal depth of occurrence for individual reflectors maybe a real reflection termination but in most cases, individual reflectors cannot be traced further up because the shallowest areas of the lake basin are not covered by the seismic and hydro-acoustic survey or reflectors could not be traced to the shallower parts due to faults (Fig. 2). In a second step, linking these reflectors to the chronological information from the DEEP site provides chronological information for the minimum water depth. Tracing a reflector from ~275 m blf at the DEEP site, i.e., a reflector located below the existing age model, supposes a minimum water depth of 300 m (Fig. 2). Reflectors at the MIS 16/15 (~240 m blf) and the MIS13/12 boundaries (~190 m blf) suggest minimum water depths of 300 m as well, thus exceeding the present day water depth of 293 m (Fig. 2). The minimum water depth was reduced to 225 m at the MIS 9/8 boundary (~140 m blf), to 200 m during MIS 8 (~100 m blf), and to 175 m during MIS 5 (47 m blf). In MIS 4 (20 m blf), the minimum water depth increased to 250 m, returning to a level similar to that observed in the lower half of the record. Note that this method for estimating water depth contains several sources of uncertainties. The actual water depth during each period may have been much higher, as individual reflectors may continue to shallower water depths or even above the present lake level but cannot be mapped due to missing data coverage in shallow water depth, or reflectors may have been eroded during a following period of a lower lake level. Ongoing subsidence might also have affected the shape of the individual reflectors and potentially increased the maximum depth difference of individual reflectors. Nonetheless, the data suggest a general trend from deeper waters from prior to MIS 16 through to MIS 13/12, followed by decreasing water depths with a minimum in MIS 5 and a subsequent deepening to present day lake level~~, which is in a broad agreement with humidity trends based on the regional vegetation cover (Sadori et al., 2016).~~. As a result, the deepening of the Lake Ohrid basin was apparently not a continuous and gradational process; we assume that short or mid-term changes reflect changes in water budgets while subsidence is a much slower process. However, already at or shortly after the end of the MPT~~,~~, at 700 ka (Clark et al., 2006), the lake showed similar or even higher water depths compared to present lake level. The seismic data do indicate periods of very low lake levels or even a ~~dry lake~~completely desiccated lake since that time.

Mapping of the hydro-acoustic reflectors indicates that the shape of the Ohrid basin slightly altered over time. Based on the isopleths, the deeper part of the basin changed from a more elongated shape to a roundish shape during the last ca. 700 kyr, with a formation of a secondary basin in the northwestern part of the lake after the MIS 13/12 boundary at 478 ka (Fig. 2). This also reflects the extension of the lake basin.

4.3 Tephrostratigraphic and environmental history

4.3.1 Tephrostratigraphy

The DEEP site sequence drilled in 2013 provides the most complete tephrostratigraphic record obtained from Lake Ohrid. A total of 39 tephra layers have been identified in the upper 247.8 mcd so far (Fig. 3; Leicher et al., 2016 and unpublished data). Major element analyses (SEM-EDS/WDS; see Leicher et al., 2016 for details) on juvenile glass fragments suggest an origin exclusively from Italian volcanic provinces. Of these tephra layers (OH-DP-0027 to OH-DP-2060), 13 could be identified and correlated with known and dated widespread eruptions (Leicher et al., 2016 and references therein). They include the Mercato tephra (OH-DP-0027, 8.43–8.63 cal ka BP) from Somma-Vesuvius, the Y-3 (OH-DP-0115, 26.68–29.42 cal ka BP), the Campanian Ignimbrite/Y-5 (OH-DP-0169, 39.6 ± 1.6 ka), and the X-6 (OH-DP-0404, 109 ± 2 ka) from the Campanian volcanoes, the P-11 (OH-DP-0499, 129 ± 6 ka) from Pantelleria, the Vico B (OH-DP-0617, 162 ± 6 ka) from the Vico volcano, the Pozzolane Rosse (OH-DP-1817, 457 ± 2 ka) and the Tufo di Bagni Albule (OH-DP-2060, 527 ± 2 ka) from the Colli Albani volcanic district, and the Fall A (OH-DP-2010, 496±3 ka) from the Sabatini volcanic field. Furthermore, a comparison of the Ohrid record with tephrostratigraphic records of mid-distal Mediterranean archives enabled the identification of less well-known tephra layers, such as the TM24-a/POP2 (OH-DP-0404, 101.8 ka; Regattieri et al., 2015) from Lago Grande di Monticchio and the Sulmona basin, the SC5 (OH-DP-1955, 493.1 ± 10.9 ka) from the Mercure basin, and the A11/12 (OH-DP-2017, 511 ± 6 ka) from the

Acerno basin, whose specific volcanic sources are still poorly constrained. OH-DP-0624 was tentatively correlated to the CF-V5/PRAD3225 layers from the Campo Felice basin/Adriatic Sea and, thus to the Pitigliano Tuff from the Vulsini volcanic field (ca. 163 ka; Leicher et al., 2016). However, recent tephrochronological results including $^{40}Ar/^{39}Ar$ of a tephra from the Fucino Basin, central Italy, suggest that these tephras correspond to an un-known eruption from the Neapolitan volcanic area at 158.8 ± 3.0 ka (Giaccio et al., 2016). In order to obtain a consistent set of ages all $^{40}Ar/^{39}Ar$ were calculated by using the same flux standard (1.194 Ma for ACs, which corresponds to FCs at 28.02 Ma). The chronological information of 11 of the well-identified tephras from Lake Ohrid was used as 1st order tie points for the age-depth model of the composite core, and complemented by tuning of sediment proxies to orbital parameters, such as summer insolation and winter season length (Francke et al., 2016).

Fifteen additional tephra horizons have been identified within the lower hemi-pelagic section of the DEEP site sequence between 248 and 450 mcd (Fig. 3) and are the subject of on-going work. Although knowledge of tephrostratigraphy for the period >637 ka is restricted, a combination of tephrochronological with paleomagnetic information should provide a robust chronology for this part of the sequence.

With a total of at least 54 tephra layers intercalated in a continuous sediment succession of > 1.3 Ma, the tephrostratigraphic record from Lake Ohrid is a strong candidate to become the template for central Mediterranean tephrostratigraphy, especially for the poorly-known and explored Lower and Middle Pleistocene period. The tephrostratigraphic record may also help to allow re-evaluation and improvement of the chronology of dated and undated tephra layers from other key sites, such as the age of the Fall A tephra (Leicher et al., 2016). Moreover, the tephras constitute valuable, independent tie points that resolve leads and lags between changes in different components of the climate system and allow a synchronisation of the Lake Ohrid record with other regional records (Zanchetta et al., 2016).

4.3.2 Environmental history

The examination of the environmental history of Lake Ohrid over the last 637 kyr focuses both on long-term changes over several glacial/interglacial periods, and short-term changes on the sub-orbital scale.

Long-term changes

The study of the long-term environmental history of Lake Ohrid and its surrounding area includes the reconstruction of minimum lake levels based on hydro-acoustic information, by vegetation changes in the catchment, and by internal lake proxies. According to the established age model (Francke et al., 2016), hydro-acoustic (Lindhorst et al., 2015~~)~~), and borehole logging data (Baumgarten et al., 2015), the sediments deposited at 637 ka are now located ~240 m blf at the DEEP site. If the altitude of the Lake Ohrid outlet or the bedrock gap used by the river Crni Drim would have been the same as it is today (693.5 m a.s.l.), the water depth of Lake Ohrid at 637 ka would have been more than 480 m. There is no evidence in the seismic or sedimentological data for such a great water depth at that time, which implies that subsidence or other tectonic activity affected the sediment succession in the lake basin or the altitude of the outlet. Nevertheless, the hydro-acoustic data suggest a fairly deep lake at the end of the MPT, with a water depth similar or even deeper than today (Figs 2 and 4). Shallower minimum water depths are tentatively indicated between MIS 9 and MIS 3, with an absolute minimum during MIS 6 or MIS 5. Tectonic activity and the relative altitude of the outlet are probably the most significant contributors to water depth variations in Lake Ohrid. ~~However, a~~A comparison of the minimum water depth data with pollen data shows some differences, but suggests that climate change may also have triggered water-depth fluctuations. Although the Lake Ohrid watershed was a refugial area for both temperate and montane trees during the glacial periods of the last 500 kyr, high amounts of herbs (grasses, chenopods, Cichorioideae and Cyperaceae) are found in the earlier glacials MIS 12, MIS 10, and MIS 8 ~~were characterized by~~and indicate the presence of open formations and grassland (Sadori et al., 2016). Such vegetation ~~would require~~requires relatively humid conditions, whereas steppe vegetation with unexpected high amounts of *Artemisia* and pioneer taxa typical of dry conditions dominated during MIS 6, MIS 4, and MIS 2 (Fig. 4; Sadori et al.,

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2016). Mesophilous communities representing a Mediterranean-type climate are found in MIS 5 and the Holocene.The pollen data suggest that in addition to glacials, a drying trend is also observed in interglacials. This is mainly based on the reduction of montane trees, particularly *Abies* and *Picea* values in MIS 5 and the Holocene (Sadori et al., 2016), which may indicate a rearrangement of vegetation in altitudinal belts. The overall progressive change from cooler and wetter conditions recorded during both interglacial and glacial periods prior to 288 ka to subsequently warmer and drier interglacials and glacials (Sadori et al., 2016) is consistentbroadly matches with the generally shallower minimum water levels reconstructed by tracing hydro-acoustic reflectors throughout the basin. Moreover, driest conditions and a maximum in steppe vegetation between 160-–129 ka (Sadori et al., 2016) correspond to a prominent lake-level lowstand and the formation of a subaquatic terrace ~60 m below the present lake level in the northeastern Ohrid basin (Fig. 4; Lindhorst et al., 2010). This lowstand was reconstructed based on hydro-acoustic studies and tephrochronological information from two short sediment cores. Two tephras deposited on the terrace were previously correlated with MIS 5 tephras C-20 (ca. 80 ka) and X5 (105 ± 2 ka) (Sulpizio et al., 2010), and it was supposed that the formation of this terrace took place during MIS 6 (Lindhorst et al., 2010). However, new tephrostratigraphic results suggest that the two tephras instead correspond with Vico B (OH-DP-0617, 162 ± 6 ka) and CF-V5/PRAD3225 (OH-DP-0624, ca. 163 ka; Leicher et al., 2016). This constrains the formation of this terrace to the earlier part of MIS 6 and the subsequent lake-level increase to late MIS 6 or early MIS 5, with a secondary lowstand around 100 ka (Fig. 4), which approximately follows the overall trend of the minimum lake-level reconstruction. 4). The lake level curve from northeastern Lake Ohrid is only partly in phase with the minimum lake level curve based on the new hydro-acoustic reconstruction (Figs 2 and 4). Whereas the terraces in the northeastern basin provide relatively precise water depths, the reconstruction based on hydro-acoustic information (Fig. 2) can give only minimum water depths and is certainly biased by subsidence.

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Internal lake proxies confirmsupport the long-term trend seen in pollen from generally wetter and cooler interglacial and glacial periods between 637 ka and ca. 300 ka to drier and warmer stages between 300 ka and the Present. The oxygen isotope composition of lake water ($\delta^{18}O_{lakewater}$), calculated from $\delta^{18}O$ of endogenic calcite, shows only moderate variability between interglacial periods with a relatively stable climate from MIS 15 to MIS 13, progressively wetter conditions during MIS 11 and MIS 9, and increasingly evaporated, drier conditions in more recent interglacials (Fig. 4; Lacey et al., 2016). In particular, higher $\delta^{18}O_{lakewater}$ through MIS 5 and the Holocene indicate higher evaporation due to dry and warm conditions prevailing under a Mediterranean-type climate. During glacials calcite is typically absent, however $\delta^{18}O_{lakewater}$ reconstructed from early diagenetic siderite shows a more pronounced long-term shift, with values being consistent with the adjacent interglacials during MIS 14, MIS 12, and MIS 10, a transition to lower values through MIS 8, and very low $\delta^{18}O_{lakewater}$ during MIS 6, MIS 4, and MIS 2 (Fig. 4). The similarity between interglacial and glacial lake water prior to ca. 300 ka suggests that Lake Ohrid may have experienced regular and complete mixing, as calcite and siderite form in different environments; calcite in surface waters during summer months and siderite as a product of early diagenesis in the surface sediments. Lower average $\delta^{18}O_{lakewater}$ before ca. 300 ka indicates moderate summer temperatures (reduced seasonality). It may also suggest higher activity of the karst system due to more precipitation and/or a higher lake level of neighbouring Lake Prespa. Subsequently, a trend to higher $\delta^{18}O_{lakewater}$ during interglacials indicates stronger rates of summer evaporation and drier conditions, and lower $\delta^{18}O_{lakewater}$ in glacial periods suggests isotopically fresh conditions most likely due to low evaporation~~ and a higher influence of winter precipitation (increased seasonality), which supports the interpretation of the palynological record.~~. Increasing summer aridity towards present is also backed by the gradual increase of Mediterranean taxa pollen percentages.

A transition from generally wetter and cooler to drier and warmer conditions is also indicated by a shift from relatively invariant and low TOC prior to ca. 300 ka towards more fluctuating and higher TOC, particularly during the more recent interglacials (Fig. 4; Francke et al., 2016). Wetter and cooler conditions after the MPT drive a high activity of the karst system and intense mixing of the water column, thus promoting decomposition of organic matter. This would, in turn, increase the supply of sulphur to the sediments and allow for the formation of greigite (Fig. 4; Just et al., 2016). A greater activity of the karst system and associated high ion (Ca^{2+}, HCO_3^-) input is further supported by the relatively high TIC during MIS 15, MIS 14, and MIS 13 (Fig. 4; Francke et al., 2016). Pollen data suggest moderate summer temperatures, i.e., conditions that would have favoured mixing and, hence, increased organic matter degradation. Conversely, drier and warmer conditions after ca. ~~300~~320 ka likely reduced mixing of the water column during the interglacials, which would lead to anoxic bottom waters and a better preservation of organic matter. Just et al. (2016) proposed a decrease in sulfide availability, either by lower sulfate concentration in lake water or ceased upward migrating fluids, changing the geochemical regime in Lake Ohrid. Such conditions are indicated by ~~the~~a shift from predominant glacial formation of Fe-sulfides to siderite ~~during these more recent glacials, when~~around 320 ka, when higher Fe concentrations and limited sulphur content of sediments may have prevented the formation of greigite (Fig. ~~4), with siderite precipitating instead.~~4; Just et al., 2016).

The maximum sedimentation rate during early MIS 6 (Francke et al., 2016) correlates well with the formation of the subaquatic terrace located at 60 m below the present lake level (Fig. 4; Lindhorst et al., 2010). The lower lake level during early MIS 6 led to exposure and erosion of formerly shallow parts of the lake and a lower distance from inlets to the central part of the lake. However, there is no indication, e.g., in isotope or redox sensitive data, for an endorheic lake at that time or any other time during the last 637 kyr. It thus seems that the outlet was ~~always active and climate driven lake-level change may have been compensated at least partly by tectonic activity.~~ active most of the time and climate driven lake-level change may have existed only for relatively short periods or has been compensated at least partly by tectonic activity. Significant variations in TOC and isotope data during early MIS 6 imply a higher variability of the climate compared to the latter period of MIS 6 (Fig. 4). These observations correspond well with palynological studies from the Ioannina basin, where distinct vegetation changes between 185–155 ka indicate a high climate variability, whereas a greater abundance of steppe taxa and other herbaceous elements, combined with lower tree pollen percentages, during the latter MIS 6 after 155 ka indicate that the landscape was predominantly open in character and more stable (Roucoux et al., 2011).

Sub-orbital changes

On a sub-orbital scale, prominent environmental changes in the Northern Hemisphere that potentially affected Lake Ohrid include Dansgaard-Oeschger (D/O) and Heinrich events (HE~~).~~) (e.g., Bond et al., 1992, 1993; Dansgaard et al., 1993; Raymo et al., 1998; McManus et al., 1999). D/O events are a pervasive feature of the last glacial (e.g., Wolff et al., 2010) and also of older glacial periods (Stein et al., 2009; Naafs et al., 2014). They are likely related to variations in the Atlantic Meridional Overturning Circulation (AMOC) and are recorded as climatic perturbations in many marine and terrestrial records (e.g., Genty et al., 2002; Rohling et al., 2003; Margari et al., 2009; Fletcher et al., 2013; Naafs et al., 2014; Seierstad et al., 2014; Stockhecke et al., 2016). In the eastern Mediterranean, D/O events may have influenced regional hydrology and led to large-scale droughts during the past four glacial cycles (Stockhecke et al., 2016). HE are distinctively represented by deposition of ice rafted debris (IRD) in North Atlantic marine cores (e.g., Hemming et al., 2004), and are also well documented to have had an imprint on marine and terrestrial records for the last glacial and beyond (e.g., Shackleton et al., 2000; Roucoux et al., 2001, 2011; Sanchez-Goni et al., 2002; Martrat et al., 2004; Margari et al., 2010; Naafs et al., 2013). At the IODP drill site U1308 in the North Atlantic, HE are first indicated during MIS 16 and are represented by ice-rafted debris (IRD) layers that are rich in detrital carbonate and poor in biogenic carbonate (Hodell et al., 2008). It has been speculated that ice volume and the duration of glacial conditions surpassed a critical threshold during MIS 16 and activated the dynamic processes responsible for Laurentide Ice Sheet instability in the region of Hudson Strait, which led to increased iceberg discharge and weakening of thermohaline circulation in the North Atlantic (Hodell et al., 2008).

MIS 12 is considered to be one of the most severe glacials during the Quaternary, with the lowest summer sea surface temperatures (SST) recorded across multiple records (e.g., Shackleton 1987; Naafs et al., 2013, 2014; Rohling et al., 2014). Abrupt sea surface warming events of 3-–6°C in the mid-latitude North Atlantic during MIS 12 likely reflect the imprint of D/O events and probably had a substantial impact on global climate (Naafs et al., 2014). In contrast to the observations from MIS 16, a temporal lag between the occurrence of IRD and surface water cooling during MIS 12 implies that HE were not the cause for a weakening of the thermohaline circulation in the North Atlantic at this time (Naafs et al., 2014).

High-resolution records from the Mediterranean region, which can be used to test a larger regional or even global impact of D/O and HE during MIS 16 or MIS 12, are scarce (e.g., Hughes et al., 2006; Tzedakis et al., 2006; Girone et al., 2013; Capotondi et al., 2016). A multi-proxy record with lithological, geochemical, and isotope data from the Sulmona basin in central Italy covering MIS 12 shows pronounced hydrological variability at orbital and millennial time scales, which replicates North Atlantic and western Mediterranean SST fluctuations (Fig. 5; Regattieri et al., 2016). Several short-term fluctuations in the MIS 12 Sulmona record most likely reflect sub-orbital scale hydrological variations, and are ~~likely~~apparently related to reduced precipitation sourcing from the North Atlantic due to episodes of iceberg melting, and IRD deposition at the west Iberian margin (Regattieri et al., 2016 and references therein). However, as the timing of these IRD events at the western Iberian margin was used to improve the chronology of the Sulmona record, the correlation of hydrological variations in central Italy and IRD deposition in the North Atlantic is not fully independent.

At Lake Ohrid and further to the East, the arboreal pollen concentration in the Tenaghi Philippon record from Greece correlates well with the general pattern of the sea surface temperatures in the North Atlantic during MIS 12 (Fig. 5; Tzedakis et al., 2006). The resolution of the existing record is too low yet to allow a clear identification of D/O or HE related climate change. The high-resolution record from Lake Van in eastern Turkey also cannot be used for testing the climatic impact of D/O or HE on the eastern Mediterranean, as the sediments of MIS 12 and the onset of MIS 11 are disturbed and lack independent age control (Stockhecke et al., 2014).

The new high-resolution record from the DEEP site in Lake Ohrid now offers the possibility to assess the impact of D/O or HE during MIS 12 on a broader regional scale, particularly as it provides two absolute tephra age control points with ages centred at 493.1 ± 10.9 and 457 ± 2 ka (Fig. 5; Francke et al., 2016; Leicher et al., 2016). During MIS 12, potassium (K) shows a long-term increase, which supports the overall trend towards colder temperatures, such as can be inferred from other marine, terrestrial, or synthetic climate records (Fig. 5). K represents the proportion of clastic, terrigenous matter relative to the content of carbonate (reflected by TIC) and organic matter (reflected by TOC and bSi). TOC was used to infer the severity of glacials at Lake Ohrid (Francke et al., 2016) and shows a remarkable saw tooth pattern during MIS 12, which resembles fluctuations in SST related to D/O variability from the North Atlantic marine record U1313 (Fig. 5; Naafs et al., 2014). Higher TOC is favoured by both increased overall productivity (on land and in the water column) as well as increased organic matter preservation, with the latter resulting from oxygen depletion of the bottom water due to enhanced thermal stratification, decreased mixing, and higher temperatures. These higher temperatures at Lake Ohrid likely correlate with higher SST in the North Atlantic. The TOC record from Lake Ohrid thus would be the first terrestrial record to indicate D/O cycle-related teleconnections between the North Atlantic thermohaline circulation and the climate in the northeastern Mediterranean region during MIS 12. Interestingly, the dominant *Pinus* pollen abundance in the vegetation record indicates a regular ~8 kyr variability during MIS 12 and 10),, for which a high-resolution analysis is now being performed (Figure 2 in Sadori et al., 2016).

The environmental impact of HE or other short-term climate events has been studied in detail for the last glacial cycle in several records from lakes Ohrid and Prespa.the Balkans (e.g., Tzedakis et al., 2004; Müller et al., 2011). Based on pollen and diatom analyses from lakes Prespa and Ohrid, HE in the North Atlantic during MIS 4 to MIS 2 led to short spells of very dry and cold conditions superimposed on the glacial conditions (Panagiotopoulos et al., 2014; Cvetkoska et al., 2015). Moreover, there is an increased formation of Fe and Mn concretions in Lake Prespa sediments, most likely driven by a significant shift in the bottom water redox conditions (Wagner et al., 2010). According to diatom studies spanning the last 92 ka, Lake Prespa experienced significant regime shifts that are correlated with lake level fluctuations and changes between (oligo-) meso- and eutrophic conditions (Cvetkoska et al., 2016). Lake Ohrid seems to be less sensitive to short-term climate change due to its higher volume--to--surface area ratio (e.g., Wagner et al., 2010; Leng et al., 2013). It does not indicate sub-orbital time scale lake-level changes and shifted between ultra oligo- and oligotrophic conditions during the last 92 kyr (Cvetkoska et al., 2016). However, the formation of Fe and Mn concretions and the occurrence of siderite indicate that Lake Ohrid is also sensitive to shifts in the bottom water redox conditions (Lacey et al., 2016). During MIS 12, Fe peaks in XRF data are positively correlated with TIC and indicate the formation of early-diagenetic siderite in response to a shift in bottom water redox conditions towards a more oxic environment (Fig. 5; Francke et al., 2016; Lacey et al., 2016). The Fe peaks during the coldest period of this glacial match particularly well with the number of IRD grains and with maxima in the quartzite- or dolomite-calcite ratio in the U1313 record from the North Atlantic (Fig. 5). The latter are interpreted as millennial ice-rafting driven events (Voelker et al., 2010; Naafs et al., 2011, 2013) and thus demonstrate that North Atlantic HE may have caused changes in internal lake conditions, such as bottom water redox conditions.

One of the HE, the H4 event at 40.4–38.4 ka, is superimposed by another short-term event, the eruption from the Campi Flegrei volcanoes 39.6 ± 1.6 ka. This eruption is one of the most severe volcanic eruptions during the Pleistocene and left a 15 cm thick tephra known as Campanian Ignimbrite or Y-5 marine tephra layer in the records from lakes Ohrid and Prespa (e.g., Wagner et al., 2009; Vogel et al., 2010b; Damaschke et al., 2013). High-resolution studies of diatoms in both lake sediment records indicated little evidence for a response of the diatom community related to the H4 event, but a clear and rapid change following tephra deposition (Jovanovska et al., 2016). This strong change is likely due to fertilisation and the availability of nutrients, particularly silica, such as it was shown in laboratory studies and leaching experiments of tephra with Lake Ohrid water (D´Addabbo et al., 2015). After the initial response, diatom community compositions in lakes Ohrid and Prespa returned to their quasi pre-disturbance state. In Lake Ohrid, the recovery time was ca. 1100 years vs. ca. 4000 years in Lake Prespa (Jovanovska et al., 2016). Although both lakes are resilient to short-term environmental change, it seems that Lake Ohrid is even more resilient than Lake Prespa, likely due to differences in geology, lake age, limnology, and intrinsic parameters of the diatom proxies (Jovanovska et al., 2016).

4.4 Drivers of biodiversity change

One of the major interdisciplinary goals of the SCOPSCO project is to infer the drivers of the extraordinary endemic biodiversity in Lake Ohrid, in general, and to evaluate the influence of major environmental events on evolutionary processes, in particular. Lake Ohrid thus serves as a model system to address questions that have puzzled evolutionary biologists for decades. These questions include the problem whether the high number of endemic species is mainly a result of an accumulation of ~~relic~~relict species (‘reservoir ~~function‘)~~function’) and/or of a high rate of intralacustrine speciation (‘cradle ~~function‘).~~function’). Moreover, if intralacustrine speciation plays a significant role, is it primarily driven by geographic or environmental

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gradients during periods of relatively constant environmental conditions, possibly supported by a high ecosystem resilience of the lake, or does ongoing environmental change lead to an increase (or decrease) in rates of species diversification? Finally, what role do potentially ’catastrophic‘ environmental fluctuations play, such as lake level change or significant changes in the trophic state?

4.4.1 Reservoir vs. cradle function of Lake Ohrid

As discussed in Föller et al. (2015), ancient lakes have often been considered to serve as evolutionary or geographic refugia, either harboring old and distinct lineages or enabling the accumulation of species from extralimital areas during periods of adverse environmental changes, respectively (‘reservoir function‘). However, previous evolutionary studies in Lake Ohrid on selected animal taxa could not demonstrate the existence of such relict species (sensu Grandcolas et al., 2014), either because ancestral distribution ranges are largely unknown (e.g., Schultheiß et al., 2008) or the native species are not extraordinarily old (e.g., Albrecht et al., 2008; Hauswald et al., 2008). Instead, intralacustrine speciation after immigration events prevails. Most endemic animal species in Lake Ohrid are considerably younger than the lake itself and form ~~a~~ monophyletic ~~clade~~clades (also see Section 4.1.2.). This suggests that the high endemic species richness in Lake Ohrid invertebrates is predominantly a result of intralacustrine diversification (‘cradle function‘, e.g., Albrecht et al., 2006, 2008; Wilke et al., 2007; Schultheiß et al., 2008; Wysocka et al., 2014; Föller et al., 2015).

Interestingly, the situation is different for plant species inhabiting the surrounding of Lake Ohrid. For example, the existing pollen record from the DEEP site sequence, which covers the last 500 kyr, indicates that the Lake Ohrid catchment has indeed been a refugial area for both temperate and montane trees during glacial periods (Sadori et al., 2016~~).~~), comparable to the Lake Ioannina catchment (Tzedakis et al., 2002).

4.4.2 Impact of environmental change on species diversification

Ancient lakes are often considered to be comparatively stable systems, potentially resulting in constant diversification rates (i.e., speciation minus extinction rates) over time. Nonetheless, several factors, often related to environmental, geological, or climatic changes, and depending on the genetic features of the species, have been suggested to affect the tempo of diversification in ancient lake species flocks. Accordingly, phases of rapid environmental fluctuations may lead to net evolutionary change. Diversification rates may be higher in the initial phase of lake colonisation and may decline once niche space is increasingly occupied. Alternately, there might be a pronounced lag phase between the colonization of a lake and the onset of subsequent diversification (reviewed in Föller et al., 2015).

Although high-resolution sediment-core analyses, covering the last 637 kyr, indicate that Lake Ohrid experienced several environmental changes, phylogenetic studies on a microgastropod group using lineage-through-time plots and diversification-rate analyses did not reveal significant changes in this rate over time (Föller et al., 2015). Moreover, diatom community analyses conducted from the DEEP sediment cores could not show extinction events due to major environmental events such as tephra deposition (Jovanovska et al., 2016; for details see section 4.3.2) and climate change over the last 92 kyr (Cvetkoska et al., 2016). However, the potential for a regime shift increases with recent human impact on the diatom flora of both lakes Ohrid (Zhang et al., 2016) and Prespa (Cvetkoska et al., 2015) although, again, Ohrid appears to be more well-buffered from eutrophication than Prespa.

The reasons for the relatively constant diversification rate over time observed in microgastropods and the lack of diatom extinction events during the Late Pleistocene/Holocene remain largely unknown. However, ~~a~~the lack of environmental induced extinction events in Lake Ohrid and/or ~~a~~the high resilience of its ecosystems may have played a role (Föller et al., 2015; Cvetkoska et al., 2016; Jovanovska et al., ~~2016).~~2016). Local buffering from extreme environmental effects in a refugial area, such as Lake Ohrid, may have not only led to reduced extinction rates, but also allowed divergence of lineages to proceed. Refugia thus may have acted both as 'museums' for the conservation of diversity and as 'cradles' for the production of new diversity (Tzedakis et al., 2002; Tzedakis, 2009).

Nonetheless, though environmental changes may have had only a minor direct effect on diversification processes in endemic taxa of Lake Ohrid during the last 637 kyr, these changes potentially altered the abundance and community compositions of diatoms and ostracods (e.g., Belmecheri et al., 2010; Reed et al., 2010; Zhang et al., 2016), thus indirectly affecting speciation processes. In fact, the analysis of the gastropod community in Lake Ohrid implied the presence of both geographical and ecological speciation due to physical barriers and divergence across environmental or life history gradients, respectively (Hauffe et al., 2016).

Another aspect of environmental change is the impact of anthropogenic activity on species composition, diversity, and diversification. As previously suggested, Lake Ohrid is facing a “creeping biodiversity crisis”, as increasing human impact in and around the lake already jeopardises endemic species (Kostoski et al., 2010). For example, the presence of globally invasive species has been recently demonstrated for Lake Ohrid (Albrecht et al., 2014). Moreover, human-mediated environmental change is also predicted to alter the trophic state of the lake (e.g., Matzinger et al., 2006). Given the small size of both the lake and its catchment, increasing negative effects on the endemic biodiversity of Lake Ohrid and the respective habitats are foreseeable and will likely foster extirpation. Only concerted and international conservation activities might help mitigating the human impact on the sensitive and highly biodiverse ecosystem of Lake Ohrid.

5 Conclusions and outlook

The SCOPSCO deep drilling project was initiated in 2004 and aimed at inferring (i) the age and origin of Lake Ohrid (Former Yugoslav Republic of Macedonia/Republic of Albania), (ii) its regional seismotectonic history, (iii) volcanic activity and climate change in the central northern Mediterranean region, and (iv) the ~~drivers of biodiversity and endemism.~~influence of major geological events on the evolution of its endemic species. The project included phylogenetic and metacommunity analyses of living invertebrates and sampling from main modern terrestrial organic matter pools from the lake and its surroundings, seismic and hydro-acoustic surveys of the ~~lake~~lake’s internal sediment architecture, and the recovery of surface sediments and sediment cores. Within the framework of the International Continental

Scientific Drilling Program (ICDP) a deep drilling in Lake Ohrid took place in spring 2013 and provided, among others, a 584 m long sediment sequence from the central part (DEEP site) of the lake. Initial results of the study of this sediment sequence in combination with the results of the biological and geophysical as well as former sedimentological studies reveal that the Ohrid basin formed during the Miocene and Pliocene. Lake Ohrid established between 1.9 and 1.3 Myr ago and provides a continuous record of distal tephra deposition and climatic and environmental change in the central northern Mediterranean region. With its geographical location, the Lake Ohrid record provides a unique opportunity to align marine records from the North Atlantic with long-term and independently dated terrestrial archives in the ~~Northern~~northern and ~~Eastern~~eastern Mediterranean, such as the records from the Sulmona basin, Tenaghi Philippon, Lake Van, or Dead Sea. This is a major precondition to disentangle longitudinal climate gradients and investigate leads and lags circumventing age model uncertainties.

More detailed studies exist meanwhile on the upper 247.8 m of the DEEP site sediment sequence and indicate that this part represents the last 637 kyr. Over this period, Lake Ohrid experienced significant environmental change, which is related to orbital-scale climate forcing and regional geological events. These changes apparently did not cause major extinction events in Lake Ohrid, as evident from both the microgastropod phylogeny and the diatom fossil record. The potential high resilience of the ecosystem to past climatic and environmental changes together with relatively low extinction rates may explain the extraordinary degree of endemic biodiversity in the lake. Ongoing biological studies and more detailed analyses of the early stages of Lake Ohrid basin, based on the now accessible sediment records, will help to better understand the drivers of biological diversification and endemism. Lake Ohrid is thus a key site to further resolve the link between biological and geological evolution and should centre our attention on protecting the endemic community from a substantial biodiversity crisis due to the increasing anthropogenic impact.

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Figure captions

Figure 1: **(a)** Location of Lake Ohrid (black rectangle) on the Balkan Peninsula at the border of the Former Yugoslav Republic of Macedonia (FYROM) and the Republic of Albania. Other records mentioned in the text are indicated by red dots (core U1313 in the North Atlantic, Sulmona basin in Italy, Tenaghi Philippon (TP) in Greece). **(b)** Map of the area of lakes Ohrid and Prespa and bathymetric map of Lake Ohrid (from Lindhorst et al., 2015). Coring locations of piston core Co1202 (red; Vogel et al., 2010) and ICDP sites (white) are shown, with DEEP and Lini sites mentioned in the text. Secondary ICDP sites P (Pestani), G (Gradiste), and C (Cerava) are not mentioned in the text. **(c)** Geological map of the Lake Ohrid catchment (modified from Lindhorst et al., 2015).

Figure 2: Selected seismic profiles and calculated water depths at different times (see text for details). The arrow of the reflector at 140 m blf (MIS 8/9) indicates the existence of a secondary basin in the northwestern part of the lake. Please note that the lake was probably larger for most periods but individual reflectors cannot be traced to the shallower water depth due to faults. This also explains, why the estimated water depth is not zero at the edges of the shown lake coverage.

Figure 3: Lithostratigraphy of the upper 247.8 mcd and tephra and crypto-tephra horizons in the DEEP sediment sequence. For nomenclature and details see Leicher et al. (2016). Tephra in bold was used as tie points for the age-depth model for the upper 247.8 mcd spanning the

last 637 kyr (Francke et al., 2016; Leicher et al., 2016). Tephrostratigraphic work on tephra from below 247.8 mcd is ongoing.

Figure 4: Lake-level reconstructions (modified from Lindhorst et al., 2010,; for details see chapter 4.3.2, and of this study), pollen (Sadori et al., 2016), sedimentological, and geochemical data over the last 637 kyr (Francke et al., 2016; Just et al., 2016; Lacey et al., 20152016) indicate a long-term shift from cooler and wetter to drier and warmer glacial and interglacial periods around 300 ka. Pollen curves have been corrected with respect to those reported in Sadori et al. (2016). MIS boundaries are according to Lisiecki and Raymo (2005).

Figure 5: Geochemical data from the DEEP site sequence with sub-orbital changes during MIS 12 in comparison with other records from a similar latitude (for location of North Atlantic core U1313, the pollen record from Tenaghi Philippon and the isotope record from Sulmona basin see Fig. 1). Arboreal pollen (AP) records are excluded of *Pinus*, *Juniperus*, and *Betula* (Sadori et al., 2016); the record from Tenaghi Philippon is based on pollen data from Wijmstra (1969) and Wijmstra and Smit (1976)), and the age model from Tzedakis et al. (2006); see also Sadori et al. (2016). Red bars and black dots at the bottom age axis indicate tephrochronological tie points and tuning points used for the age model of the DEEP site sequence (Francke et al., 2016).