

1 **Ecosystem regimes and responses in a coupled ancient lake system from MIS 5b to present:**  
2 **the diatom record of lakes Ohrid and Prespa**

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15

16 **Abstract**

17 We reconstruct the aquatic ecosystem interactions since the last interglacial period in the oldest,  
18 most diverse, hydrologically connected European lake system, by using palaeolimnological  
19 diatom and selected geochemistry data from Lake Ohrid “DEEP site” core and equivalent data  
20 from Lake Prespa core, Co1215. Driven by climate forcing, the lakes experienced two adaptive  
21 cycles during the last 92 ka: “interglacial and interstadial” and “glacial” cycle. The short-term  
22 ecosystems reorganizations, e.g. regime shifts within these cycles substantially differ between  
23 the lakes, as evident from the inferred amplitudes of variation. The deeper Lake Ohrid shifted  
24 between ultra oligo- and oligotrophic regimes in contrast to the much shallower Lake Prespa,  
25 which shifted from a deeper, (oligo-) mesotrophic to a shallower, eutrophic lake and vice versa.  
26 Due to the high level of ecosystem stability (e.g. trophic state, lake-level), Lake Ohrid appears  
27 relatively resistant to external forcing, such as climate and environmental change. Recovering in

1 relatively short time from major climate change, Lake Prespa is a resilient ecosystem. At the  
2 DEEP site, the decoupling between the lakes' response to climate change is marked in the  
3 prolonged and gradual changes during the MIS 5/4 and 2/1 transitions. These response  
4 differences and the lakes' different physical and chemical properties may limit the influence of  
5 Lake Prespa on Lake Ohrid. Regime shifts of Lake Ohrid due to potential hydrological change in  
6 Lake Prespa are not evident in the data presented here. Moreover, a complete collapse of the  
7 ecosystems functionality and loss of their diatom communities did not happen in either lake for  
8 the period presented in the study.

9 **Key words: Lake Ohrid, Lake Prespa, diatoms, regime shifts, resilience, ecosystems**  
10 **interactions**

## 11 **1 Introduction**

12 The structure and functions of the continental ecosystems constantly changed throughout the  
13 Quaternary, driven by a series of successive climate variations at different temporal scales. As  
14 dynamic entities, the ecosystems developed through these fluctuations with a “panarchy”,  
15 defined as a series of hierarchical adaptive cycles interacting across multiple scales of space and  
16 time (Holling, 2001; Delcourt and Delcourt, 2004; Allen et al., 2014). Four functional phases,  
17 controlled by top-down and bottom-up processes, have been identified within these cycles,  
18 growth ( $r$ ), conservation ( $k$ ), release ( $\Omega$ ), and reorganization ( $\alpha$ ). Change in the processes  
19 controlling the ecosystem's structure and functions can lead to regime change and creation of  
20 new self-organized structures (Holling, 1986). Regime shifts may occur within one adaptive  
21 cycle or between adaptive cycles at different scales, and cause reorganization or even sometimes  
22 a complete ecosystem collapse (Allen et al., 2014). Such catastrophic regime changes, marked by  
23 species communities loss and consequently, collapse of the ecosystem's functions have been  
24 recorded in many of the world's oldest lakes, like Baikal in Russia, Hövsgöl in Mongolia,  
25 Malawi in East Africa (Karabanov et al., 2004; Cohen et al., 2007; Burnet et al., 2011; Scholz et  
26 al., 2011). Based on the intensity of forcing, and their physical, chemical and biological  
27 properties these lakes had different capacities to adapt, restore and/or reorganize their panarchy.  
28 The adaptive capacity of an ecosystem is intrinsically related to its resilience (Allen et al., 2005;  
29 Allen and Holling, 2008), and therefore, research on sediment records from ancient lakes is

1 important for understanding the past adaptive capacities, regime changes, and resilience of these  
2 unique ecosystems.

3 In Europe, such Quaternary archives are neighboring lakes Ohrid and Prespa, located on the  
4 Balkan Peninsula. Since the Pliocene origin of their tectonic basins, more than 1 Ma co-existence  
5 and co-evolution (Stanković, 1960) resulted in the oldest and most diverse permanent lake  
6 systems in Europe (Albrecht and Wilke, 2008; Levkov and Williams, 2012). Understanding the  
7 external and internal drivers for these basins is critical for determining the high level of  
8 biological endemism of especially Lake Ohrid. At present, the lake system has unique spatial  
9 interactions due to hydrological connectivity via a karstic system in Mt. Galičica (Anovski et al.,  
10 1997, 2001). About 20% of the Lake Ohrid water inflow originates from Lake Prespa, and,  
11 therefore, the much shallower and more nutrient rich Lake Prespa can potentially drive changes  
12 in Lake Ohrid (Matzinger et al., 2006). By applying a system analytical approach, Matzinger et  
13 al. (2006) assessed the anthropogenic influence on Lake Prespa, quantified the underground  
14 water and nutrient flow and developed a linear phosphorus (P) model. By using the 1960s'  
15 water-level high-stand of Lake Prespa (~855 m above sea level) as a baseline for the calculation,  
16 the model indicates that a 20 m water level decrease of Lake Prespa can cause a five-fold  
17 increase of its P concentration, which may lead to a 30% increase of the P load from Lake Prespa  
18 to Lake Ohrid (Matzinger et al., 2006). Such a scenario can potentially trigger a regime shift in  
19 the physico-chemical properties of Lake Ohrid and affect its fragile endemic community (Watzin  
20 et al., 2002; Matzinger et al., 2006, 2007). Therefore, parallel analysis of long-term temporal  
21 variations under changing climate boundary conditions from Quaternary sedimentary records of  
22 both lakes is important for identifying the potential influence of Lake Prespa on Lake Ohrid.

23 Between 2005 and 2012, multiple cores have been retrieved at different locations from lakes  
24 Ohrid and Prespa, the oldest dating to ca. 135.0 ka (Co1202, Ohrid; Vogel et al., 2010a) and 92.0  
25 ka (Co1215, Prespa; Damaschke et al., 2013). While environmental variations in Lake Prespa  
26 were resolved at high resolution for the last ca. 92.0 ka (Aufgebauer et al., 2012; Wagner et al.,  
27 2012; Panagiotopoulos et al., 2013, 2014; Cvetkoska et al., 2014a, 2015), the presence of hiatuses  
28 in cores retrieved from Lake Ohrid (Wagner et al., 2008; Vogel et al., 2010b; Lacey et al., 2014;  
29 Zhang et al., 2016) hampered a detailed palaeoenvironmental comparison between the two lakes  
30 until today.

1 As part of the project Scientific Collaboration on Past Speciation Conditions in Lake Ohrid  
2 (SCOPSCO), a successful International Continental Scientific Drilling Program (ICDP) drilling  
3 campaign was carried out at Lake Ohrid in spring 2013. A sediment sequence spanning >1.2 Ma  
4 (Wagner et al., 2014a) was recovered at the “DEEP site” in the central part of the lake. Multi-  
5 proxy analyses of this sequence currently proceed towards understanding the influence of the  
6 past geological and environmental events on the biological evolution of the lake taxa, as one of  
7 the main project objectives.

8 Aiming to assess the potential interactions between the lakes, we compare Lake Prespa’s  
9 dynamics, as already inferred from core Co1215 diatom, pollen, and geochemistry data with the  
10 diatom and selected bio(geochemical) data from the same age interval (ca. 92.0 ka to present) of  
11 the DEEP site sediment sequence. Here, we apply the concept of panarchy and consider lakes  
12 Ohrid and Prespa as lower-scale entities of the higher hierarchical, landscape scale, as justified  
13 by their hydrological connection. Trends in the multi-proxy dataset are used to reconstruct and  
14 compare the adaptive cycles, regime shifts and assess the response mechanisms to external  
15 disturbances on ecosystem scale (e.g. lakes Ohrid and Prespa). At higher hierarchical level, we  
16 aim to assess the potential interconnectivity between the lakes in order to understand the cross-  
17 scale linkages and recognize the capacity of Lake Prespa as a driving force of regime shifts in  
18 Lake Ohrid.

## 19 **2 Environmental setting**

20 Harboring more than 300 endemic species (Föller et al., 2015), Lake Ohrid, Macedonia/Albania  
21 (41°01’N, 20°43’E, 693 m a.s.l., Fig. 1) has the highest index of endemism of all ancient lakes,  
22 when its surface area of 358 km<sup>2</sup> is taken into account (Albrecht and Wilke, 2008). With a mean  
23 and maximum water depth of 155 m and 293 m, respectively (Lindhorst et al., 2015), it is a deep,  
24 calcium-bicarbonate Ca(HCO<sub>3</sub>)<sub>2</sub> dominated, oligotrophic lake. The hydrological balance of the  
25 lake is regulated by 37.9 m<sup>3</sup> × s<sup>-1</sup> inflow, of which ~25 % derives from direct precipitation,  
26 ~25% from river input and ~50% from the karst aquifers, and the outflow through the river Crni  
27 Drim, (~60%) and evaporation (~40%, Matzinger et al., 2006). The estimated water residence  
28 time is ca. 70 years. The average monthly air temperature of the surrounding area is 26°C during  
29 summer and -1°C in winter and the annual precipitation averages to 750 mm/year (Wagner et

1 al., 2009). Recent investigations revealed an increase in total P concentration from  $\sim 1.3 \text{ mg P} \times$   
2  $\text{m}^{-3}$  in historic times (ca. 150 years ago) to  $4.5 \text{ mg P} \times \text{m}^{-3}$  today (Matzinger et al., 2006, 2007).

3 Lake Prespa, located at the border of Macedonia, Albania, and Greece ( $40^{\circ} 46' - 41^{\circ} 00' \text{ N}$ ,  $20^{\circ}$   
4  $54' - 21^{\circ} 07' \text{ E}$ , Fig. 1) is situated at 849 m a.s.l. It is a tectonic lake which belongs to a former  
5 lake complex, called Dessarets (Stanković, 1960), but its age is still uncertain. Although it hosts  
6 fewer endemic species, it has been suggested that the endemic faunal species might be older than  
7 those in Lake Ohrid (Karaman, 1971). In terms of its physical properties, Lake Prespa is a large,  
8  $254 \text{ km}^2$ , relatively shallow lake with  $\sim 14 \text{ m}$  mean and  $\sim 48 \text{ m}$  maximum water depth. At present,  
9 the estimated hydraulic residence time is ca. 11 years, but it varies highly with changing lake-  
10 levels; and for example, at  $\sim 19 \text{ m}$  mean water depth during the 1980s, this number was  $\sim 17$  years  
11 (Matzinger et al., 2006). The water input,  $16.92 \text{ m}^3 \times \text{s}^{-1}$ , is via river inflow and catchment runoff  
12 (56%), direct precipitation (35%), inflow (9%) from the nearby Lake Micri Prespa (Fig. 1), and  
13 groundwater input (no data available). The output is via evaporation (52%), water abstraction for  
14 irrigation (2%) and subsurface outflow through the karstic aquifers of Galičica Mountain (46%,  
15 Matzinger et al., 2006). The average monthly temperature in the surrounding area is  $21^{\circ}\text{C}$  in  
16 summer and  $1^{\circ}\text{C}$  in winter, and the annual precipitation varies between 720 in the lowlands and  
17  $1200 \text{ mm} \times \text{yr}^{-1}$  on the mountains (Hollis and Stevenson, 1997). The lake is highly sensitive to  
18 external disturbances (e.g. climate change) and water loss; major lake-level fluctuations  
19 including a lake-level decline of almost 10 m due to restricted precipitation and increased water  
20 abstraction for irrigation have been documented between 1950 and 2009 (Popovska and Bonacci,  
21 2007). Recent monitoring programs of the lake revealed  $\sim 31 \text{ mg} \times \text{m}^{-3}$  TP concentration  
22 (Matzinger et al., 2006), and  $\sim 162 \text{ t} \times \text{yr}^{-1}$  TP input from the river tributaries (Krstić, 2012).

### 23 **3 Methodology**

#### 24 **3.1 Core recovery and chronology**

25 Core “5045-1” was recovered at the DEEP site in the central part of Lake Ohrid within the scope  
26 of the SCOPSCO deep drilling campaign in 2013 (Fig. 1). Six parallel boreholes (A to F) at 243  
27 m water depth were drilled down to a maximum sediment depth of 569 m below the lake floor  
28 (m blf) and a total 1526 m of sediment cores were recovered. Comprehensive details of the  
29 drilling procedure, sediment recovery and results from the preliminary analyses of core catcher

1 samples are provided in Wagner et al. (2014a). The age model for the upper 247.8 m of the  
2 composite sequence of the DEEP site for the sediment core and downhole logging data is based  
3 on 11 tephrostratigraphic tie points (first order tie points), and on tuning (bio-)geochemical proxy  
4 data to orbital parameters (second order tie points) (Baumgarten et al., 2015; Francke et al.,  
5 2016). In order to compare the same age intervals in lakes Ohrid and Prespa, we analyzed the  
6 uppermost 37.5 m of the DEEP site sequence, which represent the last ca. 92.0 ka according to  
7 the age-depth model. This period is well-constrained by the occurrence of the Y5 tephra layer at  
8 ca. 39 ka, the Y3 tephra layer at ca. 29 ka, and the Mercato tephra layer at 8.5 ka in the DEEP  
9 site sediment sequence (Leicher et al., 2016).

10 The age-depth model of the 17.7 m long core Co1215 from Lake Prespa is based on 11  
11 tephrochronological tie points, radiocarbon <sup>14</sup>C dating, electron spin resonance (ESR) dating and  
12 comparison with the NGRIP ice core data. An age of ca. 92.0 cal ka BP was extrapolated for the  
13 base of the sequence; details are provided in Damaschke et al. (2013).

### 14 **3.2 Analytical work**

15 The analysis of the 37.5 m sequence from the DEEP site comprises non-destructive X-ray  
16 fluorescence scanning (ITRAX core scanner, Cox Analytical, Sweden) for potassium intensities  
17 (K), and measurements of total carbon (TC) and total inorganic carbon (TIC) by a DIMATOC  
18 100 carbon analyzer (Dimatec Corp., Germany). The total organic carbon (TOC) content was  
19 calculated from the difference between TC and TIC. Total nitrogen (TN) was analyzed using an  
20 elemental analyzer (vario MICRO cube, Elementar Corp.) after combustion at 1150°C and used  
21 to calculate the ratio between TOC and TN (abbreviated as C/N). Biogenic silica concentrations  
22 (BSi) were inferred by means of Fourier Transform Infrared Spectroscopy at the University of  
23 Bern, Switzerland following the method outlined in Vogel et al. (2008) and the calibration after  
24 Meyer-Jacob et al. (2014). All bio(geochemical) analyses are described in more detail in Francke  
25 et al. (2016).

26 Diatom analysis on the DEEP site core was performed on 235 samples in total (resolution 16 cm,  
27 ca. 0.3–0.5 ka), prepared from freeze-dried sediment subsamples according the method of  
28 Cvetkoska et al. (2012). Known aliquots of cleaned samples were used to estimate the absolute  
29 diatom concentrations, “DC” ([n] valves \* 10<sup>7</sup>/g dry sediment), employing the sedimentation tray

1 method of Battarbee (1986). Permanent diatom slides were prepared using Naphrax<sup>®</sup> as  
2 mounting medium. Around 350 diatom valves per slide were counted at 1500x magnification  
3 with an Olympus BX51 microscope. On exception, at least 100 valves per sample were counted  
4 in diatom assemblages with low species diversity and/or concentration. Species identification  
5 followed Levkov et al. (2007), Levkov and Williams (2011, 2012), Cvetkoska et al. (2012,  
6 2014b), Jovanovska et al. (2013), and Pavlov et al. (2013). Diatom accumulation rates, “DAR”  
7 ([n] valves \* 10<sup>6</sup> cm<sup>-2</sup> ka<sup>-1</sup>) were calculated by multiplying the dry sediment accumulation rates,  
8 “SAR” (g cm<sup>-2</sup> ka<sup>-1</sup>) and the DC, Anderson (1989). To assess the preservation quality in the  
9 sequence, the F index of Ryves et al. (2001) was calculated for *Cyclotella fottii* Hustedt as a  
10 proportion of the number of pristine valves and the total number of classifiable valves of the  
11 species. Values of F=0 indicate partial dissolution of all valves and F=1 means ideal  
12 preservation. The variation in the diatom data was explored by detrended correspondence  
13 analysis, “DCA”, and with a gradient length of 2.2, principle component analysis, “PCA” was  
14 appropriate (Jongman et al., 1995). To maximize the apparent variance, PCA was run on species  
15 morphotypes at a sub-species level. The Spearman’s rho rank-correlation test (“stats” version  
16 0.8-2; R Core Team, 2012) was used to analyze the correlation between the dominant diatom  
17 species abundance, the DAR, DC and the (bio)geochemistry data (Table 3). At both sites, the  
18 constrained stratigraphic diatom zones were defined by the incremental sum of squares distance  
19 metric of the CONISS program (Grimm, 1987).

20 The analytical approaches of the geochemistry, isotope, lithology, pollen, and diatom analyses of  
21 Lake Prespa core Co1215 have been extensively described in Aufgebauer et al. (2012), Wagner  
22 et al. (2012), Damaschke et al. (2013), Leng et al. (2013), Cvetkoska et al. (2014a, 2015), and  
23 Panagiotopoulos et al. (2014). Diatom analysis on core Co1215 was carried out on 222 samples  
24 in total (resolution 8 cm, ca. 0.1–0.4 ka) and the variation in the diatom data was analyzed with  
25 DCA based on the >2.5 gradient length (Cvetkoska et al., 2015). Comparative details of the  
26 diatom analytical methods applied to both site cores, DEEP and Co1215, are presented in Table  
27 1.

#### 28 **4 Principal diatom results and environmental controls**

29 In total, 141 diatom species were identified for the last ca. 92.0 ka of the DEEP site core. The  
30 diatom diagram (Fig. 2) displays 31 species and morphotypes, present at >2% in the

1 assemblages. The diatom assemblages are dominated by planktonic taxa, mainly from the genus  
2 *Cyclotella* (Kützing) Brébisson. The facultative planktonic “FP” and benthic life habitat groups  
3 are represented with higher species numbers, but low overall relative proportions due to the large  
4 depth of the coring location, which is beyond the optimal depth for their distribution in the lake.  
5 The most abundant FP and benthic genera are *Amphora* Kützing, *Cocconeis* Ehrenberg,  
6 *Gomphonema* Ehrenberg, *Diploneis* Ehrenberg ex Cleve, *Navicula* Bory, *Staurosira* Ehrenberg  
7 and *Staurosirella* D. M. Williams et F. E. Round. Following previous studies of Reed et al.  
8 (2010), Cvetkoska et al. (2012), and Wagner et al. (2014a), the dominant planktonic taxa were  
9 split in morphotypes, useful to test the link between the long-term ecosystem dynamics and  
10 species evolution in the DEEP site record. *Cyclotella fottii* was initially split in four  
11 morphotypes, based on valve size, and size and shape of the central area, while the *C. ocellata*  
12 Pantocsek complex was split in eight morphotypes based on valve size and number of ocelli in  
13 the central area.

14 Based on previous studies (Stanković 1960; Allen and Ocevski, 1976), the vertical distribution of  
15 the phytoplankton in Lake Ohrid is primarily driven by temperature, in combination with light,  
16 nutrient availability, and water mixing. The last 92.0 ka of the DEEP site diatom record are  
17 generally dominated by three planktonic species with different autecology, *C. fottii*, *C. ocellata*  
18 and *C. minuscula* (Jurilj) Cvetkoska. *Cyclotella fottii* is an oligotrophic, stenothermic species,  
19 adapted to low temperatures; viable populations of the species have been found at more than 100  
20 m water depth, where the light availability is far below the optimal intensity for photosynthesis  
21 and temperature is permanently reduced (Stanković 1960). This indicates that low light  
22 availability is not limiting *C. fottii*, while temperature is likely more important factor for its  
23 vertical distribution and abundance in the phytoplankton. *Cyclotella ocellata* is an ecologically  
24 successful species of wide distribution, though, in Lake Ohrid, it dominates in the epilimnion  
25 during the spring and summer season (Stanković 1960; Zhang et al., 2016). This is the zone of  
26 warmer temperatures, higher light availability, but lower nutrients than the hypolimnion.  
27 However, in Lake Ohrid *C. ocellata* has been interpreted as mesotrophic and an indicator of  
28 increased productivity in comparison to *C. fottii* (Wagner et al., 2009; Lorenschat et al., 2014;  
29 Zhang et al., 2016). In lack of autecological data for *C. minuscula* we relied on previous study of  
30 Cvetkoska et al. (2014a), the findings of Winder et al. (2009), and the comparison with the  
31 geochemical proxies. At the DEEP site, maxima in the relative abundance of *C. minuscula*



1 correspond to the Y5, Y3, and the Mercato tephra layers and peaks in K intensities. This is also  
2 shown by the high-resolution study of the diatom response to the Y5 tephra impact on lakes  
3 Ohrid and Prespa by Jovanovska et al. (2016). The tephra influx/deposition increases the silica  
4 availability, which is enhancing the diatom productivity, consequently leading to strong  
5 competition for nutrients and light resources.

6 At present, most of the FP and benthic species in Lake Ohrid are found between the shallow  
7 littoral zone and ~50 m water depth (Levkov et al., 2007). The overall low relative abundances,  
8 5–15 %, of these species in the DEEP site record result from the coring location, and thus add  
9 little supporting evidence to the interpretation. However, the periods of their slightly increased  
10 abundances during the last ca. 92.0 ka can be interpreted as indication for intensified transport  
11 from the shallower parts of the lake due to wind-induced wave activity and lake-internal currents  
12 (Vogel et al., 2010c).

13 The PCA (Fig. 3, Table 2), displays *C. fottii*, *C. ocellata* (3 ocelli) and *C. minuscula* aligned  
14 along the low–high values range of PCA Axis 1, reflecting the overall trend of temperature-  
15 driven diatom response, due to over-dominance of *C. fottii*. PCA Axis 2 displays clustering of  
16 the *C. ocellata* morphotypes with 4 and 5 ocelli along the positive values, reflecting their  
17 dominance during the last interglacial. For both axes, the Holocene signal appears muted  
18 between ca. 7.0–2.0 ka due to presence of taxa, like *Stephanodiscus transylvanicus* Pantocsek  
19 and *S. cf. minutulus* (Kützing) Cleve et Möller, indicative of nutrient change per se (Kilham et  
20 al., 1986; Wagner et al., 2009; Cvetkoska et al. 2012; Zhang et al., 2016).

21 The DC and DAR (Figs 2, 4) show high positive correlation values with the other  
22 (bio)geochemistry proxies (BSi, TOC, TIC, C/N, see Table 3). In Lake Ohrid sediments, BSi and  
23 TOC are of mainly authigenic origin, indicating the primary productivity in the lake (Wagner et  
24 al., 2009; Vogel et al., 2010b; Francke et al., 2016). In addition, by adjusting the DC to the  
25 sedimentation rates, DAR can be used to qualitatively assess the overall, glacial-interglacial scale  
26 trends of diatom productivity in the record.

27 Regarding the interpretation of the C/N ratios, as an indication for the source of organic matter  
28 ‘OM’, we point to the study of Lacey et al. (2014) on the Lini sequence where it was  
29 demonstrated by means of Rock Eval pyrolysis that in Lake Ohrid, the ‘OM’ is predominantly of

1 pure algal source. The contribution of vascular vegetation to the OM at the DEEP site is also  
2 highly unlikely due to the coring location. Nonetheless, low C/N ratios (~4) during the glacials  
3 can also result from enhanced supply of clay-bound ammonium following mineral soil erosion  
4 rather than algal OM, along with ongoing organic carbon degradation (Holtvoeth et al., 2016).

5 In nature, the biotic response to multiple environmental factors depends on the response to the  
6 single dominant (limiting) driver, and the chance of a driver of large effect being present  
7 increases with the number of drivers (Brennan and Collins, 2015). On a glacial-interglacial scale,  
8 multiple environmental drivers change synchronously with rising and/or declining temperatures,  
9 like the light and nutrient availability. In case of Lake Ohrid, the autecology of the species (e.g.  
10 alternations between *C. fottii* and *C. ocellata* dominance) and the significant correlation of their  
11 relative abundances with the other productivity related proxies (TOC, BSi, DC, DAR) allow us  
12 to infer the orbital timescale trends in the diatom data as primarily driven by the large-scale  
13 temperature changes. Consistently with the interpretation of the diatom response at the Lini site  
14 (core Co1262; Zhang et al., 2016) we do not exclude the influence of other drivers, like nutrients,  
15 wind-induced water mixing, thermal stratification, light etc., but consider these factors as drivers  
16 that may play more important role during millennial timescale events.

## 17 **5 Ecosystems dynamics**

18 In the DEEP site sequence, four major hierarchical diatom zones (DZ 1–4, Fig. 2), each divided  
19 into 4–6 subzones, were identified during the last ca. 92.0 ka. The diatoms are compared to  
20 selected geochemistry data, i.e. the biogenic silica content (BSi) and potassium (K) intensities  
21 inferred from XRF core scanning in the record (Fig. 4). Diatom zones are discussed according  
22 the Marine Isotope Stages (MIS) (Lisiecki and Raymo, 2005). For a detailed overview of the  
23 diatom data and palaeoenvironmental interpretation of Lake Prespa core Co1215, the reader is  
24 referred to Cvetkoska et al. (2014a, 2015).

25 The biological, chemical and physical components of the ecosystems constantly fluctuate,  
26 although sometimes at slow rates (Scheffer and Carpenter, 2003). Therefore, we apply the term  
27 regime, referring to the periods of diatom and bio(geochemistry) inferred ecosystems dynamics  
28 in terms of trophic state and/or lake-level. Changes in the diatom communities' structure related  
29 to changes in the inferred lake's dynamics are considered as regime shifts. In case of Lake

1 Prespa, multiple shifts between planktonic and benthic species-dominated assemblages mark the  
2 stratigraphic diatom data. The dominance of benthic diatom assemblages reflects the lower lake-  
3 level regimes, and the related physical changes in habitat distribution, but does not indicate  
4 higher lake productivity. Indeed, shifts in Lake Prespa trophic regimes are marked by changes  
5 within the planktonic diatom assemblages, (e.g. from *Cyclotella* to *Aulacoseira* dominated  
6 assemblages).

7 Regarding the comparison between both sediment sequences, the age models of Ohrid DEEP site  
8 core and Prespa core, Co1215 are independent and only few direct correlation points via the  
9 occurrences of well-known tephra layers exist (e.g., the Y5 and Mercato tephra). The dating  
10 errors of Ohrid DEEP site core are on the  $2\sigma$  confidence level for the tephra layers, while each  
11 cross-correlation point to orbital parameters include an error of  $\pm 2000$  years (Francke et al.,  
12 2016; Leicher et al., 2016). The dating errors of Lake Prespa core, Co1215 can be estimated to  
13  $<1000$  years for the last 40 ka, but increase significantly to several thousands of years in the  
14 lower part, where ESR dating, poorly known tephrostratigraphy, and tuning of organic matter  
15 content to marine and ice core records provide less well constrained chronological tie points  
16 (Damaschke et al., 2013). Therefore, the comparisons of the diatom data (and inferred  
17 temperature/trophic changes) need to be done carefully. This is especially the case of the single  
18 spikes, which may have easily an offset of several centuries to millennia.

## 19 **5.1 The last interglacial, MIS 5 (92.0–71.0 ka; DZ 4d-b)**

### 20 **5.1.1 MIS 5b (92.0–85.0 ka; DZ 4d)**

21 The MIS 5b period in Lake Prespa diatom record was interpreted as an unstable, transitional  
22 phase of moderate, but variable moisture availability and temperatures. Low-lake-level phases  
23 characterized by oligo-mesotrophic conditions in Lake Prespa occurred at 90.0, 88.4 and 85.6 ka  
24 (Cvetkoska et al., 2015).

25 The basal diatom zone, (DZ 4d) in Lake Ohrid DEEP site core is marked by dominance of the *C.*  
26 *ocellata* complex until 88.7 ka, when *C. minuscula* peaks with ca. 65% relative abundance,  
27 taking over a major part of the epilimnetic diatom productivity to the end of MIS 5b (Figs 2, 4).  
28 The autecology of *C. minuscula* indicates that its dominance was favored by the increased clastic  
29 input in this part of the record, rather than warmer temperatures, as it is also reflected by the

1 corresponding increase of K intensities and SAR (Fig. 4) (Francke et al., 2016). The low DAR  
2 match well with low BSi, TOC and C/N ratio, suggesting less productivity and/or preservation of  
3 the organic matter (Francke et al., 2016). The overall comparison between both records indicates  
4 that both lakes responded to the similar, transitional phase of moderate temperatures, but lake-  
5 level fluctuations in Lake Prespa do not find an equivalent in Lake Ohrid DEEP site.

### 6 **5.1.2 MIS 5a (85.0–71.0; DZ 4c, b)**

7 In Lake Prespa, a climatic drought between 85.0 and 83.0 ka causing a lake-level decline and a  
8 shift to a regime of highest productivity in the record was interpreted from the diatom and pollen  
9 data (Panagiotopoulos et al., 2014; Cvetkoska et al., 2015). A second lake-level low-stand at  
10 Lake Prespa between 77.6 and 76.6 ka, related to decreased effective precipitation, occurred  
11 before the end of the last interglacial, which is marked at 70.2 ka in the diatom record  
12 (Cvetkoska et al., 2015). Sedimentological, hydroacoustic data and bivalves indicate another  
13 lake-level low-stand around 74.0 ka (Wagner et al., 2014b), but this is not reflected in the  
14 Co1215 diatom data.

15 In Lake Ohrid DEEP site diatom record, the period between ca. 85.0 and 78.0 ka is characterized  
16 by the dominance of *C. ocellata* morphotypes with 4 and 5 ocelli (Fig. 2) and high overall DC  
17 and DAR (Figs 2, 4). Similar diversification and presence of different *C. ocellata* morphotypes  
18 during MIS 5, MIS 3 and the Holocene was observed by Reed et al. (2010) and Cvetkoska et al.  
19 (2012). To this point, the hypothesis of climatically triggered species evolution seems quite  
20 plausible, even though revealing the nature of this diversification requires more data from the  
21 earlier Quaternary. The higher productivity inferred from the diatom data in this part of the  
22 record is also seen in the increased BSi content, high TOC values and C/N ratio (Fig. 4). In a  
23 phase of constant SAR and catchment vegetation dominated by mesophilous/montane trees  
24 (Sadori et al., 2016), this implies a temperature-related increase in the diatom productivity. The  
25 diatom signal of warmer climate is also supported by the high TIC content, indicative of  
26 increased endogenic calcite precipitation and/or preservation. A small increase in the abundance  
27 of *C. fottii* at ca. 76.5 ka, correlates with a return to dominance of the typical *C. ocellata*  
28 morphotypes.

1 The diatom and geochemistry data show that the overall dynamics of the Lake Ohrid DEEP site  
2 during MIS 5 are primarily related to the regional trends in climate change, from cold/dry (MIS  
3 5b) to warmer/wetter conditions during MIS 5a (Bar-Matthews et al., 2003; Martrat et al., 2004).  
4 The absence of similar abrupt peaks in both records, DEEP and Co1215, and the lack of  
5 mesotrophic species and bio(geochemical) evidence for a lake-level decline in Lake Ohrid  
6 support the notion that the periods of low lake-levels and highest productivity in Prespa between  
7 85.0 and 71.0 ka did not affect Lake Ohrid, at least in its deepest and central parts.

## 8 **5.2 The last glacial, MIS 4–2 (71.0–14.0 ka; DZ 4–1f)**

### 9 **5.2.1 MIS 4 (71.0–57.0; DZ 4a, 3e, part of DZ 3d)**

10 In Lake Prespa, the glacial conditions during MIS 4 triggered a progressive opening of the  
11 landscape (Panagiotopoulos et al., 2014) and a regime shift to low lake-level, evident by low  
12 plankton abundances and diatom growth restricted to the shallow littoral habitats in a low  
13 productive lake (Cvetkoska et al., 2015).

14 Contrary, the glacial climate signal in Lake Ohrid DEEP site diatom record appears muted  
15 between 70.5–65.3 ka due to the high relative proportions, 30–50 %, of the epilimnetic,  
16 thermophilous, spring/summer species *C. ocellata* (Fig. 2, DZ 4a). At the same time, the low  
17 DAR, BSi and TOC point to low diatom productivity and/or enhanced OM decomposition. High  
18 *C. minuscula* abundance and K intensities in this period (Fig. 4), indicative of enhanced clastic  
19 supply due to catchment erosion, are consistent with climate cooling. Nonetheless, the high  
20 relative abundances of *C. ocellata* between ca. 70.5 and 65.3 ka indicate that probably the  
21 spring/summer temperatures of the epilimnetic zone were still favorable for its growth. This  
22 implies a gradual transition of Lake Ohrid from interglacial to glacial conditions, unlike Lake  
23 Prespa, where the MIS 5/4 transition is marked with a sharp boundary at ca. 70.2 ka.

24 The low proportions of epilimnetic taxa and dominance of *C. fottii* between 65.3 and 60.0 ka  
25 (Fig. 2) in a zone of low preservation quality is indicative of low water temperatures and weak  
26 thermal stratification of the lake. In addition, the high proportions and/or dominance of *C. fottii*  
27 morphotypes >30 µm can be related to ultra(-oligotrophic) conditions, and consequently low  
28 competition and decreased grazing pressure, reflecting the cold glacial climate conditions.  
29 Similarly, large-celled diatom populations have been noted in other ancient lakes (e.g. Baikal,

1 Hövsgöl) and it is supposed that they reflect oligotrophy, in contrast to smaller-celled diatoms  
2 which are more competitive in conditions of limiting nutrients and light (Stoermer et al., 1989;  
3 Edlund et al., 2003).

#### 4 **5.2.2 The interstadial, MIS 3 (57.0–29.0 ka; part of DZ 3d, DZ 3c-a, DZ 2d, c)**

5 In Lake Prespa, the increased moisture availability at the interstadial onset prompted an  
6 increasing lake-level, but the productivity remained low until 38.2 ka. Aridification and/or  
7 cooling were inferred from the diatom and pollen data at ca. 29.0 ka (Panagiotopoulos et al.,  
8 2014; Cvetkoska et al., 2015).

9 The start of the interstadial warming in the DEEP site diatom record is documented between ca.  
10 57.5 and 52.0 ka by a successive increase in the relative proportions of *C. ocellata* (25–35%, Fig.  
11 2) and BSi concentrations (Fig. 4), as well as decreasing K intensities. However, low BSi, TOC,  
12 DAR and DC in assemblages dominated by *C. fottii* and *C. minuscula* between 57.5 ka and 35.0  
13 ka suggest low productivity and/or enhanced decomposition, and similarly, as in Prespa indicate  
14 that the interstadial warming was insufficient to enhance the dominance of the epilimnetic,  
15 thermophilous species. The decline of *C. ocellata* to <5% and increased abundances of *C. fottii*  
16 (Fig. 2) indicate the return to colder conditions after ca. 33.0 ka, culminating in the return to  
17 glacial climatic conditions in Lake Ohrid at ca. 28.3 ka.

18 During MIS 3, a change in the structure and productivity of the diatom assemblages in Lake  
19 Prespa core Co1215 was related to the joined effect of the CI/Y5 tephra and the inferred climate  
20 aridity/cooling at ca. 39.3 ka (Wagner et al., 2012; Leng et al., 2013; Panagiotopoulos et al., 2014;  
21 Cvetkoska et al., 2015).

22 Similarly, the most notable features of MIS 3 in Lake Ohrid are two maxima in DAR and DC  
23 between 39.2–38.8 ka and at ca. 29.0 ka, prompted by ca. 85% and ca. 55% relative abundance  
24 of *C. minuscula*, respectively (Fig. 2). Both events coincide with high K intensities (Fig. 4), and  
25 correspond to the Y5 and Y3 tephra layers in the DEEP site sequence (Leicher et al., 2016). The  
26 diatoms indicate that the Y5 and Y3 tephra deposition disturbed the diatom communities by  
27 creating conditions of low transparency and high silica availability that enhanced the dominance  
28 of small celled *Cyclotella* species, due to the strong competition for nutrients and light resources.  
29 In a case study with leaching experiments on fresh ash samples from Etna eruptions, D’Addabbo

1 et al. (2015) showed that there is only a little impact of tephra on Lake Ohrid water, except for Si  
2 and F saturation. Here, for example, the over-dominance of *C. minuscula* after the Y5 tephra  
3 impact in both lakes (this study, Cvetkoska et al., 2015; Jovanovska et al., 2016), is compensated  
4 by its small valve size (3–7 µm) as superior adaptation enhancing its competitive strength during  
5 such conditions.

### 6 **5.2.3 The last glacial maximum, MIS 2 (29.0–14.0 ka; DZ 2b, a, 1f)**

7 During the LGM, Lake Prespa experienced low productivity and low lake-levels until 15.7 ka,  
8 and the diatom communities were dominated by facultative planktonic and benthic species  
9 (Cvetkoska et al., 2014a, 2015).

10 In Lake Ohrid, minima in DAR, DC, and low BSi content between ca. 29.0 and 13.6 ka (Fig. 2)  
11 indicate low productivity and low temperatures. The low TOC and TIC (Fig. 4) support this  
12 interpretation and suggest enhanced decomposition of the organic matter due to cold/dry glacial  
13 regime (Wagner et al., 2009; Vogel et al., 2010b; Francke et al., 2016). Similar conditions with  
14 winter-ice cover at least in the littoral zone, frequent complete overturn of the lake, substantial  
15 opening of the landscape and reduction of vegetation belts were interpreted from multi-proxy  
16 analyses of other Lake Ohrid cores Lz1120 and Co1202 (Wagner et al., 2009; Vogel et al.,  
17 2010b), and from the DEEP site pollen record as well (Sadori et al., 2016).

18 In terms of diatom response, the similar pattern of glacial assemblages dominated by large,  
19 robust valves of *C. fottii*, were also observed in the previous diatom records from Lake Ohrid  
20 (Wagner et al., 2009; Reed et al., 2010; Cvetkoska et al., 2012). Such similarity indicates that  
21 this is a “glacial-climate” driven regime of low productivity and diversity, and not just an artifact  
22 of taphonomic bias due to weak preservation. In general, both lakes seem to have buffered  
23 climate change during the LGM, since no major changes of the diatom communities, and/or  
24 species extinctions have been observed in the diatom records.

### 25 **5.3 Termination I and the Holocene, MIS 1 (14.0 ka to present; DZ 1e-a)**

26 Unlike the strong response of Lake Prespa to the wet-dry-wet phases between 15.7–12.3 ka due  
27 to the Bølling/Allerød (B/A) and Younger Dryas (YD) (Panagiotopoluos et al., 2013; Cvetkoska  
28 et al., 2014a), a first signal of climate warming subsequent to the LGM in Lake Ohrid derives

1 from an unusual 15% abundance of “Janus”, e.g., heterovalvate cells of *C. ocellata* at ca. 14.0 ka  
2 (Fig. 2). The formation of heterovalvate cells is a phenomenon observed in many diatoms and  
3 often related to variation in nutrients, pH or temperatures (McBride and Edgar, 1998; Stoermer,  
4 1967; Teubner, 1995). Their increased abundances at Lake Ohrid DEEP site core can be  
5 tentatively related to improved temperature and light conditions at the end of the LGM, as  
6 supported by somewhat higher DAR, DC, TOC and BSi between 13.6 and 11.2 ka (Figs 2, 4). At  
7 the same time, low TIC implies frequent mixing of the water column and dissolution of calcite  
8 during cold/dry winters (Vogel et al., 2010b; Francke et al., 2016).

9 Indeed, Lacey et al. (2014) and Zhang et al. (2016) interpreted the changes between 12.3 and  
10 11.8 ka in the bio(geochemical) and diatom dataset of the “Lini” core Co1262 as reflection of the  
11 YD climate reversal. However, this record dates back to 12.4 ka only and does not provide  
12 complete insights into the MIS 2/1 transition. Due to the sampling resolution and presence of  
13 hiatuses, cores Lz1120 and Co1202 from Lake Ohrid (Fig. 1) only provided incomplete or  
14 inconclusive results for this period (Wagner et al., 2009, 2012; Reed et al., 2010; Vogel et al.,  
15 2010a; Cvetkoska et al., 2012). We thus tentatively relate the weakness of response observed at  
16 the DEEP site to a combination of the depth at the coring location, low temperatures, and low  
17 nutrient availability prior to 11.2 ka.

18 While rapid water-level increase in Lake Prespa was inferred between 10.0 and 8.0 ka  
19 (Panagiotopoulos et al., 2013; Cvetkoska et al., 2014a), in Lake Ohrid DEEP site record, the  
20 presence of *Stephanodiscus* species, indicative of increased nutrient availability, and slightly  
21 increased DC and DAR during low SAR imply enhanced productivity between 11.2–9.0 ka. A  
22 comparable trend of increased productivity was observed at the Lini site (Lacey et al., 2014),  
23 while Zhang et al. (2016) found similar trends of water temperature-induced lake productivity  
24 with an interruption between 10.2 and 9.5 ka.

25 Based on core Co1215 diatom data, sustained moisture availability, high lake-levels, and oligo-  
26 mesotrophic regime prevailed in Lake Prespa between 7.9 and 1.9 ka (Cvetkoska et al., 2014a,  
27 2015). At Lake Ohrid DEEP site, maximum BSi content, high TIC and TOC concentrations, and  
28 diatom assemblages co-dominated by *C. ocellata* and *S. transylvanicus* between ca. 8.9–4.8 ka  
29 (Figs 2, 4) indicate high lake productivity. These conditions are rather indicative of warm mid-  
30 Holocene climate, than high nutrient supply from Lake Prespa. Rising water-levels at Prespa



1 could have led to higher water supply to Lake Ohrid, but rising lake-level would have also led to  
2 a decrease of the nutrient concentrations in the water (Matzinger et al., 2006).

3 The mid-Holocene at Lake Ohrid is punctuated by two synchronous peaks of *C. ocellata* (ca. 5–7  
4  $\mu\text{m}$ ) and *C. minuscula*, with sum abundances of ca. 50% and 75% at ca. 8.5 ka and 7.9 ka,  
5 respectively, co-occurring with peaks in K (Figs 2, 4). These pronounced signals are likely  
6 related to the Mercato tephra layer in the DEEP site sequence (Leicher et al., 2016; Francke et  
7 al., 2016) and the “8.2 ka” cold event. But, delineating the exact reasons for the delay of the  
8 peaks in diatoms by ca. 300 or 400 years requires a high-resolution study.

9 Around 1.0 ka, the combination of human impact, climate aridification and decreased summer  
10 precipitation during the “Medieval Climate Anomaly”, MCA was considered as the tipping point  
11 that led to significant lake-level decline at Lake Prespa (Cvetkoska et al., 2014a and references  
12 therein). In fact, Prespa’s decline of ~20 m at time of the MCA, as also evident in the position of  
13 the historic settlements around the lake (Sibinoviç, 1987), is a close analogue to the modelled  
14 lake-level decline of 20 m that can potentially increase the P load in Lake Ohrid by almost 30%  
15 (see Fig. 11 in Matzinger et al., 2006). However, the lack of meso-eutrophic species and low  
16 TOC, in combination with the high water depth at the DEEP site coring location and the sample  
17 resolution do not support enhanced nutrient levels and, by extension, significant influence from  
18 Lake Prespa. Moreover, the co-dominance of *C. ocellata* and *C. minuscula* between 1.5 ka and  
19 present can be related to a combination of warm climate and/or anthropogenic influence at the  
20 DEEP site, as also shown from the diatom study of core Co1262 from the Lini site (Zhang et al.,  
21 2016).

## 22 **6 Ecosystems internal dynamics and interactions**

### 23 **6.1 Adaptive cycles: thresholds, regimes, resistance and resilience**

24 From the above interpretation and comparison between the lakes, shifts in the diatom  
25 communities, and by inference the lakes’ response, are triggered by critical thresholds at  
26 different scales of intensity and by different external factors. As pointed out by Cvetkoska et al.  
27 (2015) while the diatom response in Lake Prespa is primarily driven by moisture availability, the  
28 multi-proxy approach in this study shows that regime shifts in Lake Ohrid are tipped by  
29 temperature thresholds, inducing changes in wind activity, light and nutrient availability.

1 Apart from the encountered differences, two adaptive cycles can be identified at orbital scale:  
2 “interglacial and interstadial” and “glacial” cycle. The glacial cycle of Lake Prespa is  
3 characterized by much lower productivity than the interglacial/interstadial cycle and dominated  
4 by facultative planktonic and benthic species (Cvetkoska et al., 2015). The lake experienced  
5 multiple regime shifts on sub-orbital time scale, resulting in low or high lake-levels, and changes  
6 between (oligo-) meso- and eutrophic trophic states.

7 Lake Ohrid’s glacial cycle is mainly dominated by the hypolimnetic planktonic *C. fottii* and is  
8 characterized by a lower productivity than the interglacial/interstadial cycles (Fig. 2). Within  
9 these cycles, short-term regime shifts in the diatom communities occur at sub-orbital time scale,  
10 but the lake remained ultra- to oligotrophic. Based on the presented proxy data, there is no  
11 indication for lake-level changes throughout the entire studied period.

12 More importantly, all diatom data show that during the last 92.0 ka both lakes did not underwent  
13 catastrophic ecosystem collapses imprinted by loss of the diatom communities, and/or  
14 ecosystems functionality, such as happened at other ancient lakes during the LGM, like Baikal  
15 and Hövsgöl (Karabanov et al., 2004; Khurshevic et al., 2006).

16 Assessing the capacity of both ecosystems to absorb disturbances and reorganize in order to  
17 retain their functional and structural characteristics implies that both lakes have different  
18 response mechanisms. The concept of the “ecosystems resilience” (Holling, 1973) is widely  
19 accepted, but also controversial because of its definition of mechanisms and components  
20 (Carpenter et al., 2001; Scheffer, 2001; Walker et al., 2004; Lake, 2013). Here, we consider the  
21 “resistance” and “resilience” as different components of the ecosystems response to disturbance;  
22 by interpreting the resistance in this case as the capacity of the ecosystem to absorb and  
23 withstand the disturbance and the resilience as the capacity to reorganize and/or restore or  
24 “recover” from the disturbance (Westman, 1978; Webster et al. 1983). As evident from the  
25 diatom and bio(geochemical) data, and the comparison of the lakes (Fig. 4), the amplitude of  
26 Lake Ohrid’s response, though, appears smaller and in some cases shifting more gradually into  
27 the new regime, like for example at the MIS 5/4 transition (Figs 2, 4).

28 This implies a high capacity of Lake Ohrid to absorb the disturbances and retain, and/or  
29 reorganize its structure, in order to maintain its functionality. Similarly, once pushed into a new

1 regime, a tipping point of much higher intensity is required so the system can reorganize and/or  
2 restore a similar dynamic regime. In the DEEP site record, this pattern is evident from the  
3 gradual, prolonged “recovery” periods after climate disturbances, as the gradual transition and  
4 muted response to the two-step deglaciation pattern of Termination I (cf. Lowe et al., 2008).

5 Relatively low intensity disturbances in Lake Prespa, however, are occasionally already  
6 sufficient to trigger high-amplitude changes in lake-levels and productivity (DCA Axes 1 and 2  
7 in Fig. 4), emphasizing a lower lake capacity to absorb disturbance. An example is the abrupt  
8 shift from oligo-mesotrophic to eutrophic conditions during MIS 5b (Fig. 4). Interestingly, the  
9 relatively short periods of “recovery” after these climate-induced disturbances, like for example  
10 the rapid lake-level increase after the LGM, demonstrates that Lake Prespa is a resilient  
11 ecosystem. These lakes’ specific differences can be attributed to their different physical  
12 properties and hydrological balances.

## 13 **6.2 Lake ecosystem interactions**

14 Understanding the interactions between lakes Prespa and Ohrid requires assessment of several  
15 parameters which influence the dynamics of their hydrological connection through the karst  
16 system of Mt. Galičica: i) Lake Prespa water balance, ii) the P load and TP concentration in the  
17 lake, iii) the underground outflow from Lake Prespa, and iv) the P load from Lake Prespa to  
18 Lake Ohrid. Matzinger et al. (2006) assessed these parameters, demonstrating that currently  
19 about 20% of Lake Ohrid water inflow and 7% of the P load originate from Lake Prespa.  
20 However, a large part, ~ 65%, of the P load from Lake Prespa is retained in the karst aquifers.  
21 Lake Prespa is highly sensitive to water loss and a 5 m lake-level decrease corresponds to a  
22 ~25% loss of the total lake volume, with significantly increasing concentration of dissolved  
23 nutrients (Matzinger et al., 2006).

24 In order to understand the role of Lake Prespa as possible driver of lake-level and/or nutrient  
25 shifts in Lake Ohrid over the past 92.0 ka, we explored the panarchy within the “sister lake  
26 system” by identifying possible cross-scale linkages between the adaptive cycles and regime  
27 changes of both lakes as lower-scale entities of the landscape dynamics.

28 From the comparison of the multi-proxy inferred lake-levels and productivity of both lakes (see  
29 Ecosystem dynamics, Fig. 4), it is evident that the low lake-level and eutrophic conditions at

1 Prespa during the interglacials, such as during MIS 5a and the MCA, do not counterpart with  
2 similar regimes at Lake Ohrid DEEP site. On the contrary, Lake Ohrid recharge was probably  
3 reduced during the glacial, when lake-level at Prespa was low and discontinuous permafrost  
4 prevailed in the catchment (Belmecheri et al., 2009). Indeed, Lacey et al. (2014) already  
5 discussed the potential scenario for reduced water input from Prespa during the glacials resulting  
6 in lower lake-water  $\delta^{18}\text{O}$ . The palynological analyses of the last ca. 0.5 Ma from the DEEP site  
7 sequence (Sadori et al., 2016) and pollen based reconstructed LGM temperatures (Peyron et al.,  
8 1998) support the existence of discontinuous permafrost and suggest that the karst aquifer system  
9 was not completely shut off during the glacials. Distinct water-level reductions are not evident in  
10 the DEEP site diatom record from the last ca. 92.0 ka, nor have been observed in the  
11 geochemistry and diatom data from the previous studies covering the last interglacial-glacial  
12 cycle (Wagner et al., 2009; Reed et al., 2010; Cvetkoska et al., 2015; Zhang et al., 2016).

13 As pointed by Matzinger et al. (2006) the P load to Lake Ohrid changes with decreasing Lake  
14 Prespa water level, but it highly depends on the following factors: (i) a smaller subaquatic  
15 outflow is reducing the P input, (ii) declining volumes of Lake Prespa lead to increase in P  
16 concentration in the lake and (iii) shorter hydraulic residence time of Lake Prespa decreases its P  
17 concentration. On glacial-interglacial scale, this would imply that potentially higher P supply to  
18 Ohrid due to lower lake-level in Prespa is probably compensated by smaller subaquatic outflow.

19 On a Quaternary scale, it can be argued that climate disturbances leading to changes in lake-level  
20 and trophic states in Lake Prespa were probably insufficient to affect Lake Ohrid's productivity.  
21 This decoupling results from the high resistance of Lake Ohrid, or at least the DEEP site, against  
22 the disturbances which could have been introduced from Lake Prespa. Moreover, the data shows  
23 that from MIS 5b to present, Lake Ohrid did not undergo regime changes introduced by Lake  
24 Prespa and did not experienced a phase of collapse, or release ( $\Omega$ ) as defined by Holling (1986).

## 25 **7 Conclusions**

26 From the presented data, it is evident that apart from the climatically triggered regime shifts, the  
27 lack of similar abrupt peaks in the lake-levels and/or productivity in the sediment records of  
28 lakes Ohrid and Prespa, there is no clear indication for a direct link between the lakes' regime  
29 changes. While Lake Prespa shifted from shallow eutrophic to deep (oligo-)mesotrophic regimes

1 and vice versa, Lake Ohrid changed between ultra oligo- and oligotrophic, deep lake system over  
2 the last glacial-interglacial period.

3 In general, both lakes display different response mechanisms to external disturbances. While  
4 Lake Ohrid is more resistant to climate change, Lake Prespa is very sensitive, but a resilient  
5 ecosystem, and recovers in relatively short time. Nonetheless, both lakes did not experience loss  
6 of the diatom communities and/or catastrophic ecosystem collapses.

7 The overall comparison provides sufficient evidence to disregard the theory of Prespa-dependent  
8 regime shifts in Ohrid, at least in its central and deepest parts. This may give future research on  
9 Lake Ohrid a more confident interpretation of the earlier parts of the DEEP site sediment  
10 sequence in terms of climate change.

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1 Table 1. Locations, sediment recovery and summary of methods used for the diatom analyses of  
 2 cores 5045-1 from Lake Ohrid and Co1215 from Lake Prespa.

	Lake Ohrid ‘5011-1’	Lake Prespa Co1215
Drill site location	N 41°02’57’’, E 020°42’54’’	N 40° 57’ 50’’, E 20° 58’ 41’’
Water depth (m)	243	14 m
Length of composite record (this study; m)	37.5	17.7 m
Age (ka BP)	92.0	92.0
Sample resolution for diatom analysis (cm, ka)	16, ca. 0.3–0.5	8, ca. 0.1–0.4
Total number of slides	235	222
Stratigraphic plots of relative diatom abundances	Tilia/TGView v. 1.7.16. (Grimm, 1987)	
Diatom assemblages zonation	CONISS (Grimm 1987)	
Multi-proxy stratigraphic diagrams	C2(Juggins 1991–2007)	
Ordination	PCA (SD = 2.2), Canoco 5 (ter Braak and Šmilauer 1997–2014)	DCA (SD > 2.5), R “stats” v. 0.8-2 (R Core Team 2012)

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5 Table 2. Summary results of the unconstrained PCA ordination of 235 diatom samples from  
 6 Lake Ohrid DEEP core and the DCA ordination of the 222 samples from Lake Prespa core  
 7 Co1215 (modified from Cvetkoska et al., 2015).

8 SD (PCA) = 2.2, SD (DCA) > 2.5

Lake Ohrid, PCA Axes	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.44	0.13	0.09	0.06
Explained variation (cumulative)	44.46	57.08	66.30	72.24
Lake Prespa, DCA Axes	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.47	0.23	0.17	0.14
Decorana values	0.50	0.32	0.12	0.08

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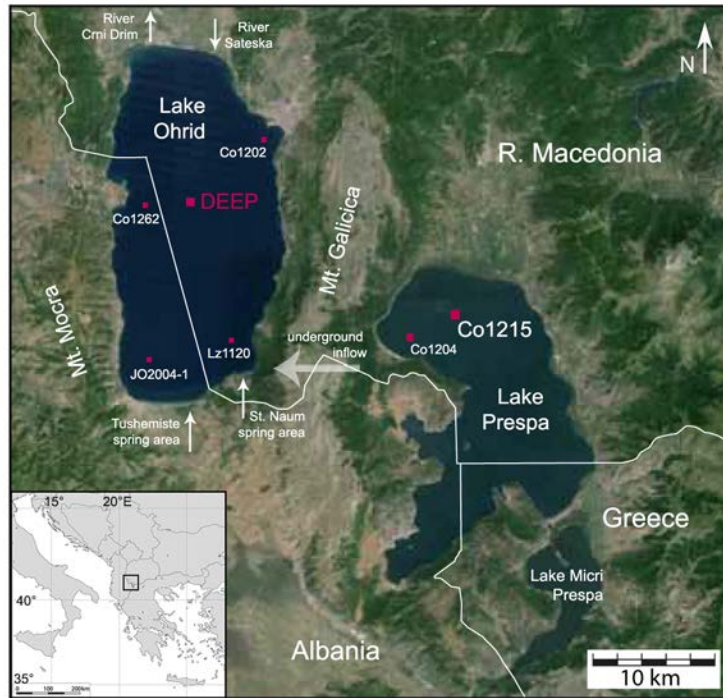
2 Table 3. Spearman's rho ( $\rho$ ) coefficient values for the correlations between selected diatom data,  
3 and geochemical proxies from Lake Ohrid DEEP site core.

<b>Spearman's correlation</b>	<i>Cyclotella fottii</i>	<i>C. ocellata</i>	<i>C. minuscula</i>	<b>DC</b>	<b>DAR</b>
TIC (%)	-0.48	0.47	0.32	0.45	0.35
TOC (%)	-0.36	0.50	/	<b>0.64</b>	<b>0.50</b>
BSi	-0.45	<b>0.53</b>	0.30	<b>0.75</b>	<b>0.7</b>
C/N	-0.40	<b>0.53</b>	/	<b>0.63</b>	0.47
K	0.38	-0.41	/	<b>-0.60</b>	<b>-0.43</b>

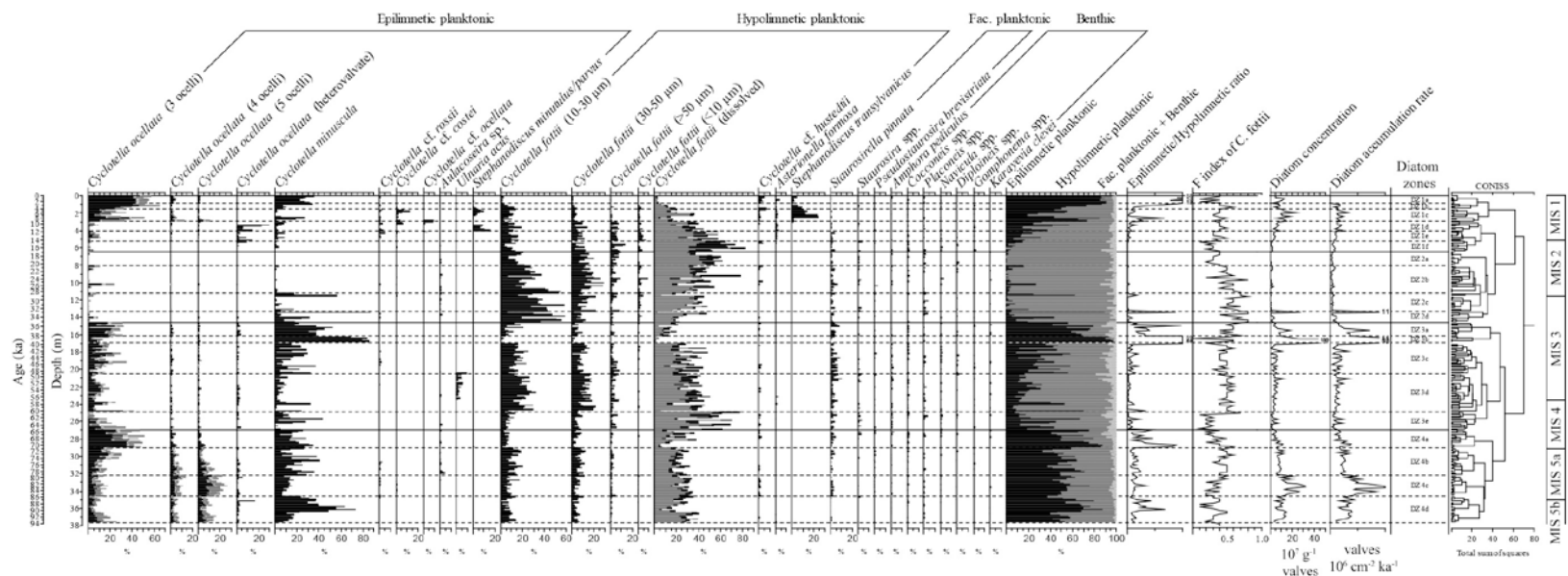
4 All presented values are significant at  $p < 0.05$

5 "/" low values and/or no significant correlation

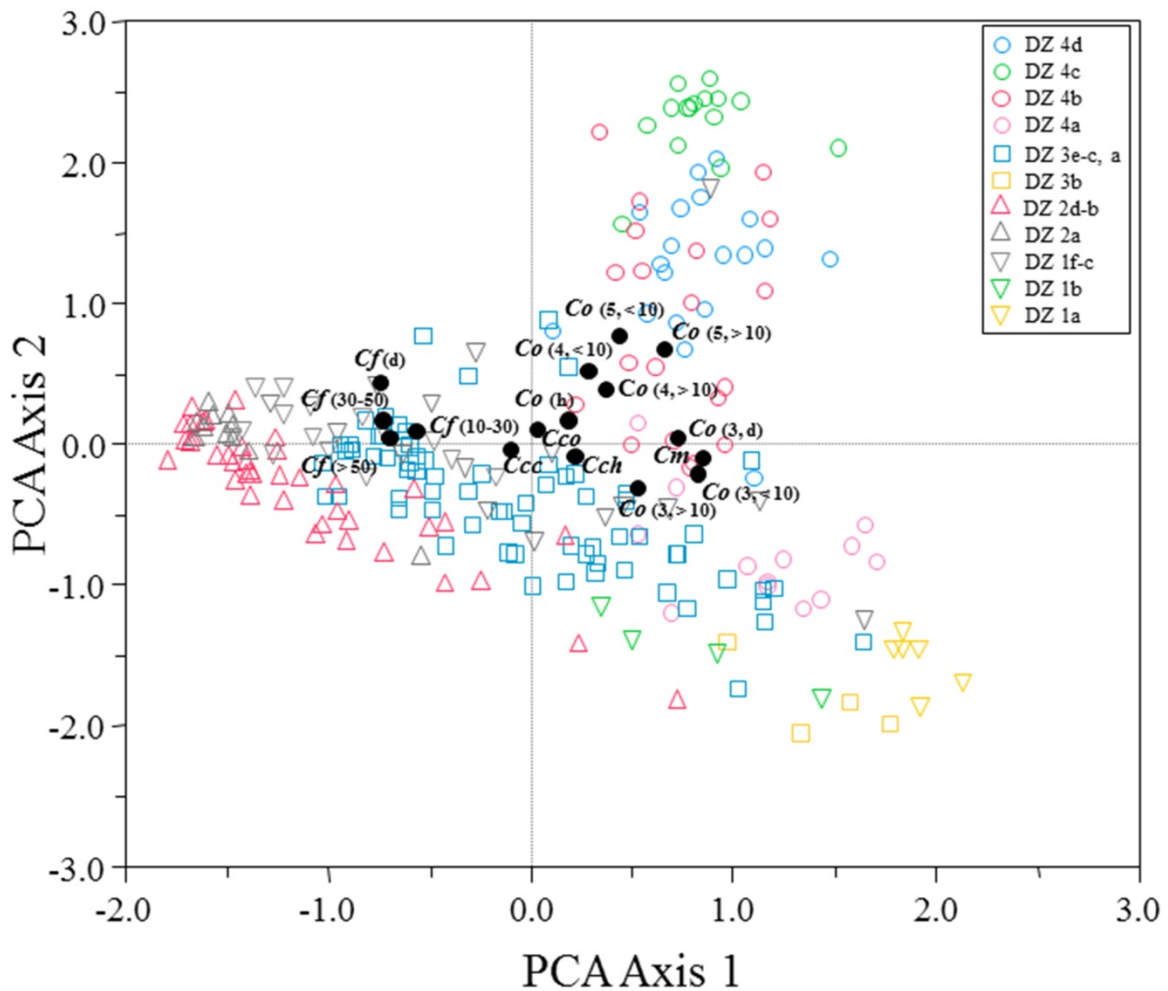
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13 Fig. 1. Map of the northern Mediterranean region showing the location of lakes Ohrid and  
14 Prespa. Marked in purple are the locations of the cores: JO2004 (Belmecheri et al., 2009), Lz  
15 1120, Co1202, Co1262 and from field campaigns at Lake Ohrid between 2005–2012, cores  
16 Co1204 and Co1215 recovered from Lake Prespa during field campaigns in 2009 and 2011;  
17 (Wagner et al., 2009, 2010, 2012) and the DEEP site core 5045-1, retrieved during the  
18 SCOPSCO deep drilling campaign at Lake Ohrid in 2013 (Wagner et al., 2014a). Modified from  
19 Francke et al. (2016).



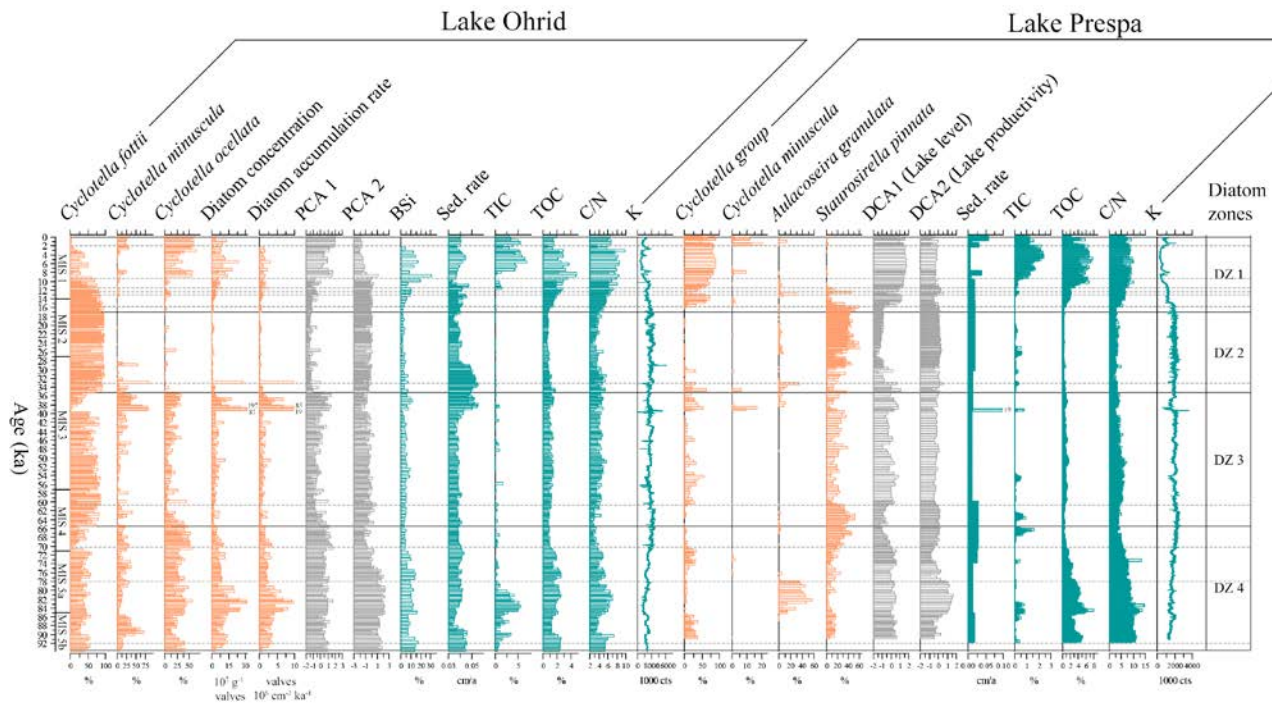
1  
 2 Fig 2. Stratigraphic diatom diagram showing species with >2 % abundance in Lake Ohrid DEEP site core 5045-1, F index of  
 3 *Cyclotella formii*, diatom concentrations ([n] valves  $\times 10^7/g$  dry sediment) and diatom accumulation rates ([n] valves  $\times 10^6/cm^2/ka$ ).  
 4 Diatom zone boundaries are defined by CONISS, Marine Isotope Stages (MIS) boundaries after Lisiecki and Raymo (2005).



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2 Fig. 3. Biplot of PCA Axis 1 vs. PCA Axis 2 sample and species scores from Lake Ohrid DEEP  
 3 site core (5045-1). Symbol keys for diatom zones and sub-zones in top right corner. Selected  
 4 diatom taxa and morphological splits of *Cyclotella fottii* (*Cf*, size in  $\mu\text{m}$ ) and *Cyclotella ocellata*  
 5 (*Co*) are plotted, where numbers in brackets refer to size splits ( $\mu\text{m}$ ) and ocelli number in *C*.  
 6 *ocellata*. Explanation: *Cm* = *Cyclotella minuscula*, *Cch* = *Cyclotella cf. hustedtii*, *Ccc* =  
 7 *Cyclotella cf. costei*, *Cco* = *Cyclotella cf. ocellata*, (d)=dissolved.

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 2 Fig. 4. Comparison diagram between Lake Ohrid core 5045-1 and Lake Prespa core Co1215 showing the relative abundance data of  
 3 selected diatom species, the PCA 1 and 2 sample scores; DC and DAR, the sediment accumulation rates (SAR) and the biogenic silica  
 4 content (BSi, % weight) of Lake Ohrid core DEEP. Prespa DCA 1 and 2 sample scores represent lake level and productivity.  
 5 Displayed are the diatom zones (DZ 1–4) of Lake Ohrid core DEEP; the dotted lines mark the six major diatom zones of Lake Prespa  
 6 core Co1215 (Cvetkoska et al., 2015). Selected geochemical proxies from Lake Ohrid core DEEP: total organic carbon (TOC), total  
 7 inorganic carbon (TIC), C/N ratio and potassium (K); data from Francke et al. (2016); Lake Prespa core Co1215: TOC, TIC, C/N  
 8 ratio, K; data from Wagner et al. (2012) and *S. pinnata* (%), data from Cvetkoska et al. (2015); The MIS boundaries are from Lisiecki  
 9 and Raymo (2005).

