

1 **Differential resilience of ancient sister lakes Ohrid and Prespa to**  
2 **environmental disturbances during the Late Pleistocene**

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16

17 **Abstract**

18 Ancient lakes, like lakes Ohrid and Prespa on the Balkan Peninsula, have become model  
19 systems for studying the link between geological and biotic evolution. Recently, the scientific  
20 deep drilling project “Scientific Collaboration on Past Speciation Conditions in Lake Ohrid”  
21 (SCOPSCO) was initiated to better understand the environmental, climatic and limnological  
22 evolution of the lake. It revealed that Lake Ohrid experienced a number of environmental  
23 disturbances during its ca. 2.0 million year long history. They are comprised of disturbances  
24 that lasted over longer periods of time (“press events”) such as Heinrich events, as well as  
25 sudden and short disturbances (“pulse events”) like the deposition of volcanic ashes. The  
26 latter includes one of the most severe volcanic episodes during the Late Pleistocene; the  
27 eruption of the Campanian Ignimbrite (known as Y-5 marine tephra layer) from the Campi  
28 Flegrei caldera, dated at 39.6±0.1 thousand years ago. The event is recorded by the deposition

1 of a ca. 15 cm thick tephra layer in sediment cores of lakes Ohrid (DEEP-5045-1) and Prespa  
2 (Co1204). Coincidentally, this pulse event is superimposed by the Heinrich H4-event,  
3 40.1–38.1 thousand years ago.

4 In the current paper, diatoms were used as proxies to compare the responses of these lakes to  
5 the Y-5 (pulse) and the H4 (press) disturbances. Based on stratigraphically constrained  
6 incremental sum of squares cluster (CONISS) and unconstrained Partitioning Around  
7 Medoids (PAM) analyses, we found little evidence that diatom community compositions in  
8 either lake responded to the H4 event. However, the Y-5 influx caused clear and rapid diatom  
9 community changes. After the initial response, community compositions in Lake Ohrid and,  
10 to a lesser extent, in Lake Prespa slowly returned to their quasi pre-disturbance state.  
11 Moreover, there is no evidence for disturbance-related extinction events. The combined  
12 evidence from these findings suggests that lakes Ohrid and Prespa likely did not experience  
13 regime shifts. It is therefore concluded that both lakes show resilience to environmental  
14 disturbance. However, it seems that Lake Ohrid is more resilient than Lake Prespa as the  
15 recovery of diatom communities is more pronounced and as its estimated recovery time is  
16 only ca. 1,100 years vs. ca. 4,000 years in Lake Prespa. The reasons for the differential  
17 responses remain largely unknown, but differences in geology, lake age, limnology, and  
18 intrinsic parameters of the diatom proxies may play an important role.

## 19 **1 Introduction**

20 Ancient lakes, i.e., extant lakes that have continuously existed since before the last glacial  
21 maximum (Albrecht and Wilke, 2008), have become model systems for studying the link  
22 between geological and biological evolution over extended periods of time. For some ancient  
23 lakes, such as Baikal (Russia) and Hövsgöl (Mongolia), it has been demonstrated that the  
24 evolution of their species was largely shaped by massive environmental disturbances, like  
25 extreme lake-level fluctuations and glacial-interglacial cycles (Karabanov et al., 2004).

26 However, for other ancient lakes, like the sister lakes Ohrid and Prespa on the Balkan  
27 Peninsula, the link between geological and biotic evolution is not well understood. In order to  
28 better understand the environmental, climatic, and limnological evolution of Lake Ohrid, the  
29 SCOPSCO project was initiated. Early results revealed that the lake experienced a number of  
30 environmental disturbances during its ca. 2.0 million year (Ma) long history (Lindhorst et al.,  
31 2015). Some of these events lasted over longer periods of times and covered, for example,  
32 glacial/interglacial cycles (Wagner et al., 2014) or Heinrich events (Wagner et al., 2010), i.e.,

1 episodes of massive iceberg discharges that caused cooling of the North Atlantic during the  
2 last glacial period (Bond et al., 1993). These events presumably intensified the aeolian  
3 activity, lowered the temperature, and increased the aridity in the Ohrid region (Wagner et al.,  
4 2010). From a biological perspective, long-lasting disturbances (> several centuries) are  
5 referred to as “press disturbances” (Niemi et al., 1990). In contrast, sudden disturbances with  
6 a short and clearly defined duration (< few decades) are called “pulse disturbances” (Niemi et  
7 al., 1990). Examples include landslides (Lindhorst et al., 2014), earthquakes (Hoffmann et al.,  
8 2010; Wagner et al., 2012b; Lindhorst et al., 2015), and volcanic ash depositions (Sulpizio et  
9 al., 2010; D’Addabbo et al., 2015).

10 The eruption of the Campanian Ignimbrite from Campi Flegrei caldera, dated at  $39.6 \pm 0.1$   
11 thousand years (ka) ago, is considered to be one of the most severe volcanic events during the  
12 Late Pleistocene (De Vivo et al., 2001; Fedele et al., 2003; Costa et al., 2012; Fitzsimmons et  
13 al., 2013; Leicher et al., 2015). The corresponding Y-5 tephra plume dispersed across the  
14 Mediterranean and central Europe, and even reached the Black Sea, the Russian plain and the  
15 northern African coast (see Fig. 1A; Fitzsimmons et al., 2013). The tephra also discharged  
16 into lakes Ohrid and Prespa, directly through atmospheric precipitation and/or indirectly  
17 through catchment runoff (sensu Fitzsimmons et al., 2013). The volcanic event is recorded by  
18 a ca. 15 cm thick and well-preserved tephra layer in sediment cores of both lakes (Sulpizio et  
19 al., 2010; Wagner et al., 2012a; Leicher et al., 2015).

20 It has been suggested that the interaction of volcanic ash deposition with a receiving lake  
21 triggers perturbations, primarily through the effect of tephra weathering, but also through  
22 changes in pH, mineral concentration, organic matter input, and short-term light deprivation  
23 (e.g., Harper et al., 1986; Barker et al., 2003; Telford et al., 2004; Cruces et al., 2006; Urrutia  
24 et al., 2007; D’Addabbo et al., 2015). Depending on the magnitude of the disturbance and the  
25 resilience of the respective ecosystem (i.e., the amount of disturbance an ecosystem can  
26 tolerate without changing its regime; Holling et al., 1973, 1986; Scheffer and Carpenter,  
27 2003; Baho et al., 2014), lake biota may react with extinction events and/or changes in  
28 community structures and functions.

29 Some organisms, like diatoms (single-celled siliceous algae), react very sensitively to pulse  
30 disturbances, such as tephra depositions (e.g., Harper et al., 1986; Barker et al., 2003; Cruces  
31 et al., 2006). Moreover, they are remarkably well-preserved in the sediment records of lakes  
32 Ohrid and Prespa (e.g., Reed et al., 2010; Cvetkoska et al., 2012, 2014, 2015a; Zhang et al.,

1 2015). These aspects make diatoms excellent proxies for studying how the lakes responded to  
2 environmental disturbances. In fact, previous sediment core analyses suggest alterations in  
3 diatom assemblage structure and abundances due to tephra influxes in both lakes (Cvetkoska  
4 et al., 2012, 2014, 2015a, b). However, the low temporal resolution did not allow the diatom  
5 data to be linked to distinct pulse events or used to estimate recovery periods (i.e., the time an  
6 ecosystem needs to return to pre-disturbances conditions; the recovery period serves as  
7 measure for resilience strength; Carpenter, 2013). Therefore, it remains unclear how the lakes  
8 responded to such changes, and whether there were differences in response.

9 Given this lack of knowledge, the general goal of this paper is to use diatom community data  
10 from the sediment records of lakes Ohrid (core DEEP-5045-1) and Prespa (core Co1204) as a  
11 proxy to comparatively study the responses of these lakes to one of the most severe pulse  
12 disturbance events during the late Pleistocene – the Y-5 tephra influx. Our specific objectives  
13 are to study:

- 14 1) Whether lakes Ohrid and Prespa had the resilience to tolerate this disturbance without  
15 changing their regimes (i.e., without exceeding a critical threshold). Operational criteria  
16 for resilience are the lack of disturbance-related extinction events in the diatom record  
17 and a subsequent return of diatom communities to a quasi pre-disturbance state.
- 18 2) If resilience can be demonstrated for one or both lakes, whether there are differences in  
19 resilience strength between the two systems. The operational criterion for resilience  
20 strength is the length of the recovery period, which is measured as the time the diatom  
21 communities need to return to their quasi pre-disturbance state.

22 Lake Ohrid has long been considered to have a high level of ecosystem stability (sensu  
23 Stanković, 1960; Föller et al., 2015), principally due to its depth, age, and peculiar karst  
24 limnology. Hence, our working hypothesis is that Lake Ohrid is more resilient to  
25 environmental disturbances than Lake Prespa.

26 Coincidentally, the Y-5 tephra deposition ( $39.6 \pm 0.1$  ka ago) is superimposed by the Heinrich  
27 H4-event that occurred 40.1–38.1 ka ago (see Wutke et al., 2015 for the temporal gap  
28 between Y-5 and H4), and left signatures in the sediment records of both lakes (Wagner et al.,  
29 2010; Panagiotopoulos et al., 2014; Cvetkoska et al., 2015b). This provides a unique  
30 opportunity to obtain information on the differential effect of a short pulse and a longer press  
31 disturbance event.

1 We believe that this study can contribute to one of the major goals of the SCOPSCO deep  
2 drilling program – to evaluate the influence of major geological events on the evolution of  
3 endemic taxa in Lake Ohrid (Wagner et al., 2014). It might also provide insight into the  
4 response of lakes to massive environmental disturbances.

## 5 **2 Material and methods**

### 6 **2.1 Site description**

7 Ancient lakes Ohrid and Prespa are located on the Balkan Peninsula (Fig. 1) within karstic  
8 steep-sided graben systems with a rift-formation origin (Stanković, 1960; Matzinger et al.,  
9 2006a; Albrecht et al., 2008). They are separated by the Galicica Mountain range, but share an  
10 underground connection (Matzinger et al., 2006a).

11 Lake Ohrid is located at 693 m a.s.l., covers a surface area of 358 km<sup>2</sup>, and has a maximum  
12 water depth of 293 m (Lindhorst et al., 2014). The hydrological regime of the lake is highly  
13 regulated with inflow from karstic aquifers (sublacustrine and surface springs), while the  
14 outflow occurs via the River Crn Drim (Matzinger et al., 2006a). Oligotrophic Lake Ohrid is  
15 phosphorus limited (Allen and Ocevski, 1977) with an average total phosphorus (TP)  
16 concentration of 4.5 mg·m<sup>-3</sup> (Matzinger et al., 2007) and total nitrogen (TN) concentration of  
17 171–512 mg·m<sup>-3</sup> (Watzin et al., 2002). The lake's silica (SI) concentration is < 200 mg·m<sup>-3</sup> in  
18 the trophogenic zone during summer (Stanković, 1960), the average water pH and water  
19 conductivity are 8.48 and 208 µS cm<sup>-1</sup>, respectively (Schneider et al., 2014). The average  
20 Secchi depth is ca. 14 m (Matzinger et al., 2006b).

21 Neighbouring Lake Prespa is situated ca. 160 m above Lake Ohrid (849 m a.s.l.), has a  
22 surface area of 254 km<sup>2</sup>, and a maximum water depth of 58 m (Matzinger et al., 2006a;  
23 Albrecht et al., 2008). The water balance is regulated through inputs from Lake Mikri Prespa,  
24 catchment and river runoff, groundwater, and direct precipitation. Water output occurs  
25 through karstic aquifers, irrigation, and water surface evaporation (Matzinger et al., 2006a).  
26 Mesotrophic Lake Prespa has an average TP concentration of 31 mg·m<sup>-3</sup> (Wagner et al.,  
27 2010), an average TN concentration of ca. 2000 mg·m<sup>-3</sup>, an average water pH of ca. 8.3, and  
28 an average Secchi depth of ca. 2.6 m (Levkov et al., 2007).

### 29 **2.2 Core recovery and geochronology**

30 During the SCOPSCO deep-drilling campaign in spring 2013, a 569 m long core (DEEP-  
31 5045-1) was retrieved from the central part of the Ohrid Basin at ca. 243 m water depth (Fig.

1 1B; Wagner et al., 2014). To date, only sediments of the upper 247.8 meter composite depth  
2 (mcd) of the DEEP site sequence have become available (Francke et al., 2015). The age-depth  
3 model of the composite sequence, which is based on 11 tephrostratigraphic tie points (1st  
4 order tie points) and on tuning of biogeochemical proxy data to orbital parameters (2nd order  
5 tie points), suggest that this sequence covers the last 637 ka (Baumgarten et al., 2015; Francke  
6 et al., 2015). In this study, we focused on the Y-5 tephra layer at  $39.6 \pm 0.1$  ka ago, according  
7 to the age estimations provided by Leicher et al. (2015).

8 The Lake Prespa core (Co1204) was recovered in October 2011 from the northwestern part of  
9 the lake (Fig. 1B; Wagner et al., 2010). The age model of the 17.76 m long sequence was  
10 established using radiocarbon dating of macrofossil remains as well as three major tephra  
11 layers as control points. The resulting age model covers ca. 48 ka (Sulpizio et al., 2010;  
12 Wagner et al., 2010).

### 13 **2.3 Diatom analyses**

14 In total, 193 sediment sub-samples were collected and analysed from the Ohrid and Prespa  
15 cores (18.19–14.19 mcd and 9.21–7.47 mcd, respectively). In the Prespa core, the tephra  
16 boundaries were sharp and clearly distinguishable. In the Ohrid core, only the lower boundary  
17 was clear; the upper boundary appeared relatively diffuse, presumably due to post-  
18 depositional tephra input from the catchment area, bioturbation, and/or drilling artefacts.  
19 Within and around the actual tephra layer, the cores were sliced in 5 mm intervals,  
20 corresponding to a temporal resolution of approx. 10 years. With increasing distance above  
21 and below the tephra layer, resolution was decreased first to 4 cm and then to 16 cm.

22 For diatom analyses, weighed samples of freeze-dried sediments were acid-cleaned with cold  
23 35%  $\text{H}_2\text{O}_2$  and 10% HCl, and left overnight for the removal of carbonates. The samples were  
24 then boiled in a water bath for 2 h in 37% HCl for oxidization of the organic matter (Renberg,  
25 1990; Cvetkoska et al., 2012). The treated samples were rinsed several times with distilled  
26 water and subsequently centrifuged for removing the products of the oxidation reaction.  
27 Defined aliquots of the cleaned samples were settled onto coverslips and then mounted on  
28 glass slides using Naphrax®. In each sample, random transects were selected and 200–400  
29 diatom valves per slide were counted and identified by one of us (EJ) at 1000x magnification  
30 with a Carl Zeiss, Axioplan 2 microscope equipped with a Nikon D5700 digital camera. All  
31 samples and microscopic slides are hosted at the University of Giessen Systematics and  
32 Biodiversity Collection (UGSB), Department of Animal Ecology and Systematics, Justus

1 Liebig University, Giessen, Germany. Diatom identification followed Levkov et al. (2007),  
2 Levkov and Williams (2011), Cvetkoska et al. (2012, 2014), Jovanovska et al. (2013), and  
3 Pavlov et al. (2013).

4 Diatom counts were converted to percentages and displayed using the package rioja 0.9.3  
5 (Juggins, 2014) for the R statistical environment 3.2.1 (R Core Team, 2015). For  
6 characterizing diatom based stratigraphic zones, a constrained incremental sum of squares  
7 cluster analysis (CONISS; Grimm, 1987) was performed in rioja.

8 In addition, we determined community response phases based on distinct changes in  
9 community structures using the stratigraphically unconstrained clustering approach of  
10 Partitioning Around Medoids (PAM; Kaufman and Rousseeuw, 1990). PAM clusters pair-  
11 wise Bray-Curtis dissimilarities (Bray and Curtis, 1957) of communities into k groups of  
12 minimum intragroup sum-of-distances, with an optimum of k chosen by the silhouette  
13 criterion (Kaufman and Rousseeuw, 1990). The PAM analyses were performed with the  
14 package cluster 2.0.3 (Maechler et al., 2013) for R. Using Bray-Curtis dissimilarities, we  
15 performed a metric multidimensional scaling in R and plotted the scores of the first axes  
16 according to their respective age.

17 Recovery times were calculated by estimating the time differences between the same group-  
18 membership assigned by the PAM analyses before and after the tephra influx. As the diatom  
19 communities sampled in Lake Ohrid are biased towards planktonic species due to the deep-  
20 water coring location, we determined recovery times both for planktonic and overall  
21 communities in lakes Ohrid and Prespa.

### 22 **3 Results**

23 In total, 94 and 213 diatom species were identified in the cores of lakes Ohrid and Prespa,  
24 respectively. Due to the difference in water depth of the coring locations (ca. 243 m for Lake  
25 Ohrid vs. 14 m for Lake Prespa), planktonic species were dominant in Lake Ohrid, especially  
26 members of the genus *Cyclotella*. Though many benthic species had been found, they only  
27 occurred in low abundance. In Lake Prespa, planktonic and benthic species were roughly  
28 balanced (Figs. 2 and 3).

29 Some planktonic species showed a high morphological variability with respect to valve size,  
30 shape of the central area, and number of ocelli in the central area (e.g., *Cyclotella fottii* and

1 *Cyclotella ocellata*). In order to fully cover the magnitude of potential community changes,  
2 we assigned them to distinct morphotypes and identification units (see Figs. 2 and 3).

### 3 **3.1 Identification of community response phases and diatom zones**

4 The stratigraphically unconstrained PAM analyses identified three major community response  
5 phases in lakes Ohrid and Prespa: A phase that corresponds to pre-disturbance conditions  
6 (pre-tephra-disturbance phase; Fig. 4, also see the lower blue bars in Figs. 2 and 3), a distinct  
7 disturbance phase (tephra-disturbance phase; Fig. 4, also see the green and yellow bars in  
8 Figs. 2 and 3), and a phase in which communities had returned to quasi pre-disturbance  
9 conditions (post-tephra-disturbance phase; Fig. 4, also see the upper blue bars in Figs. 2 and  
10 3).

11 The stratigraphically constrained CONISS analyses identified three distinct diatom zones  
12 together with several subzones each for lakes Ohrid (ODZs) and Prespa (PDZs). They largely  
13 corresponded to the pre-tephra-disturbance phase (ODZ 3b–a and PDZ 3b–a), the tephra-  
14 disturbance phase (ODZ 2b–a and PDZ 2, 1d–b), and the post-tephra-disturbance phase (ODZ  
15 1b–a and PDZ 1a) (see Figs. 2 and 3).

### 16 **3.2 Diatom analyses of the Ohrid core**

#### 17 **3.2.1 Pre-tephra-disturbance phase (ODZ 3b–a; age 43.00–39.60 ka)**

18 Diatom subzones ODZ 3b–a (Fig. 2) were characterized by the presence of the planktonic  
19 taxa *Cyclotella fottii*, *C. ocellata* complex, and *C. minuscula*, of which *C. fottii* was the most  
20 dominant with up to 50% relative abundance. In contrast, the benthic and facultative  
21 planktonic species had abundances of up to 10% when taking the whole profile into account.  
22 Examples include *Staurosirella* spp., *Staurosira* spp., *Amphora* spp., *Cocconeis* spp.,  
23 *Diploneis* spp., *Planothidium frequentissimum*, and *Navicula* spp.

#### 24 **3.2.2 Tephra-disturbance phase (ODZ 2b–a; age 39.60–38.50 ka)**

25 Within ODZ 2b, *C. fottii* and *C. ocellata* were replaced by *C. minuscula* (Fig. 2), which  
26 reached almost 100% relative abundance. Abundances of facultative planktonic and benthic  
27 species (e.g., *Navicula* spp., *Diploneis* spp., *Staurosirella* spp.) gradually decreased to values  
28 < 5%. The subzone ODZ 2a is marked by the absence of benthic species, and the slight  
29 decline of *C. minuscula* to ca. 70 % relative abundance.

#### 30 **3.2.3 Post-tephra-disturbance phase (ODZ 1b–a; age 38.50–34.75 ka)**



1 Diatom subzone ODZ 1b (Fig. 2) is marked by a decline of *Cyclotella minuscula* down to ca.  
2 20%, reaching relative abundance of 10% towards the upper subzone boundary ODZ 1a. In  
3 contrast, *C. fottii* and *C. ocellata* gradually increase in abundances of up to 75% and 30%,  
4 respectively. The latter decreased to < 5% in ODZ 1a. The facultative planktonic taxa,  
5 especially *Staurosirella* spp., were present at abundances of ca. 5% in ODZ 1b, and gradually  
6 decreased to ca. 2% relative abundance towards the upper ODZ 1a boundary. The combined  
7 abundances of benthic species remained low with < 2%; they almost disappeared in ODZ 1a.

### 8 **3.3 Diatom analyses of the Prespa core**

#### 9 **3.3.1 Pre-tephra-disturbance phase (PDZ 3b–a; age 43.00–39.60 ka)**

10 The diatom assemblages in this zone were dominated by facultative planktonic species (e.g.,  
11 *Staurosirella pinnata*, *Staurosira venter*, and *Pseudostaurosira brevistriata*) and the benthic  
12 species *Eolimna submuralis* (Fig. 3). The latter reached relative abundances between 5 and  
13 20%. The planktonic species *C. minuscula* was present at ca. 2% abundance in PDZ 3a.  
14 Benthic species were consistently low in abundance.

#### 15 **3.3.2 Tephra-disturbance phase (PDZ 2, PDZ 1d–b; age 39.60–37.00 ka)**

16 In zone PDZ 2, facultative planktonic species (e.g., *S. pinnata*, *Staurosirella* sp. 1, *Fragilaria*  
17 cf. *capucina*, and *P. brevistriata*) were replaced by planktonic species (e.g., *C. minuscula* with  
18 up to 50%, *C. ocellata* with up to 30%, and *C. paraocellata* with up to 5% relative  
19 abundances). Note that *Cyclotella* aff. *minuscula* had relative abundances of up to 30%. Most  
20 benthic species decreased in abundances (e.g., *E. submuralis*, *Placoneis balcanica*,  
21 *Khursevichia* cf. *explorata*); and only few increased (e.g., *Fallacia* spp., *Hippodonta* spp.,  
22 *Nitzschia* spp., and *Navicula* spp.).

23 Subzones PDZ 1d–b are characterized by a decline of *C. minuscula* abundances to < 5%, and  
24 a renewed dominance of facultative planktonic and benthic species. However, some  
25 planktonic species maintained their abundances throughout PDZ 1d–b. *Cyclotella* aff.  
26 *minuscula* sharply decreased in subzone PDZ 1d and almost disappeared in PDZ 1c–b.  
27 *Asterionella formosa* and *S. minutulus* increased the abundances in subzone PDZ 1c and  
28 decreased in subzone PDZ 1b. The planktonic *Cyclotella ocellata* and *C. paraocellata*, and  
29 the benthic *E. submuralis* increased their relative abundances in subzones PDZ 1c–b.

#### 30 **3.3.3 Post-tephra-disturbance phase (PDZ 1a; age 37.00–34.75 ka)**

1 The diatom subzone PDZ 1a, is characterized by a gradual decline of planktonic species (e.g.,  
2 *C. paraocellata* and *C. ocellata*), dropping to < 2% relative abundances in the upper part of  
3 this subzone. *Cyclotella minuscula* decreased to an abundance of < 2% at the upper subzone  
4 boundary. In contrast, benthic species moderately increased in their abundances; only few  
5 decreased (e.g., *Hippodonta* spp., *Fallacia* spp., *Nitzschia* spp.).

### 6 **3.4 Community composition analyses and estimations of recovery times**

7 The first ordination axis of the metric multidimensional scaling analyses indicates that the Y-  
8 5 tephra deposition caused very rapid changes in the diatom communities of lakes Ohrid (Fig.  
9 4A) and Prespa (Fig. 4B). Given that the communities in Lake Ohrid's DEEP core were  
10 dominated by planktonic species, the respective curves for overall (i.e., planktonic and  
11 benthic communities) and planktonic communities in Fig. 4A showed similar patterns over  
12 time. After the drastic change of community composition, coinciding with the tephra  
13 deposition, communities reverted to a quasi pre-disturbance state (green bar in Fig. 2).

14 In Lake Prespa, where planktonic and benthic species were roughly balanced, the overall  
15 community structure (grey curve in Fig. 4B) rapidly changed, following the Y-5 event and  
16 then gradually approached a quasi pre-disturbance state. Both the stratigraphically  
17 unconstrained PAM and the constrained CONISS analyses, suggest recovery through a direct  
18 and prolonged phase (see the yellow and green bars on Figs. 3 and 4). PAM suggests a  
19 recovery until the beginning of subzone PDZ 1a. In this study, we used PAM as a  
20 representative for the recovery period. For the planktonic communities of Lake Prespa, the  
21 change coinciding with the tephra deposition was not as abrupt. However, the return to the  
22 pre-eruption community state occurred even more gradually.

23 The diatom communities in both lakes Ohrid and Prespa did not display a strong response to  
24 the onset of the H4 event 40.1 ka ago. In Lake Ohrid, H4 specific PAM clusters or CONISS  
25 zones could not be detected. However, in Lake Prespa a distinct CONISS subzone coincides  
26 with H4 (see Fig. 3).

27 The Ohrid communities had converted back to the quasi pre-disturbance state shortly before  
28 the cessation of the H4 event 38.1 ka ago (grey and black dashed lines in Fig. 4A; also see the  
29 upper blue bar in Fig. 2), whereas this process in the Prespa communities extended beyond  
30 the end of the Heinrich event (grey and black dashed lines in Fig. 4B; also see the upper blue  
31 bar in Fig. 3). The PAM analyses clearly show that the Ohrid and Prespa communities did

1 return to their quasi pre-disturbance states (see the upper blue bars in Figs. 2 and 3 and the  
2 PAM clusters in Fig. 4), indicating that no regime shift occurred.

3 According to the age models of the two cores, the recovery times (i.e., the time differences  
4 between the same group-membership assigned by the PAM analyses before and after the  
5 tephra influx) for planktonic communities in lakes Ohrid and Prespa were ca. 1,100 and ca.  
6 4,000 years, respectively (Fig. 4), following the Y-5 tephra influx.

## 7 **4 Discussion**

8 Our results indicated only mild effects of the H4-event on diatom community compositions in  
9 lakes Ohrid and Prespa, though the impact is slightly greater in the latter one. In contrast, the  
10 Y-5 influx caused clear and rapid responses in both lakes (Fig. 4). Whereas the overall  
11 community composition in Lake Prespa partially recovered within a few decades, mostly  
12 driven by benthic species, and then slowly returned to the quasi pre-disturbance state over an  
13 extended period of time, the planktonic community needed a longer period of time for  
14 recovery (compare the grey and black curves in Fig. 4B).

15 In Lake Ohrid, both overall and planktonic community composition indicated similar  
16 reactions to the Y-5 tephra influx (Fig. 4A), owing the fact that planktonic communities  
17 strongly dominated in the lake due to the depth of the drilling location.

18 When comparing changes in planktonic communities in lakes Ohrid and Prespa, overall  
19 patterns are similar. An initial rapid response phase was followed by a phase in which  
20 communities slowly returned to the quasi pre-disturbance state. However, as noted above, the  
21 quasi pre-disturbance state in the Ohrid communities was reached shortly before the H4  
22 cessation, whereas the Prespa communities recovered only long after the end of the Heinrich  
23 event.

### 24 **4.1 Diatom responses to disturbances in Lake Ohrid**

25 The communities in the Ohrid core were mainly characterized by planktonic species (Fig. 2).  
26 Although at low abundances, the benthic species likely indicate wind induced water currents,  
27 water mixing, and/or sediment redistribution in the lake (cf. Vogel et al., 2010b; Cvetkoska et  
28 al., 2015a). The latter process might explain the prevalence of benthic species at 243 m water  
29 depth. Almost all of the identified benthic taxa have been reported from contemporary  
30 communities in the littoral zones (0–60 m water depth) of Lake Ohrid (Levkov et al., 2007;  
31 Levkov and Williams, 2012; Jovanovska et al., 2013; Pavlov et al., 2013). The benthic species

1 slightly increased in abundances with the onset of the H4, indicating the possibility of  
2 intensified wind transport and mixing of the water column during the H4 stadial (40.1–38.1  
3 ka ago). However, distinct changes in community composition were not revealed. The minor  
4 influence of the H4 event on Lake Ohrid is also reflected in the previously published  
5 geochemical data (Wagner et al., 2010).

6 In contrast to the onset of this press disturbance event, the Y-5 pulse disturbance event  
7 triggered an immediate reaction by the lake's diatom communities. The deposition of silica-  
8 rich volcanic ashes (ca. 60% SiO<sub>2</sub>, Sulpizio et al., 2010) likely had an impact on the water  
9 chemistry by increasing the silica content in the water column (D'Abbabbo et al., 2015).  
10 Indications of these changes are the rapid replacement of the dominant hypolimnetic *C. fottii*  
11 with the epilimnetic *C. minuscula* (Fig. 2). The latter species (only 3–7 μm in diameter) has  
12 high silica incorporating rates and low transparency preferences, which makes it a strong  
13 competitor for light and nutrients under tephra-altered environmental conditions (Cvetkoska  
14 et al., 2014, 2015a; Zhang et al., 2015). These conditions were temporally maintained before  
15 communities gradually returned to the quasi pre-disturbance state. During the recovery period  
16 (until ODZ 1b), the nutrient pool of the lake likely changed, yet continued silica enrichment  
17 from the catchment area may still have played a role. Whereas *C. minuscula* slightly  
18 decreased in abundance during the recovery period, other planktonic species maintained their  
19 elevated abundances until ODZ 1b.

20 The point of return to quasi pre-disturbance state was probably reached in subzone ODZ 1b,  
21 when nutrient levels in the water column likely had recovered and silica levels had decreased.  
22 This is indicated by the increase in abundances of the endemic *C. fottii* to pre-tephra-  
23 disturbance levels. As the recovery of planktonic communities was achieved prior to the end  
24 of the H4 event (ca. 1,100 years), we here suggest that this press disturbance possibly  
25 amplified the impact of the Y-5 and prolonged the recovery, but did not prevent it.

#### 26 **4.2 Diatom responses to disturbances in Lake Prespa**

27 In contrast to the diatom communities in the Ohrid core, Prespa communities were  
28 characterized by significant abundances of both planktonic and benthic species. During the  
29 pre-tephra-disturbance phase (42.9–39.6 ka ago), the ordination (Fig. 4B) indicates only little  
30 change in overall community composition. However, planktonic communities did show  
31 moderate fluctuations in structure even before the onset of the H4 event 40.1 ka ago.  
32 Moreover, the geochemical properties of the lake changed only moderately with the onset of

1 the H4 (Wagner et al., 2010). Therefore, it remains difficult to quantify the immediate  
2 community impact of this press disturbance event.

3 The Y-5 associated silica fallouts (PDZ 2) rapidly altered the water chemistry by increasing  
4 the silica content (ca. 60% SiO<sub>2</sub> in the tephra layer, Sulpizio et al., 2010) in the water column,  
5 and likely affected the nutrient pool in the lake. The increased silica content favoured the  
6 growth of planktonic species like *C. minuscula*, *C. ocellata*, *C. paraocellata*, and *C. aff.*  
7 *minuscula*. The latter taxon has never been reported before. It occurs exclusively during the  
8 recovery period and failed to establish permanently.

9 In contrast to the planktonic species, epiphytic and facultative planktonic species like  
10 *Cocconeis pseudothumensis*, *Staurosirella pinnata*, and *Pseudostaurosira brevistriata*  
11 temporally decreased in relative abundance (i.e., for a period of few decades). This may be  
12 explained by a short-term destruction of the littoral macrophytic habitats as a result of the Y-5  
13 influx.

14 In subzone PDZ 1d, nutrient levels likely increased in the water column, favouring species  
15 with high phosphorus and silica preferences, such as *Stephanodiscus minutulus* (Kilham et al.,  
16 1986). Due to increased nutrient availability and water transparency (Cvetkoska et al., 2014,  
17 2015b), benthic species (e.g., *Diploneis exigua*, *Placoneis balcanica*, *Karayevia clevei*)  
18 increased in abundances. Moreover, the increased relative abundance of *Asterionella formosa*  
19 in subzone PDZ 1c indicates nutrient pool recovery (Holm and Armstrong, 1981). However,  
20 the overall community structure did not return to the pre-disturbance state until PDZ 1a (see  
21 the upper blue bar in Fig. 3).

22 This long recovery period (planktonic communities) of almost 4,000 years – exceeding the  
23 end of the H4 event – is striking and may reflect the joint impact of a press (H4) and a pulse  
24 (Y-5) event. Although we see a little effect at the initiation of the H4 event, it probably  
25 amplified the Y-5 impact and prolonged the recovery period of diatom communities in Lake  
26 Prespa. The combined effects of the H4 and Y-5 events are corroborated by previously  
27 published palynological data (Panagiotopoulos et al., 2014).

28 Interestingly, Cvetkoska et al. (2014) found evidences that the H2, H5, and H6 events  
29 influenced the diatom communities in Lake Prespa. Yet their low-resolution study could not  
30 disentangle the almost simultaneous impacts of the H4 and Y-5 events.

1 From the current study, it becomes clear that the changes in community composition are  
2 largely caused by the Y-5 event. However, relating our data to those of Cvetkoska et al.  
3 (2015a), we suggest that Heinrich and volcanic events, which are very different in nature,  
4 may drive communities in different directions.

### 5 **4.3 Disturbance related regime shifts in diatom communities**

6 The first specific objective of this study was to evaluate whether lakes Ohrid and Prespa had  
7 the resilience to tolerate environmental disturbances without changing their regimes (i.e.,  
8 without exceeding a critical threshold sensu Scheffer and Carpenter, 2003). Our operational  
9 criteria for assessing resilience were i) the lack of disturbance-related extinction events in the  
10 diatom records and ii) a subsequent return of diatom communities to their quasi pre-  
11 disturbance state.

12 The data obtained are informative in this regard: we do not see extinction events directly  
13 related to the H4 and/or Y-5 events (see Figs. 2 and 3). Moreover, community compositions  
14 appear to subsequently return to their quasi pre-disturbance states (see Fig. 4A, B). However,  
15 whereas the latter patterns are clear for both overall and planktonic communities in Lake  
16 Ohrid as well as for overall communities in Lake Prespa, the return to the quasi pre-  
17 disturbance state in planktonic communities in Lake Prespa is less obvious (see the black  
18 curve in Fig. 4B). Accordingly, neither lake underwent regime shifts. We, therefore, conclude  
19 that lakes Ohrid and Prespa have a high ecosystem resilience. This is in contrast to findings  
20 from some lakes where instability was hypothesized to increase susceptibility to regime shifts  
21 (cf. Spanbauer et al., 2014).

22 However, the drivers for the resilience in lakes Ohrid and Prespa remain unclear at this stage.  
23 They are likely multifactorial, involving parameters such as water depth, hydrological regime,  
24 and chemical buffer processes. As the resilience of the lakes was indirectly inferred using  
25 diatom communities as proxies, the results were likely also affected by intrinsic biotic  
26 parameters of the diatoms.

### 27 **4.4 Differential resilience in lakes Ohrid and Prespa**

28 Given that ecosystem resilience has been demonstrated for both lakes, our second specific  
29 objective was to investigate whether there were differences in resilience strength between the  
30 two systems. As an operational criterion for resilience strength, we used the length of the

1 recovery periods (sensu Carpenter, 2013). Our working hypothesis was that Lake Ohrid is  
2 more resilient to environmental disturbances than Lake Prespa.

3 Concluding from the length of the recovery periods, Lake Ohrid is more resilient than Lake  
4 Prespa (ca. 1,100 years vs. ca. 4,000 years, respectively). The reasons for the differential  
5 responses of the two neighbouring lakes remain less well understood (also see Wagner et al.,  
6 2010; Leng et al., 2013), but as discussed above, may be related to differences in their  
7 geology, limnology, and lake age.

#### 8 **4.5 Limitations and outlook**

9 We believe that the data and conclusions provided in the present paper are robust. The  
10 analyses show that the diatom communities in both lakes recovered after major environmental  
11 disturbances and that there are differences in recovery times between the two lakes.

12 Nonetheless, given the nature of our data, a number of limitations have to be noted. Firstly,  
13 the resolution of the age models used and potential bioturbation may hamper the precise  
14 estimation of community change above and below the actual tephra deposition. Additionally,  
15 our findings are based on single core locations in lakes Ohrid and Prespa. Moreover, as  
16 former littoral core sediments from Lake Ohrid were characterized by the presence of hiatuses  
17 (e.g., Wagner et al., 2008; Vogel et al., 2010a), we had to use a core that was retrieved from a  
18 greater water depth (see Fig. 1). This, in turn, resulted in a bias of the Ohrid communities  
19 towards planktonic species. Finally, our study lacked high-resolution geochemical core data  
20 for the timeframe of interest.

21 In order to mitigate these problems, we used relative time information (i.e., diatom zones) for  
22 describing community changes, whenever possible. We focused in the comparative resilience  
23 and recovery time analyses on changes in the planktonic communities, as they were directly  
24 comparable in the two lakes (see black curves in Fig. 4). We also used previously published  
25 Y-5 geochemical data, especially SiO<sub>2</sub> content in the tephra layers (Sulpizio et al., 2010).

26 Despite these limitations, the response curves for the planktonic diatom communities in Ohrid  
27 and Prespa were similar. Differences mainly concerned the duration of the individual phases  
28 of community response. We take this as another indication for the robustness of our data.

29 Nevertheless, given the interesting and partly unexpected patterns observed, we encourage  
30 future projects that aim at studying resilience processes in lakes Ohrid and Prespa in more  
31 detail. This would not only be of interest from a conceptual, but also from an applied point of

1 view relative to current and future human impact scenarios for these model lakes (e.g.,  
2 Kostoski et al., 2010).

3 In particular, we recommend high-resolution studies of more and/or other pulse and press  
4 disturbance events (e.g., earthquakes, lake level fluctuations, orbital-suborbital climate  
5 changes) in order to better understand the interplay of multiple disturbances. Given the  
6 unexpectedly long recovery times found in this study, we also suggest studying post-  
7 disturbance patterns in higher resolution and over extended periods of time.

## 8 **5 Conclusions**

9 In the present study, we demonstrated that diatom communities in ancient lakes Ohrid and  
10 Prespa reacted strongly to one of the most severe volcanic eruptions in the central  
11 Mediterranean region during the Late Pleistocene – the Y-5 event ( $39.6 \pm 0.1$  ka ago). After a  
12 rapid initial response, community compositions slowly returned to their quasi pre-disturbance  
13 states. In contrast to the Y-5 pulse disturbance event, signatures of the superimposed H4 press  
14 disturbance event were less distinct. However, the latter likely contributed to the extended  
15 recovery periods of  $> 1,000$  years seen in both lakes. In the case of Lake Prespa, the H4 event  
16 may have prolonged full recovery from the Y-5 pulse event until after the end of the H4.

17 Nonetheless, the data suggest that the communities in lakes Ohrid and Prespa likely did not  
18 experience regime shifts (but see above for the complex pattern in planktonic communities in  
19 Lake Prespa). We, therefore, conclude that both lakes show a high resilience to environmental  
20 disturbances. However, the estimated recovery times, which can be used as measure for  
21 resilience strength, differed between lakes Ohrid and Prespa (i.e., ca. 1,100 vs. ca. 4,000  
22 years, respectively). This finding supports our working hypothesis that Lake Ohrid is more  
23 resilient to environmental disturbances than Lake Prespa. The exact reasons for the  
24 differential responses remain unknown, but differences in geology, lake age, limnology, as  
25 well as intrinsic parameters of the diatom proxies may play an important role.

26 We do note some limitations of our study such as the resolution of the age models and the  
27 different depths of the drilling locations, causing a bias towards planktonic species in Lake  
28 Ohrid. Nonetheless, we believe that the results presented here are robust as indicated by  
29 similar response curves for the overall communities in lakes Ohrid and Prespa. Yet, the curves  
30 for the planktonic communities show no concurrence due to the complex response of Lake  
31 Prespa.



1 We also believe that this study provides important new insights into the response of ancient  
2 lakes to (multiple) environmental disturbances. Moreover, it contributes to one of the main  
3 goals of the SCOPSCO deep drilling program – to evaluate the influence of major geological  
4 events onto the evolution of endemic taxa in Lake Ohrid.

5

#### 6 **Author contribution**

7 E.J., C.A. and T.W. conceived the study. E.J. and A.C. conducted the lab work. E.J., A.C.,  
8 and T.H. performed the community analyses. The manuscript was written by E.J. and T.W.  
9 with contributions from all co-authors. All authors gave final approval for publication.

10

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24

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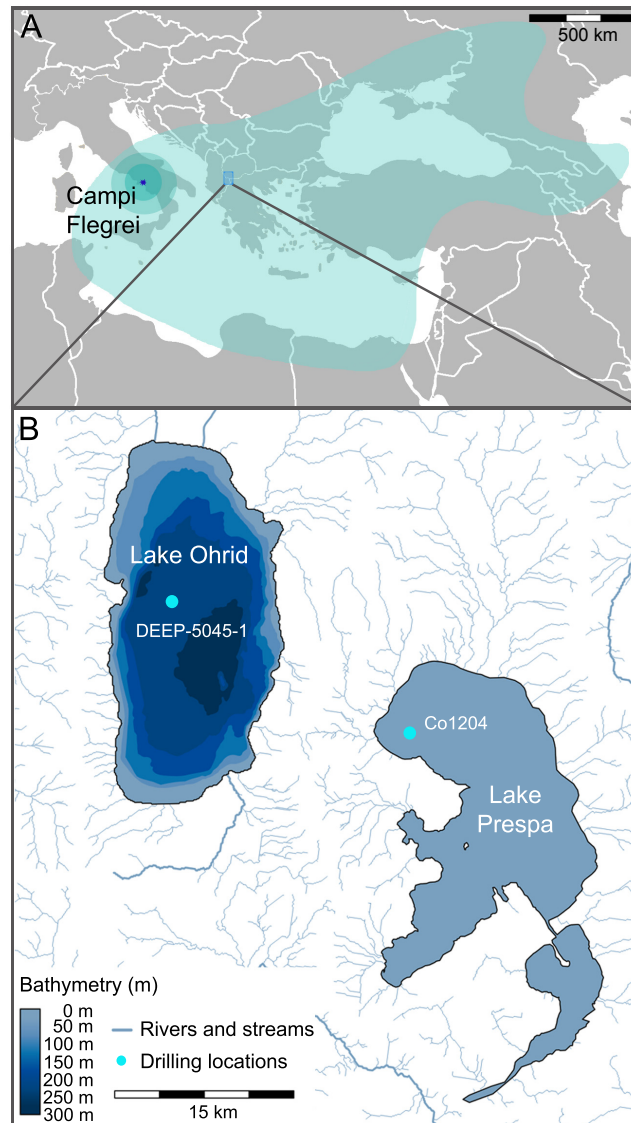
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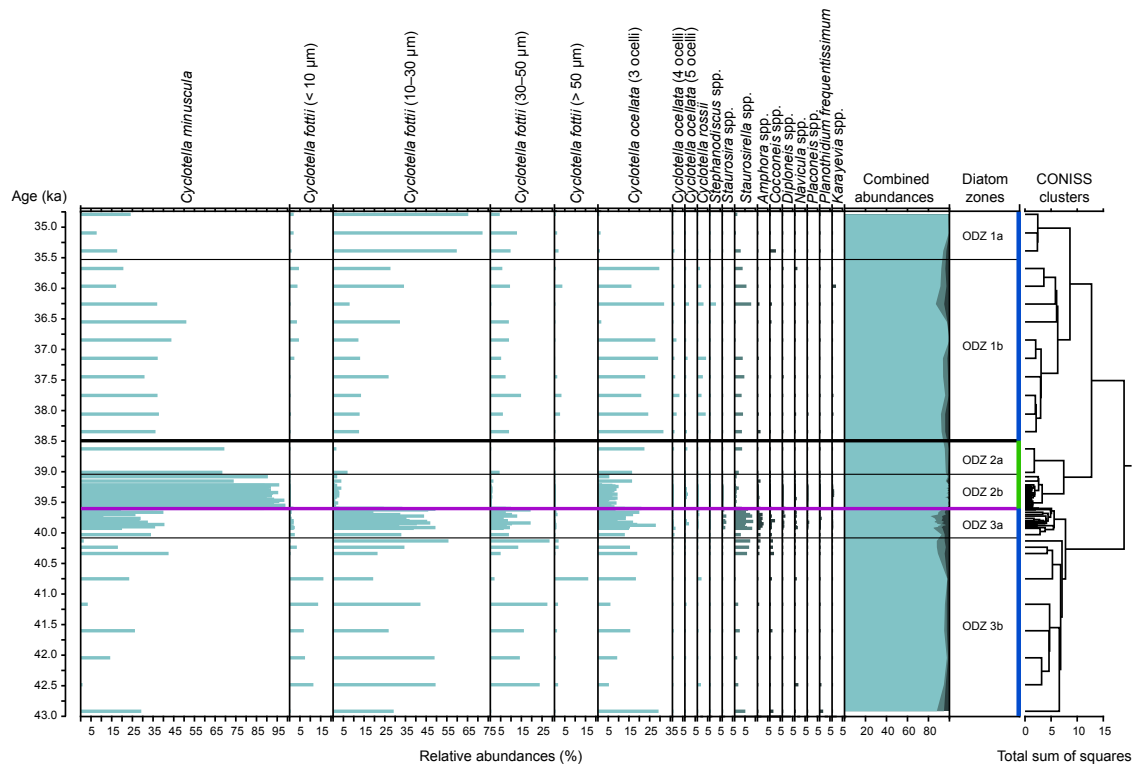
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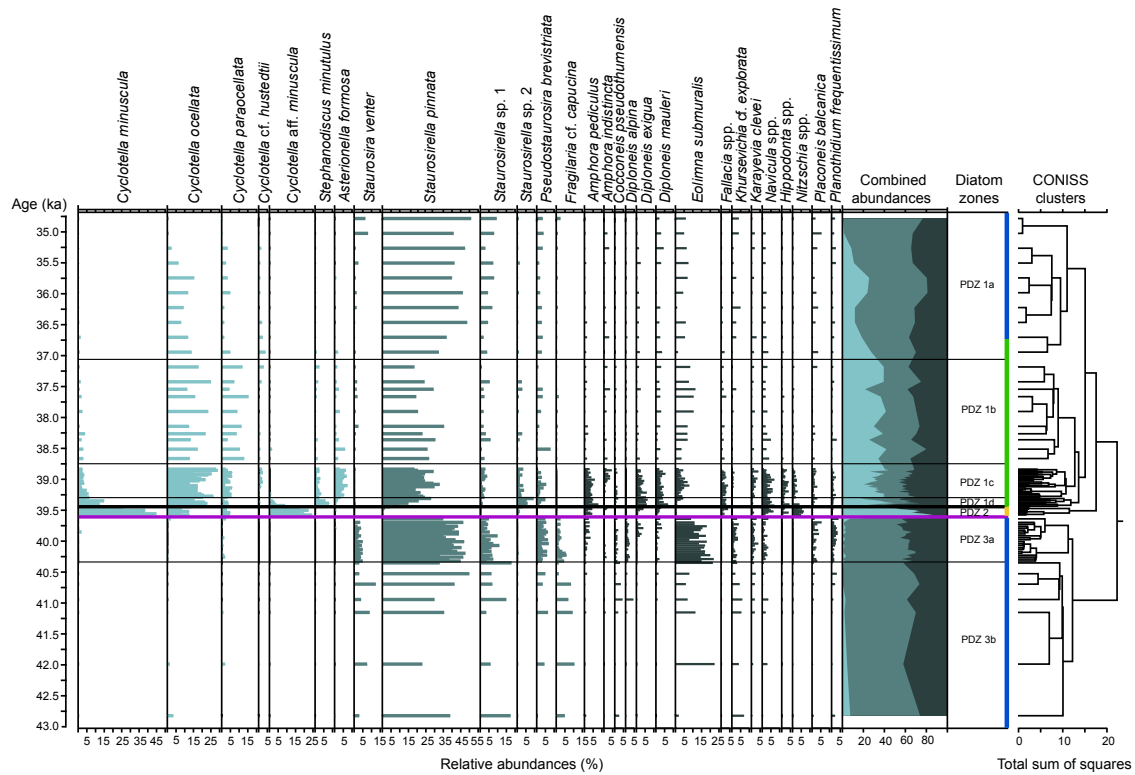




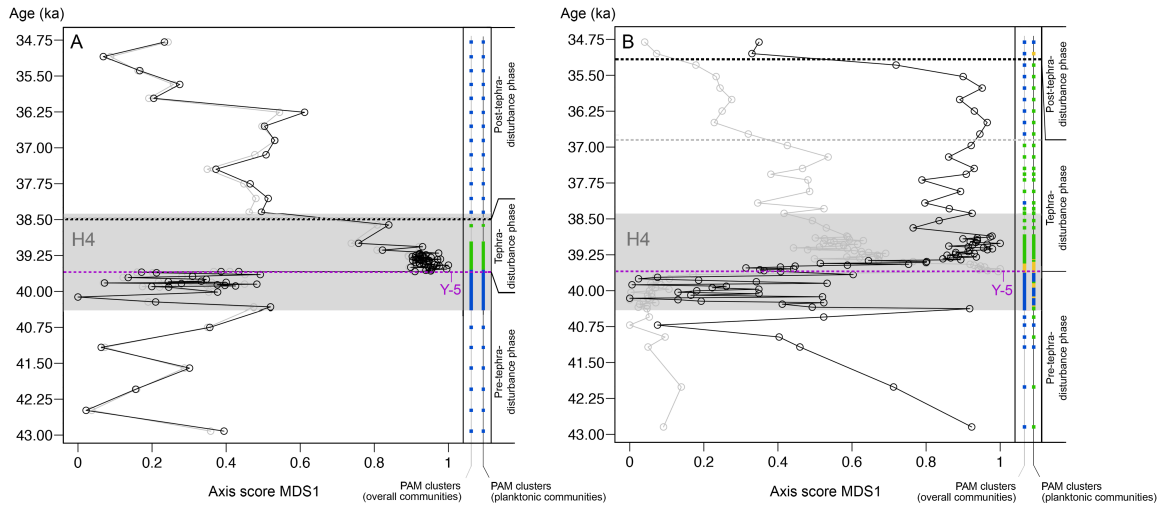
**Figure 1.** Maps showing (A) the Y-5 tephra distribution from the Campi Flegrei caldera in Europe (blueish-green shading, sensu Fitzsimmons et al., 2013) and (B) the drilling sites in lakes Ohrid (DEEP-5045-1) and Prespa (Co1204).



**Figure 2.** Summary diatom diagram for the Ohrid core (DEEP-5045-1). Only diatom taxa with relative abundances of  $> 2\%$  are shown. Individual abundances are color-coded according to life style (light blue: planktonic, medium blue: facultative planktonic, dark blue: benthic). Diatom zones and subzones were defined by CONISS; zone boundaries are represented with thick solid lines, subzone boundaries with thin solid lines. PAM community clusters are color-coded according to Fig. 4A. The purple line indicates the timing of the Y-5 eruption; the greyish area the timing of the H4 event. Note that the diatom communities had reached the quasi pre-disturbance state (upper blue bar) before the end of the H4 event.



**Figure 3.** Summary diatom diagram for the Prespa core (Co1204). Only diatom taxa with relative abundances of  $> 4\%$  are shown. Individual abundances are color-coded according to life style (light blue: planktonic, medium blue: facultative planktonic, dark blue: benthic). Diatom zones and subzones were defined by CONISS; zone boundaries are represented with thick solid lines, subzone boundaries with thin solid lines. PAM community clusters are color-coded according to Fig. 4B. The purple line indicates the timing of the Y-5 eruption; the greyish area the timing of the H4 event. Note that the diatom communities had reached the quasi pre-disturbance state (upper blue bar) only after the end of the H4 event.



**Figure 4.** Diagrams showing changes in MDS diatom community compositions (black curves: planktonic communities; grey curves: overall communities) and respective PAM community assignments (colored rectangles) for lakes Ohrid (A) and Prespa (B). The purple dashed lines indicate the timing of the Y-5 eruption; the greyish areas the timing of the H4 event; and the black and grey dashed lines the return of the respective planktonic and overall community compositions to quasi pre-disturbance state.