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

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Differential resilience of ancient sister lakes

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Abstract

Ancient lakes, like lakes Ohrid and Prespa on the Balkan Peninsula, have become model systems for studying the link between geological and biotic evolution. Recently the scientific deep drilling program "Scientific Collaboration on Past Speciation Conditions in Lake Ohrid" (SCOPSCO) has been launched to better understand the environmental, climatic and limnological evolution of the lake. It revealed that Lake Ohrid experienced a number of environmental disturbances during its ca. 2.0 million year long history. They comprise disturbances that lasted over longer periods of times ("press events") such as Heinrich events as well as sudden and short disturbances ("pulse events") like the deposition of volcanic ashes. The latter include one of the most severe volcanic episodes during the Late Pleistocene, the eruption of the Campanian Ignimbrite (known as Y-5 marine tephra layer) from the Campi Flegrei caldera, dated at 39.6 ± 0.1 ka ago. The event is recorded by the deposition of a ca. 15 cm thick Y-5 tephra layer in sediment cores of lakes Ohrid (DEEP-5045-1) and Prespa (Co1204). This pulse event is overlain by the Heinrich event 4 (H4), 40.0–38.0 ka ago.

In the current paper, diatoms were used as proxies to compare the responses of these lakes to the Y-5 (pulse) and the H4 (press) disturbances. Based on stratigraphically constrained incremental sum of squares cluster (CONISS) and unconstrained Partitioning Around Medoids (PAM) analyses, we found ~~only~~ little evidence that ~~the~~ diatom community compositions in either lake responded to the H4 event. However, the Y-5 influx caused clear and rapid diatom community changes. After the initial response, community composition in Lake Ohrid and, to a lesser extent, in Lake Prespa slowly returned to their quasi pre-disturbance state. Moreover, there is no evidence for disturbance-related extinction events. The combined evidence from these findings suggest~~s~~ that lakes Ohrid and Prespa likely did not experience regime shifts. It is therefore concluded that both lakes show resilience to environmental disturbance. However, it seems that Lake Ohrid is more resilient than Lake Prespa as the recovery of diatom communities is more pronounced and as its estimated recovery time is only

ca. 1400 years vs. ca. 3600 years in Lake Prespa. The reasons for the differential responses remain largely unknown, but differences in geology, lake age, limnology, and intrinsic parameters of the diatom proxies may play a role.

Given the relative robust results obtained, this study provides important new insights into the response of lakes to (multiple) environmental disturbances. Moreover, it contributes to one of the major goals of the SCOPSCO project – to evaluate the influence of major geological events onto the evolution of endemic taxa in Lake Ohrid.

1 Introduction

Ancient lakes, i.e. extant lakes that have continuously existed since before the last glacial maximum (Albrecht and Wilke, 2008), have become model systems for studying the link between geological and biological evolution over extended periods of time. For some lakes, such as Malawi (Van Bocxlaer et al., 2012) or Titicaca (Kroll et al., 2012), it has been demonstrated that the evolution of their species was largely shaped by massive environmental disturbances, leading to (near-) desiccation and/or salinization events, followed by mass extinction of many biota.

However, for other lakes, like the sister lakes Ohrid and Prespa on the Balkan Peninsula, the link between geological and biotic evolution is not well understood. In order to better understand the environmental, climatic and limnological evolution of Lake Ohrid, the SCOPSCO project has been conducted recently. The project revealed that the lake experienced a number of environmental disturbances during its ca. 2.0 million year (Ma) long history (Lindhorst et al., 2015). Some of these events lasted over longer periods of times and covered, for example, glacial/interglacial cycles (Wagner et al., 2014) or Heinrich events (Wagner et al., 2010), i.e., episodes of massive iceberg discharges that caused cooling of the North Atlantic during the last glacial period (Bond et al., 1993). The latter events presumably intensified aeolian activities, lowered the temperature, and increased the aridity in the Ohrid region (Wagner et al., 2010). Such long-lasting disturbances (> several centuries) are referred to as "press disturbances"

(Niemi et al., 1990). In contrast, sudden disturbances with a short and clearly defined duration (< few decades) are called "pulse disturbances" (Niemi et al., 1990). Examples include landslides (Lindhorst et al., 2014), earthquakes (Hoffmann et al., 2010; Wagner et al., 2012b; Lindhorst et al., 2015), and volcanic ash depositions (Sulpizio et al., 2010; D'Addabbo et al., 2015).

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

It has been suggested that the interaction of volcanic ash deposition with a receiving lake triggers perturbations, primarily through the effect of tephra weathering, but also through changes in pH value, mineral concentration, organic matter input, and due to a short-term light deprivation (e.g., Harper et al., 1986; Barker et al., 2003; Telford et al., 2004; Cruces et al., 2006; Urrutia et al., 2007; D'Addabbo et al., 2015).

Depending on the magnitude of the disturbance and the resilience of the respective ecosystem (i.e., the amount of disturbance an ecosystem can tolerate without changing its regime; Holling et al., 1973, 1986; Scheffer and Carpenter, 2003; Baho et al., 2014), lake biota may react with extinction events and/or changes in community structures.

Some organisms, like diatoms (single-celled siliceous algae belonging to the Protista), react very sensitively to pulse disturbances, such as tephra deposition (e.g., Harper et al., 1986; Barker et al., 2003; Cruces et al., 2006). Moreover, they are often remarkably well-preserved in the sediment records of lakes Ohrid and Prespa (e.g.,

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Reed et al., 2010; Cvetkoska et al., 2012, 2014, 2015b). These aspects make diatoms excellent proxies for studying how the lakes responded to massive environmental disturbances. In fact, previous sediment core analyses suggest alterations in diatom assemblage structure and abundances due to tephra influxes in both lakes (Cvetkoska et al., 2012, 2014, 2015a, b). However, ~~the~~ low temporal resolution did not allow the diatom data to be linked to distinct pulse events or to estimate recovery periods (i.e., the time an ecosystem needs to return to pre-disturbances conditions; the recovery period serves as measure for resilience strength; Carpenter, 2013). Therefore, it remains unclear how the lakes responded to such changes and whether there ~~are~~ differences in response between the lakes.

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

1. Whether lakes Ohrid and Prespa had the resilience to tolerate this disturbance without changing their regimes (i.e., without exceeding a critical threshold). Operational criteria for resilience are the lack of disturbance-related extinction events in the diatom record and a subsequent return of diatom communities to a quasi pre-disturbance state.

2. If resilience can be demonstrated for one or both lakes, whether there are differences in resilience strength between the two systems. The operational criterion for resilience strength is the length of the recovery period, which, is measured as the time the diatom communities need to return to their quasi pre-disturbance state.

Given that Lake Ohrid has long been considered to have a high ecosystem stability (sensu Stanković, 1960; Föller et al., 2015) due to its depth, age, and peculiar karst

limnology, our working hypothesis is that Lake Ohrid is more resilient to environmental disturbances than Lake Prespa.

Coincidently, the Y-5 tephra deposition (39.6 ± 0.1 ka ago) is overlain by the Heinrich event 4 (H4) that occurred 40.0–38.0 ka ago and which left signatures in the sediment records of both lakes (Wagner et al., 2010; Panagiotopoulos et al., 2014; Cvetkoska et al., 2015a). This provides a unique opportunity to obtain ~~preliminary~~ information on the differential effect of a short pulse and a longer press disturbance event.

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

2 Material and methods

2.1 Site description

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

Lake Ohrid is located at 693 m a.s.l., covers a surface area of 358 km^2, and has a maximum water depth of 293 m (Lindhorst et al., 2014). The hydrological regime of the lake is highly regulated with inflow from karstic aquifers (sublacustrine and surface springs), while the outflow occurs via the River Crn Drim (Matzinger et al., 2006a). Oligotrophic Lake Ohrid is phosphorus limited (Allen and Ocevski, 1977) with an average total phosphorus (TP) concentration of 4.5 mg m^{-3} (Matzinger et al., 2007), and an average Secchi depth of ca. 14 m (Matzinger et al., 2006b).

Neighbouring Lake Prespa is situated ca. 150 m above Lake Ohrid (849 m a.s.l.), has a surface area of 254 km^2, and a maximum water depth of 58 m (Matzinger et al.,

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2006a; Albrecht et al., 2008). The water balance is regulated through inputs from Lake Mikri Prespa, catchment inflow and river runoff, groundwater, and direct precipitation. The outflow occurs through the karstic aquifers of Mt. Galicica, irrigation and water surface evaporation (Matzinger et al., 2006a). Mesotrophic Lake Prespa has an average TP concentration of $31\,\mathrm{mg\,m^{-3}}$ (Wagner et al., 2010) and an average Secchi depth of ca. $6.2\,\mathrm{m}$ (Zacharias et al., 2002).

2.2 Core recovery and geochronology

During the SCOPSCO deep-drilling campaign in spring 2013, a $569\,\mathrm{m}$ long core (DEEP-5045-1) was retrieved from the central part of the Ohrid Basin at ca. $255\,\mathrm{m}$ water depth (Fig. 1; Wagner et al., 2014). Until today, sediment cores of the upper 247.8 mcd (meter composite depth) of the DEEP site sequence have become available (Francke et al., 2015). The age-depth model of the composite sequence, which is based on nine tephrostratigraphic tie points (1st order tie points), and on tuning of biogeochemical proxy data to orbital parameters (2nd order tie points) and to the global benthic isotope stack LR04 (Liesecki and Raymo, 2005; 3rd order tie points), suggest that this upper part of the DEEP site sequence covers the last 640 ka (Baumgarten et al., 2015; Francke et al., 2015). In this study, we focused on the Y-5 tephra layer at 39.6 ± 0.1 ka ago, according to the age estimations provided by Leicher et al. (2015).

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

2.3 Diatom analyses

In total, 157 sediment sub-samples were collected from the Ohrid and Prespa cores and analysed (18.03–15.63 m and 9.21–7.57 m, respectively). In the Prespa core, the

tephra boundaries were sharp and clearly distinguishable. In the Ohrid core, only the lower boundary was clear; the upper boundary appeared relatively diffuse, presumably due to post-depositional tephra input from the catchment area and/or a drilling artefact. Within and around the actual tephra layer, the cores were sliced in 5 mm intervals for a high temporal resolution of ca. 10 years. With increasing distance above and below the tephra layer, resolution was decreased first to 4 cm and then to 16 cm.

For diatom analyses, weighed samples of freeze-dried sediments were acid-cleaned with cold H_2O_2 and 10 % HCl, and then boiled for 2 h in 37 % HCl for oxidization of organic matter and for removing carbonates (Renberg, 1990; Cvetkoska et al., 2012). Permanent diatom slides were mounted with Naphrax[®].

As a proxy for productivity, diatom concentrations were calculated according to the following equation: DC = # valves $\times 10^7 \times g^{-1}_{dry \ sediment}$ (Battarbee, 1986). In each sample, 200–400 diatom valves per slide were counted and identified by one of us (EJ) at 1000× magnification either with a Carl Zeiss, Axioplan 2 microscope equipped with a Nikon D5700 digital camera or a Nikon Eclipse 80i microscope equipped with a Canon EOS 600D digital camera. Diatom identification followed Levkov et al. (2007), Levkov and Williams (2011), Cvetkoska et al. (2012, 2014), Jovanovska et al. (2013), and Pavlov et al. (2013).

Diatom counts were converted to percentages and displayed using Tilia and TGView v. 1.7.16. (Grimm, 1987). For characterizing the relationship between diatom constrained incremental sum of squares cluster analysis (CONISS; Grimm, 1987). In order to prevent a bias caused by rare species, only diatom taxa with a relative abundance of > 2 % were used for the CONISS analyses.

In addition, we determined community response phases based on distinct changes in community structures using the stratigraphically unconstrained clustering approach of Partitioning Around Medoids (PAM; Kaufman and Rousseeuw, 1990). PAM clusters pair-wise Bray–Curtis dissimilarities (Bray and Curtis, 1957) of communities into k groups of minimum intragroup sum-of-distances, with an optimum of k chosen by the silhouette criterion (Kaufman and Rousseeuw, 1990). The PAM analyses were per-

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formed using the package cluster 2.0.3 (Maechler et al., 2013) for the R statistical environment 3.2.1 (R Core Team, 2015). Using Bray–Curtis dissimilarities, we preformed metric multidimensional scaling in R and plotted the scores of the first axes according to their respective age.

⁵ The recovery time was calculated by estimating the time differences between the same group-membership assigned by the PAM analyses before and after the tephra influx. As the overall diatom communities in Lake Ohrid are biased towards planktonic species, we determined recovery times from planktonic communities only.

3 Results

¹⁰ In total, 82 and 210 diatom species were identified in the cores of lakes Ohrid and Prespa, respectively. Due to the difference in water depth of the coring locations (ca. 255 m for Lake Ohrid vs. 14 m for Lake Prespa), planktonic species dominated in Lake Ohrid, especially members of the genus *Cyclotella*. Though many benthic species had been found, they only occurred in low abundance. In Lake Prespa, planktonic and

¹⁵ benthic species were roughly balanced (Figs. 2 and 3).

Some planktonic species showed a high morphological variability in respect to valve size, shape of the central area or number of ocelli in the central area (e.g., *Cyclotella fottii* and *Cyclotella ocellata*). In order to fully cover the magnitude of potential community changes, we assigned them to distinct morphotypes.

²⁰ **3.1 Identification of community response phases and diatom zones**

The stratigraphically unconstrained PAM analyses identified three major community response phases in lakes Ohrid and Prespa: A phase that corresponds to pre-disturbance conditions (pre-tephra-disturbance phase; Fig. 4, also see lower red bars in Figs. 2 and 3), a distinct disturbance phase (tephra-disturbance phase; Fig. 4, also

²⁵ see yellow and blue bars in Figs. 2 and 3), and a phase in which communities had re-

turned to quasi pre-disturbance conditions (post-tephra-disturbance phase; Fig. 4, also see upper red bars in Figs. 2 and 3).

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

3.2 Diatom analyses of the Ohrid core

3.2.1 Pre-tephra-disturbance phase (ODZ 3c–a; age 42.0–39.6 ka)

Diatom subzones ODZ 3c–a (Fig. 2) were characterized by the presence of the planktonic taxa *Cyclotella fottii* complex, *C. minuscula*, and *C. ocellata*, of which *C. fottii* was the most dominant with up to 50 % relative abundance. The benthic and facultative planktonic species had abundances of up to 10 % when taking the whole profile into account. Examples include *Staurosirella* spp., *Staurosira* spp., *Amphora* spp., *Cocconeis* spp., *Diploneis* spp., *Planothidium frequentissimum*, and *Navicula* spp. The diatom concentration (DC) values were low in subzone ODZ 3c and slightly increased towards the upper subzone boundary of ODZ 3a.

3.2.2 Tephra-disturbance phase (ODZ 2d–a; age 39.6–ca. 38.2 ka)

Within subzones ODZ 2d–c, *C. fottii* and *C. ocellata* were replaced by *C. minuscula* (Fig. 2), which reached almost 100 % relative abundance. Abundances of facultative planktonic and benthic species (e.g., *Navicula* spp., *Diploneis* spp., and *Encyonopsis* spp., *Staurosirella* spp., *C. ocellata*) gradually decreased to values of ca. 10–20 %. DC reached maxima of ca. 1200×10^7 valves $\times$ g$^{-1}_{\text{dry sediment}}$ in subzones ODZ 2c–d.

Subzones ODZ 2b–a were characterized by increasing abundances of *C. fottii* and *C. ocellata* of up to 10 and 30 %, respectively. *Cyclotella minuscula* gradually de-

creased towards the upper subzone boundary ODZ 2a. DC values ~~gradually~~ declined to ca. ~~510~~ $\times$ 10^7 valves $\times$ g $_{\text{dry sediment}}^{-1}$ in subzone ODZ 2b, and to $< 50 \times 10^7$ valves $\times$ g $_{\text{dry sediment}}^{-1}$ in subzone ODZ 2a.

3.2.3 Post-tephra-disturbance phase (ODZ 1a; age ca. 38.2–37.25 ka)

Diatom subzone ODZ 1a (Fig. 2) was marked by a return of *Cyclotella minuscula* to ~~the~~ initial abundance of ca. 30 % and a continued increase in abundances of *C. fottii* towards the upper boundary of the subzone. The facultative planktonic species, especially *Staurosirella* spp., were present at abundances of ca. 5 %, while the benthic species abundances remained low with < 2 %. DC values decreased almost below 5×10^7 valves $\times$ g $_{\text{dry sediment}}^{-1}$.

3.3 Diatom analyses of the Prespa core

3.3.1 Pre-tephra-disturbance phase (PDZ 3c–a; age 42.9–39.6 ka)

The diatom assemblages in this zone were dominated by facultative planktonic species (e.g., *Staurosirella pinnata*, *S. venter*, and *Pseudostaurosira brevistriata*) and the benthic species *Eolimna submuralis.* The latter reached a relative abundance of up to 5–20 %. The planktonic species *C. minuscula* was present at ca. 2 % abundance in PDZ 3a. Benthic species were ~~rare and~~ low in abundance. The planktonic *C. ocellata* and *C. paraocellata* were highly dissolved in ~~this~~ subzone. DC values fluctuated throughout the zone, with highest values of ca. 50×10^7 valves $\times$ g $_{\text{dry sediment}}^{-1}$ in subzones PDZ 3c and 3a.

3.3.2 Tephra-disturbance phase (PDZ 2d–a; age 39.6–37.45 ka)

At the base of subzone PDZ 2d, facultative planktonic species (e.g., *Staurosirella* sp. 1, *Fragilaria* cf. *capucina*, and *P*. *brevistriata*) were ~~quickly~~ replaced by planktonic species

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(e.g., *C. minuscula*, which reached relative abundances of up to 50 % but also *C. ocellata*, *C. paraocellata*, and *Cyclotella* cf. *hustedtii*). Note that *Cyclotella* aff. *minuscula* had abundances of up to 30 % throughout PDZ 2d–a. Most benthic species increased in abundances (e.g., *Diploneis* cf. *peterseni*, *Fallacia* spp., *Nitzschia* spp., and *Navicula* spp.); only few species decreased (e.g., *E*. *submuralis*, *Placoneis balcanica*, *Kurshevichia* cf. *exploranta*). DC values increased to ca. 120×10^7 valves $\times$ g$^{-1}_{\text{dry sediment}}$ in PDZ 2d.

Subzones PDZ 2c–a were characterized by a decline of *C. minuscula* abundance to ca. 7 % and a renewed dominance of facultative planktonic species. The planktonic species maintained their abundances throughout PDZ 2c–a, with a peak of *C. paraocellata* in lower parts of subzone PDZ 2a. *Cyclotella* aff. *minuscula* gradually decreased in subzone PDZ 2a and disappeared within subzone PDZ 1a. Benthic species decreased in abundances towards PZD 2a (e.g., *F*. cf. *capucina* and *Nitzschia* spp.). After a maximum of ca. 200×10^7 valves $\times$ g$^{-1}_{\text{dry sediment}}$ in subzone PDZ 2c, DC values declined to ca. 25×10^7 valves $\times$ g$^{-1}_{\text{dry sediment}}$ towards the upper boundary of PDZ 1a.

3.3.3 Post-tephra-disturbance phase (PDZ 1a; age ca. 36.85–35.50 ka)

The diatom subzone PDZ 1a was characterized by a decline of planktonic species (e.g., *C. paraocellata* and *C. ocellata*) to ca. 7 % relative abundance. In contrast, benthic species moderately increased in their abundances. DC values decreased to a minimum of ca. 10×10^7 valves $\times$ g$^{-1}_{\text{dry sediment}}$.

3.4 Community composition analyses and estimations of recovery times

The first ordination axis of the metric multidimensional scaling analyses indicates that the Y-5 tephra deposition caused very rapid changes in the diatom communities of lakes Ohrid (Fig. 4a) and Prespa (Fig. 4b). Given that the communities in Lake Ohrid's DEEP core were dominated by planktonic species, the respective curves for overall (i.e., planktonic and benthic communities) and planktonic communities in Fig. 4a

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showed similar patterns over time. After the drastic change of community composition, coinciding with the tephra deposition, communities slowly reverted to ~~the~~ quasi pre-disturbance state (yellow bar in Fig. 2).

In Lake Prespa, where planktonic and benthic species were roughly balanced, the overall community structure (grey curve in Fig. 4b) rapidly changed, following the Y-5 event and then gradually approached ~~the~~ quasi pre-disturbance state. For the planktonic communities of Lake Prespa, the change coinciding with the tephra deposition was not as abrupt. However, the return to the pre-eruption community state occurred even more gradually.

The diatom communities in both lakes Ohrid and Prespa did not show a strong response to the onset of the H4 event 40 ka ago (but see the appearance of several benthic species during this period; Figs. 2 and 3). Nonetheless, the Ohrid communities had converted back to the quasi pre-disturbance state before the end of the H4 event 38 ka ago (blue dashed curve in Fig. 4a; also see the upper red bar in Fig. 2), whereas this process in the Prespa communities extended beyond the end of the Heinrich event (blue dashed curve in Fig. 4b; also see the upper red bar in Fig. 3). ~~Nonetheless~~, the PAM analyses showed that the Ohrid and Prespa communities did return back to their quasi pre-disturbance states (see the upper red bars in Figs. 2–4 and the PAM clusters in Fig. 4), indicating that no regime shift occurred.

According to the age models of the two cores, the recovery times (i.e., the time differences between the same group-membership assigned by the PAM analyses before and after the tephra influx) for planktonic communities in lakes Ohrid and Prespa were ca. 1400 and ca. 3600 years, respectively (Fig. 4), following the Y-5 tephra influx.

4 Discussion

Our results indicated little immediate effects of the H4 event on diatom community compositions in either of the lakes. However, the Y-5 influx caused clear and rapid responses (Fig. 4). Whereas the overall community composition in Lake Prespa partially

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recovered within a few decades, mostly driven by benthic species, and then slowly returned to the quasi pre-disturbance state over an extended period of time, the plank-tonic community needed ~~an even~~ longer period of time for recovery (compare the grey and black curves in Fig. 4b).

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

When comparing changes in planktonic communities as well as productivity rates in lakes Ohrid and Prespa, overall patterns are similar. An initial rapid response phase was followed by a phase in which communities slowly returned to the quasi pre-disturbance state. However, as ~~stated~~ above, the quasi pre-disturbance state in the Ohrid communities was reached prior to the end of the H4 event, whereas the Prespa communities ~~had~~ recovered only long after the end of the Heinrich event.

4.1 Diatom responses to disturbances in Lake Ohrid

The communities in the Ohrid core were ~~mainly~~ characterized by planktonic species. Dominant taxa in the pre-tephra-disturbance phase ~~(42.0–39.6 ka ago) were the epilim-netic~~ *Cyclotella ocellata*, *C. minuscula*, and the hypolimnetic endemic *C. fottii* (Fig. 2). ~~This community is~~ indicative of the MIS 3 warming (Cvetkoska at al., 2015b). Although at low abundances, the benthic species likely indicate wind induced water currents, wa-ter mixing and/or sediment redistribution in the lake (Cvetkoska at al., 2015b). Almost all of the identified benthic taxa ~~also~~ have been reported from contemporary communi-ties in the littoral zones (0–60 m water depth) of Lake Ohrid (Levkov et al., 2007; Levkov and Williams, 2012; Jovanovska et al., 2013; Pavlov et al., 2013). The increased abun-dances of benthic species at ca. 40.0 ka ago likely reflect the response to intensified wind transport and mixing of the water column during the H4 event (ca. 40.0–38.0; also see Wagner et al., 2010).

In contrast to the onset of this press disturbance event, the Y-5 pulse disturbance event triggered an almost immediate reaction by the lake's diatom communities. The

deposition of silica rich volcanic ashes (ca. 60 % SiO$_2$, Sulpizio et al., 2010; Leicher et al., 2015) likely had an impact on the water chemistry by increasing the silica content in the water column (D'Abbabbo et al., 2015), and potentially ⬛️nd P in the sediment (sensu Barker et al., 2003). Indications of these changes are the rapid replacement of the dominant hypolimnetic *C. fottii* with the epilimnetic *C. minuscula* (Fig. 2). The latter species (only 3–7 μm in diameter) has high silica incorporating rates and low transparency preferences, which makes it a strong competitor for light and nutrients under tephra-altered environmental conditions (Cvetkoska et al., 2014, 2015b; Zhang et al., 2015). Due to the strong growth of its population, D⬛️values (i.e., a proxy for productivity) also increased rapidly. They reached maximum values in ODZ 2d–c (Fig. 2). These conditions were temporally maintained before communities gradually returned to the quasi pre-disturbance state. During the recovery period (until ODZ 1a), the nutrient pool of the lake likely changed due to the recycling of internally buried P and N, but continued silica enrichment from the catchment area may still have played a role. This assumption is supported by community and productivity data. Whereas *C. minuscula* slightly decreased in abundance duri⬛️he recovery period, other planktonic species maintained their elevated abundances until ODZ 1a.

The point of return to quasi pre-disturbance state was probably reached in subzone ODZ 1a. At that time, P and N levels in the water column likely had recovered and silica levels had decreased. This is indicated by the increase in abundances of the endemic *C. fottii* to pre-tephra-disturbance levels and the decline of DC values.

The overall recovery period (planktonic communities) in Lake Ohrid lasted ca. 1400 years. As recovery was achieved prior to the end of the H4 event, we here suggest that this press disturbance event possibly prolonged the recovery but did not prevent it.

4.2 Diatom responses to disturbances in Lake Prespa

In contrast to the diatom communities in the Ohrid core, Prespa communities were characterized by significant abundances of both planktonic and benthic species. Dominant planktonic taxa in the pre-tephra-disturbance phase (42.9–39.6 ka ago) w⬛️*C.*

ocellata and *C. paraocellata*; dominant benthic species were *Eolimna submuralis and Kurshevicia* cf. *exploranta*. The ordination (Fig. 4b) indicates only little change in over-all community composition during this time. However, planktonic communities did show moderate fluctuations in structure even before the onset of the H4 event 40.0 ka ago.

5 Therefore it remains difficult to quantify the immediate community impact of this press disturbance event.

The Y-5 associated silica fallouts (PDZ 2d) rapidly altered the water chemistry by increasing the silica content (ca. 60 % SiO_2 in the tephra layer, Sulpizio et al., 2010) in the water column of Lake Prespa. The tephra impact likely affected the P cycles and

10 the Si/P ratio in the water column as well (sensu Barker et al., 2003). The increased silica content favoured the growth of planktonic species like *C. minuscula*, *C. ocellata*, *C. paraocellata*, and *C.* aff. *minuscula*. The latter taxon has never been reported before. It occurs exclusively during the recovery period and failed to establish permanently.

In contrast to the planktonic species, epiphytic and facultative planktonic species like

15 *Cocconeis pseudothumensis*, *Staurosirella pinnata*, and *Pseudostaurosira brevistriata* temporally decreased in relative abundance (i.e., for a period of few decades). This may be explained by a short-term destruction of the littoral macrophytic habitats as a result of the Y-5 influx.

In subzone PDZ 2c, nutrient level slowly increased in the water column, favouring

20 species with high nutrient and silica preferences, such as *Asterionella formosa* (Holm and Armstrong, 1981). The combination of high silica, P and N contents in the water column also caused an increase in productivity (Fig. 3).

Due to increased nutrient availability and water transparency (Cvetkoska et al., 2014, 2015a), benthic species (e.g., *Diploneis exigua*, *Placoneis balcanica*, *Karayevia clevei*)

25 significantly increased in abundances. However, overall community structure and DC values did not return to the pre-disturbance state until PDZ 1a (see upper red bar in Fig. 3).

This long recovery period (planktonic communities) of almost 3600 years – exceed-ing the end of the H4 event – is striking and may reflect the joint impact of a press

(H4) and a pulse (Y-5) event. Although we do not see a direct effect at the initiation of H4, it likely prolonged the recovery period of diatom communities in Lake Prespa. It might even have prevented a full recovery prior to the end of the H4 period, although an additional effect of the MIS 3 warming period cannot be excluded.

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

From the current study, it becomes clear that the changes in community composition are largely caused by the Y-5 event. However, relating our data to those of Cvetkoska et al. (2014), we suggest that Heinrich and volcanic events, which are very different in nature, may drive communities in different directions. The potentially ~~strong~~ signatures of the H4 event ~~are~~ likely superimposed by ~~even~~ stronger ~~signatures~~ of the Y-5 event.

4.3 Disturbance related regime shifts in diatom communities

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

The data obtained are informative in this regard: we do not see extinction events directly related to the H4 and/or Y-5 events (see Figs. 2 and 3). Moreover, community composition appears to subsequently return to their quasi pre-disturbance states (see Fig. 4a and b). However, whereas the latter patterns are clear for both overall and planktonic communities in Lake Ohrid as well as for overall communities in Lake Prespa, the return to the quasi pre-disturbance state in planktonic communities in Lake Prespa is less obvious (see black curve in Fig. 4b). We therefore also considered the corresponding productivity values (see green curves in Fig. 4a and b). Acknowledging that these values cannot be used to directly characterize community changes, they

nicely correspond to the results of the PAM analyses. We therefore conclude that both lakes have a high ecosystem resilience.

However, the drivers for the resilience remain poorly understood. They are likely multifactorial, involving parameters such as water depth, hydrological regime, and chemical buffer processes. As the resilience of the lakes was indirectly inferred using diatom communities as proxies, our results were likely also affected by intrinsic biotic parameters of the diatoms.

4.4 Differential resilience in lakes Ohrid and Prespa

Given that ecosystem resilience has been demonstrated for both lakes, our second specific objective was to investigate whether there were differences in resilience strength between the two systems. As operational criterion for resilience strength, we used the length of the recovery periods (sensu Carpenter, 2013). Our working hypothesis was that Lake Ohrid is more resilient to environmental disturbances than Lake Prespa.

Concluding from the length of the recovery periods, Lake Ohrid is, indeed, more resilient than Lake Prespa (ca. 1400 years vs. ca. 3600 years, respectively). The reasons for the differential responses of the two sister lakes, which are located in close proximity, remain not fully understood, but, as discussed above, may be related to, for example, differences in their geology, limnology, and lake age.

4.5 Limitations and outlook

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

Nonetheless, given the nature of our data, a number of limitations have to be noted. First, our averaged age model may not allow for a precise estimating of short time in-

tervals (i.e., sub-millennium scale) above and below the actual tephra deposition. Also, our findings are based on single core locations in lakes Ohrid and Prespa. Moreover, as former littoral core sediments from Lake Ohrid were characterized by the presence of hiatuses (e.g., Wagner et al., 2008; Vogel et al., 2010), we had to use a core that was retrieved from a greater water depth (see Fig. 1). This, in turn, resulted in a bias of the Ohrid communities towards planktonic species. Finally, our study lacked high-resolution geochemical core data for the timeframe of interest.

In order to mitigate these problems, we used relative time information (i.e., diatom zones) for describing community changes, whenever possible. We focused in the comparative resilience and recovery time analyses on changes in the planktonic communities, as they were directly comparable in the two lakes (see black curves in Fig. 4). We also used previously published Y-5 geochemical data, especially SiO_2 content in the tephra layers (Sulpizio et al., 2010).

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

Nevertheless, given the interesting and partly unexpected patterns observed, we encourage future projects that aim at studying resilience processes in lakes Ohrid and Prespa in more detail. This would not only be of interest from a conceptual, but also from an applied point of view relative to current and future human impact scenarios for these model lakes (e.g., Kostoski et al., 2010).

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

5 Conclusions

In the present study, we demonstrated that diatom communities in ancient lakes Ohrid and Prespa reacted strongly to one of the most severe volcanic eruptions in the central Mediterranean region during the Late Pleistocene – the Y-5 event (39.6 ka ago). After a rapid initial response, community compositions slowly returned to their quasi pre-disturbance states. In contrast to the Y-5 pulse disturbance event, signatures of the overlaying H4 press disturbance event were less distinct. However, the latter likely contributed to the extended recovery periods of > 1000 years seen in both lakes. In the case of Lake Prespa, the H4 event may have delayed full recovery from the Y-5 pulse event until after the end of the H4.

Moreover, given that pulse and press events may drive community state in different directions, a potentially strong signature of the H4 event could have been superimposed by the even stronger signature of the Y-5 event.

Nonetheless, the data suggest that the communities in lakes Ohrid and Prespa likely did not experience regime shifts (but see above for the complex pattern in planktonic communities in Lake Prespa). We therefore conclude that both lakes show a high resilience to environmental disturbances. However, the estimated recovery times, which can be used as measure for resilience strength, differed between lakes Ohrid and Prespa (i.e., ca. 1400 vs. ca. 3600 years, respectively). This finding supports our working hypothesis that Lake Ohrid is more resilient to environmental disturbances than Lake Prespa. The exact reasons for the differential responses remain unknown, but differences in geology, lake age, limnology, as well as in intrinsic parameters of the diatom proxies may play a role.

We do note some limitations of our study such as the resolution of our age model and the different depths of the drilling locations, causing a bias towards planktonic species in Lake Ohrid. Nonetheless we believe that the results presented here are robust as indicated by similar overall response curves for the planktonic communities in lakes Ohrid and Prespa.

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

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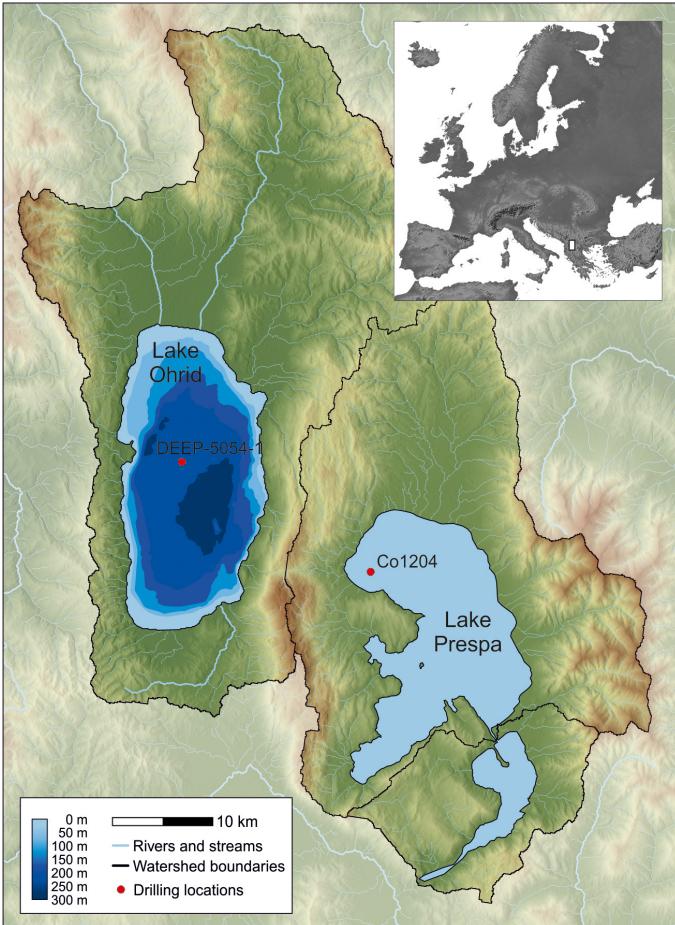
Figure 1. Map showing the drilling sites (red circles) in lakes Ohrid (DEEP-5045-1) and Prespa (Co1204).
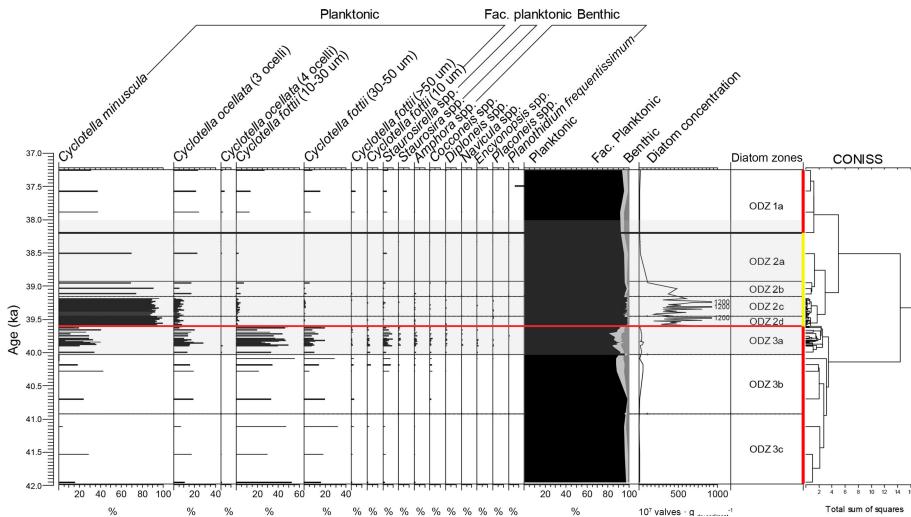
Figure 2. Summary diatom diagram for the Ohrid core (DEEP-5045-1). Only diatom taxa with a relative abundance of > 2 % are shown. Diatom zones and subzones were defined by CONISS; zone boundaries are represented with thick solid lines, subzone boundaries with thin solid lines. PAM community clusters are color-coded according to Fig. 4a. The red 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 red bar) before the end of the H4 event.

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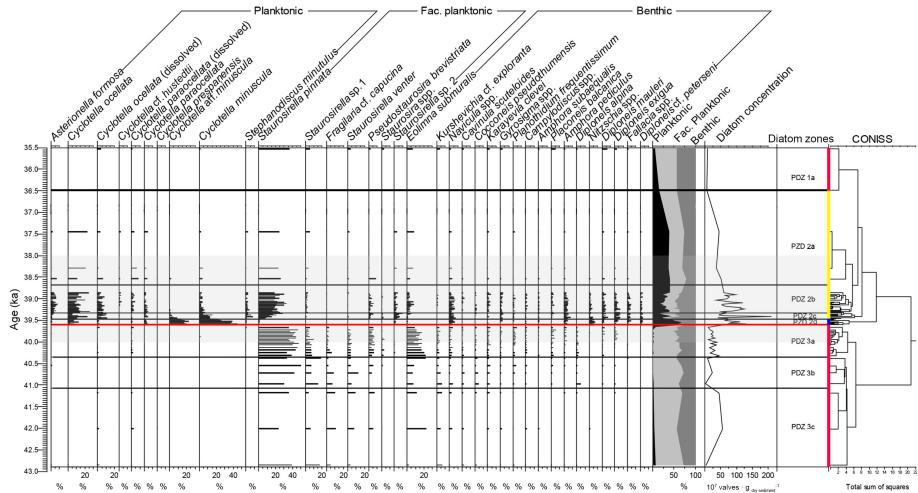
Figure 3. Summary diatom diagram for the Prespa core (Co1204). Only diatom taxa with a relative abundance of > 2 % are shown. Diatom zones and subzones were defined by CONISS; zone boundaries are represented with thick solid lines, subzone boundaries with thin solid lines. PAM community clusters are color-coded according to Fig. 4b. The red 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 red bar) only after the end of the H4 event.
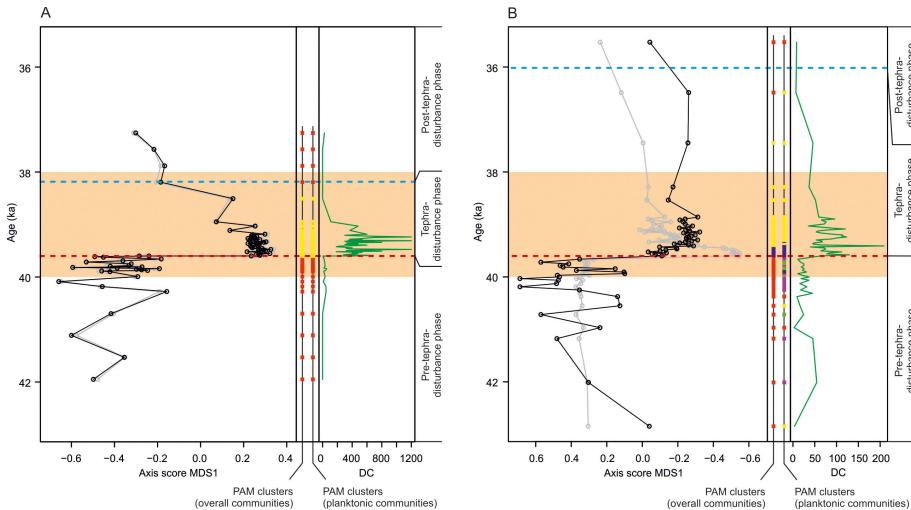
Figure 4. Diagrams showing changes in MDS diatom community compositions (black curves: planktonic communities; grey curves: overall communities), respective PAM community assignments (colored rectangles), and changes in overall diatom concentrations (DC in # valves × 107 × $g^{-1}_{dry\ sediment}$; green curve) for lakes Ohrid **(a)** and Prespa **(b)**. The red dashed lines indicate the timing of the Y-5 eruption; the light-brownish areas the timing of the H4 event, and the blue dashed lines the return of planktonic communities to quasi pre-disturbance state.