

Reply to referees' comments on Jovanovska et al. discussion paper

The authors would like to thank both reviewers for the detailed and constructive comments on the manuscript. We took their suggestions into consideration and will incorporate them in the revised manuscript.

Below we list all comments and suggestions of the reviewers (in italics), together with our point-by-point reply.

Reviewer #1

General comments:

1. *“The characterization of Heinrich events as press events seems somewhat peculiar to me given that in the paleoclimate literature Heinrich events are viewed as relatively short term events, and H4 in particular is characterized as being abrupt and extreme...I think the paper would be better if it simply relied on contrasting the abrupt impacts of tephra with the longer-term impacts of climate variation, without the jargon”.*

Response: We do agree with the reviewer that the used terminology might be inadequate from a geological viewpoint. However, biologically, the H-4 event is, indeed, a long period, especially when taken into account the biology of the diatom species studied (short generation time of ca. 1.1 divisions per day, Crawford et al., 2011). Moreover, this terminology is commonly accepted in ecosystems resilience/resistance studies, which are the main focus of this paper. We therefore would prefer to retain the term in the revised ms.

2. *“The paper concludes that the diatoms do show an abrupt response to tephra deposition but do not respond to the H4 event (but this latter statement is not consistently supported by the data - see my comments below). Differentiating the onset of these two “events”, of course, hinges on chronology – as the Heinrich event precedes the tephra deposition by just 400 yr. Yet no comments are made on the errors associated with the chronology, so it is not clear how well supported this statement is ... In addition, for Lake Ohrid, the sampling resolution prior to the onset and after the cessation of H4 is very low, so it is difficult to make a clear assessment of the impacts of H4, because of the changes in resolution ... see comments below”.*

Response: Thank you for raising this important point. However, our results in independency of the exact timing of the onset of the H-4 compared to Y-5, indeed, do not show an impact of H-4, which is as strong as the Y-5 impact. This, additionally, is supported by the previously published geochemical data (Wagner et al., 2010, 2012). Importantly, the sample resolution allows such interpretation, and therefore the impact of the H-4 seems to be relatively low compared to the impact of Y-5.

More importantly, the onset of the H-4 event has just been refined by Wutke et al. (2015). This new study specifies the timing of both events, H-4 and Y-5, based on sediment records recovered from Lago Grande di Monticchio in Italy. Accordingly, the timing of H-4 precedes the Y-5 event by ca. 800-700 years. In our revised ms, we will use this new chronological information.

However, it is important to note i) that this new information will not change the results and conclusions of our study and ii) that the primary aim of our study never was to precisely distinguish between Y-5 and H-4 events. Rather we are interested to see whether there is a differential response of lakes Prespa and Ohrid to these events.

3. I also think the sampling resolution is a significant problem in the discussion of the extent to which the floras recover their pre-disturbance state, which is not acknowledged adequately in the discussion of the data. Based on Figure 3, for example, there are really only two samples above the gray Heinrich layer – how does one know what is signal versus what is noise?

Response: Both reviewers pinpointed difficulties when comparing the recovery periods of lakes Ohrid and Prespa, mainly due to the uneven sampling resolution and the different timeframe observed. We fully agree with both reviewers and added 27 new sampling points to the Lake Prespa diagram and 9 to Lake Ohrid. Both diagrams now cover the same time frame and show a denser sampling. The refined analyses indicate that the overall diatom community in Lake Prespa, indeed, did recover (now supported by a total of 9 sampling points, instead of just 2 as in the original ms; see revised Fig. 3).

As for the signal-noise-ratio, the Y-5 impact (i.e., the signal) now shows a magnitude of change of ~0.6 units and a subsequently reduced variability of ~0.2 units. Therefore, the given variability of the sampling resolution should not blur the strong signal of the Y-5.

Specific comments:

4. Page 3, lines 13–15: “This sentence should be less definitive. In both lakes, speciation patterns have been inferred for only one faunal group– hence there is not sufficient data to make generalizations, such as “the evolution of their species”...alternatively, it might be more appropriate to summarize what is observed in the diatom records of Lake Baikal and Lake E, for example, which arguably are more similar to Ohrid and Prespa than the two tropical lakes”.

Response: We accept the reviewer suggestion and will include in the revised ms information on diatom stratigraphic records from lakes Baikal (Russia) and Hövsgöl (Mongolia).

5. P. 7, l. 10: It is not clear what is meant by “Until today.” Recently? Please change the wording to be clearer.

Response: Modified.

6. P. 13, l. 10: *As I indicated above, how good is your age model? How much error is associated with your characterization of the onset of H4?*

Response: Please see response #2.

7. P. 13, l. 17: *I think the basis for saying the Prespa community recovered is rather weak given that there are only 2 samples in the upper part of the diagram, and they are very widely spaced.*

Response: Please see response #3.

8. P. 13, l. 25: *Most of the prior discussion has centered on the impacts of the tephra deposition – Heinrich events are mentioned only briefly – so I think it would be better to start the discussion with a focus on the major theme (tephra deposition) – and later move into assessing how climate affected the flora.*

Response: In principle, we agree with this comment. However, as mentioned above, the primary aim of our study was not to precisely distinguish between Y-5 and H-4 events. Rather we are interested to see whether there is a differential response of lakes Prespa and Ohrid to these events.

9. P. 14, l. 23–26: *You start the Discussion section by saying that the Heinrich events had little effect on the diatom community – yet here you say that there is increased representation of benthic species, likely because of mixing at the onset of H4. The two statements are inconsistent.*

Response: We agree and will revise our discussion accordingly.

10. P. 15, l. 24: *Do you mean that climate may have delayed the recovery (rather than prolonged)? And again, saying that climate variation associated with the Heinrich event may have affected the rate of change in the diatom community structure is inconsistent with your statement that Heinrich events had little effect.*

Response: Our new analyses, indeed, suggest that climate change likely prolonged the recovery period. Moreover, the revised CONISS shows a mild influence of the H-4 event, particularly in Lake Prespa (see revised Fig. 3). We will discuss this in the revised paper.

11. P. 18, l. 20: *I think the variable sampling resolution, particularly the coarse resolution in some sections of each core, imposes some serious constraints on the ability to differentiate real trends versus sample to sample variation. This section should acknowledge this.*

Response: Please see response #3.

12. P. 19, l. 6: *The paper by Spanbauer (2014), which discusses long-term responses of diatom communities to perturbations, would be relevant to the discussion here. Spanbauer, T.L., C.R. Allen, D.G. Angeler, T. Eason, S.C. Fritz, A.S. Garmestani, K.L. Nash, J. R. Stone. 2014. Prolonged instability prior to a regime shift. PLoS ONE 9: e108936, doi:10.1371/journal.pone.0108936*

Response: The suggested paper will be included in the revised manuscript.

Reviewer #2

General comments:

1. *The concurrent/ongoing Heinrich “press” event (H4) did not have an impact on the diatoms, although the sampling around the initiation and termination of the event (Lake Ohrid: pre- samples, post: 3 samples; Lake Prespa: pre- 13 samples, post 3 samples) was uneven and restricted for analysis. However, the degree of the impact by the Campanian Ignimbrite eruption was substantive, well beyond any hint of an impact from the Heinrich “press” event.*

Response: Thank you for pointing out this issue, which has also been raised by reviewer #1. For our response, please see comment #3 above.

2. *Lake Ohrid In the discussion it was implied that valve densities for *C. ocellata* and *C. fottii* increased, but the relative composition decreased. This can be deceiving because the reader thinks that numbers declined (based on figs 2 and 3) when in fact numbers (DC) increased for all the prominent taxa. Clarify differences between taxa relative abundance and taxa density changes.*

Response: We agree with the reviewer. As a pragmatic solution, we will remove diatom concentrations (DC) as a proxy for productivity from the revised ms. This proxy is not essential for reaching the goals of our study as it was only used as supporting data for the interpretation of the nutrient pool status.

3. *Lake Prespa is there a count at 36.5? If so it cannot be seen. The DC count graph indicates a count as well as the PAM data. Move the zone boundary line so we can see the data.*

Response: We revised the figure accordingly (see Fig. 3 below).

Specific comments:

4. *In the introduction there are a number of extended. Compound sentences, which make for difficult reading. Try to keep sentences to less than 35 words.*

Response: We will consider this point in our revised version of the ms.

5. *A picture of the core section including the tephra for each lake would be helpful (as a supplement figure).*

Response: We appreciate this suggestion, but, as we consider that this is not of crucial importance for the ms, we decided to not include pictures from the cores.

6. P. 16055, l.15: *Lisiecki spelling*; P. 16056, l.08: *Expand the explanation on how the samples were treated*; P.16058, l.12: *Expand the explanation on how cell densities were determined*; *Documentation of the taxa with images (supplemental) or archiving the samples for possible future referencing and validation should be included.*

Response: We appreciate the suggestions and will expand the information provided for the cleaning process and samples archiving in the revised version. As mentioned above we will exclude DC from the revised version of the ms.

7. *“Diatom concentrations are replicated figs 2 & 3 versus 4. I can see why this was done, but it may not be necessary. As listed below expand on the valve density changes for the prominent taxa after the tephra event...P. 16077&16078: Label: : :.. g ash free dry weight, text is very small, maybe exclude from the label and include in the legend”.*

Response: We will apply the suggested corrections.

8. P. 16062, l. 16: *this sentence is repeating the results. Modify or remove.*

Response: The sentence will be modified.

9. P. 16062, l. 18: *This is the first time MIS 3 has been mentioned. This could be further defined/outlined in the Introduction or here.*

Response: In the revised ms, we will remove the statement about the potential influence of the MIS 3 climate conditions, since the Y-5 event occurs in the middle of the interstadial. Therefore, the communities should be already in equilibrium with the interstadial climate conditions of this period, and thus, MIS 3 unlikely influenced the recovery in lakes Ohrid and Prespa.

10. P. 16063, l. 03: *In Sulpizio et al. 2010, EDS data in the upper levels of the core would suggest that P levels were not altered that much during tephra events (?). If this is true, then P and possibly N were not significant. However the presence of A. formosa (in low numbers) does suggest P levels were changing? I would suggest adding more about the P and Si data from Sulpizio et al. paper in here. Your data is better than Barker et al. with respect to diatom proxies for TP. Limit the referencing to Barker et al. since they do not develop proxies for P & N. 20.*

Response: Thank you for these suggestions. Unfortunately, TP concentration data is not available from the bulk sediments for either lake. The low-resolution TN values (Wagner, unpublished data) show no significant change after the tephra influx. Therefore, we decided to tone down the respective interpretation and include suitable references.

11. P. 16064, l. 08: *Prespa and Ohrid had the same % SiO₂ tephra composition. I would add (either here or possibly in the methods) that you had similar "chemical" tephra compositions between the two lakes and reference Sulpizio et al. 2010. This further supports the idea that both lakes received the same impact.*

Response: We will consider this suggestion in our revised ms.

12. P. 16064, l. 10: *Since Barker et al. (2003) does not present chemistry/geochemistry data, but inference results for Conductivity and pH, I would suggest not using this reference to account for SI/P results.*

Response: Will be removed from the ms.

13. P. 16064, l. 16: *"The smaller graph interval is 50 years, not decades. 23. 16064-17: Benthic diatoms also "tended" to have an initial delay in response recovery but for a shorter period of time, which supports your argument of substratum availability...P. 16064, l. 26: Fig. 3 suggests that "recovery" of the benthics occurred in PZD 2a? Maybe stick to the planktonic forms for your discussion on return to pre-disturbance or use the MDS/PAM results"*.

Response: We agree and will change the ms accordingly.

14. *Addition minor comments and suggested sentence format changes are found on the manuscript.*

Supplement: All changes will be taken into consideration and incorporated in the revised manuscript. We really appreciate the efforts made by the reviewer.

References

Crawford, K. J., Raven, J. A., Wheeler, G. L., Baxter, E. J., and Joint, I.: The Response of *Thalassiosira pseudonana* to Long-Term Exposure to Increased CO₂ and Decreased pH, PLoS ONE, 6(10), e26695, doi:10.1371/journal.pone.0026695, 2011.

Wagner, B., Vogel, H., Zanchetta, G., and Sulpizio, R.: Environmental change within the Balkan region during the past ca. 50 ka recorded in the sediments from lakes Prespa and Ohrid, Biogeosciences, 7(10), 3187–3198, doi:10.5194/bg-7-3187-2010, 2010.

Wagner, B., Aufgebauer, A., Vogel, H., Zanchetta, G., Sulpizio, R., and Damaschke, M.: Late Pleistocene and Holocene contourite drift in Lake Prespa (Albania/F.Y.R. of Macedonia/Greece), *Quat. Int.*, 274, 112–121, doi:10.1016/j.quaint.2012.02.016, 2012.

Wutke, K., Wulf, S., Tomlinson, E. L., Hardiman, M., Dulski, P., Luterbacher, J., and Brauer, A.: Geochemical properties and environmental impacts of seven Campanian tephra layers deposited between 40 and 38 ka BP in the varved lake sediments of Lago Grande di Monticchio, southern Italy, *Quaternary Science Reviews*, 118, 67–83, doi: 10.1016/j.quascirev.2014.05.017, 2015.

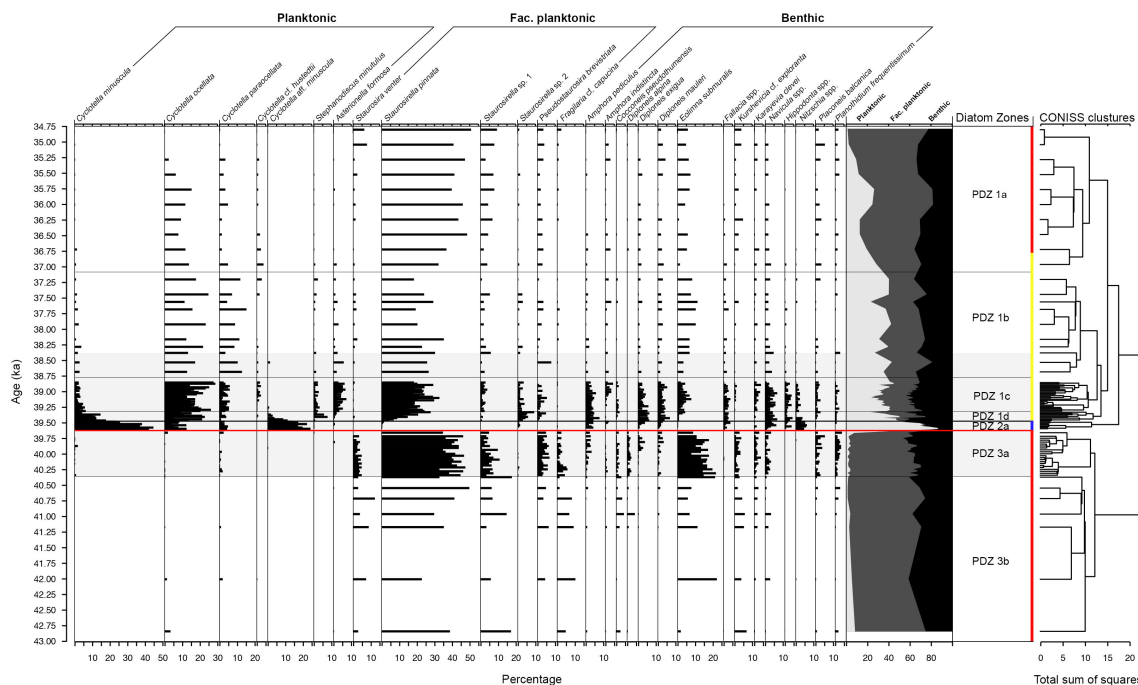


Figure 3. Summary diatom diagram for the Prespa core (Co1204). Only diatom taxa with a relative abundance of $> 2\%$ are shown. Diatom zones and subzones were defined by CONISS; zone boundaries are represented with thick solid lines, subzone boundaries with thin solid lines. PAM community clusters are 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).

List of relevant changes to MS Jovanovska et al. (2015):

1. We increased the sampling resolution and the number of diatom samples for both lakes (for Lake Prespa, we added 27 new sampling points; for Lake Ohrid 9). As a result, both diatom diagrams now cover the same time frame of 43.00-34.75 ka. The figures and figure captions were modified accordingly.
2. We now discuss the impact of the Heinrich H4-event more carefully and assured consistency throughout the manuscript.
3. We used the new data of Wutke et al. (2015) for the timing of the H4 event. This, in turn, allowed us to more precisely define the temporal gap between the H4 and Y-5 events.
4. We removed the diatom concentration (DC) as a proxy for productivity from the manuscript.

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±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±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 km², 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⁻³ (Matzinger et al., 2007) and total nitrogen (TN) concentration of
17 171–512 mg·m⁻³ (Watzin et al., 2002). The lake's silica (SI) concentration is < 200 mg·m⁻³ in
18 the trophogenic zone during summer (Stanković, 1960), the average water pH and water
19 conductivity are 8.48 and 208 µS cm⁻¹, 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 km², 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⁻³ (Wagner et al.,
27 2010), an average TN concentration of ca. 2000 mg·m⁻³, 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 ± 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% H₂O₂ 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% SiO₂, 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% SiO₂ 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 SiO₂ 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±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

25 **References**

26 Albrecht, C. and Wilke, T.: Ancient Lake Ohrid: biodiversity and evolution, *Hydrobiologia*,
27 615, 103–140, doi:10.1007/s10750-008-9558-y, 2008.

28 Albrecht, C., Wolff, C., Glöer, P., and Wilke, T: Concurrent evolution of ancient sister lakes
29 and sister species: the freshwater gastropod genus *Radix* in lakes Ohrid and Prespa,
30 *Hydrobiologia*, 615, 157–167, doi:10.1007/s10750-008-9555-1, 2008.

1 Allen, H. L. and Ocevski, B. T.: Limnological studies in a large, deep, oligotrophic lake (Lake
2 Ohrid, Yugoslavia). A summary of nutritional radiobioassay responses of the pelagial
3 phytoplankton, *Arch. Hydrobiol.*, 53, 1–21, doi:10.1007/BF00021231, 1977.

4 Baho, D. L., Drakare, S., Johnson, R. K., Allen, C. R., and Angeler, D. G.: Similar resilience
5 characteristics in lakes with different management practices, *PLoS ONE*, 9, e91881,
6 doi:10.1371/journal.pone.0091881, 2014.

7 Barker, P., Williamson, D., Gasse, F., and Gibert, E.: Climatic and volcanic forcing revealed
8 in a 50,000 year diatom record from Lake Massoko, Tanzania, *Quaternary Res.*, 60, 368–376,
9 doi:10.1016/S0033-5894(03)00114-5, 2003.

10 Baumgarten, H., Wonik, T., Tanner, D. C., Francke, A., Wagner, B., Zanchetta, G., Sulpizio,
11 R., Giaccio, B., and Nomade, S.: Age depth-model for the past 630 ka in Lake Ohrid
12 (Macedonia/Albania) based on cyclostratigraphic analysis of downhole gamma ray data,
13 [Biogeosciences, 12, 7453–7465, doi:10.5194/bg-12-7453-2015, 2015.](#)

14 Bond, G., Broecker, W., Johnsen, S., McManus, J., Labeyrie, L., Jouzel, J., and Bonani, G.:
15 Correlations between climate records from North Atlantic sediments and Greenland ice,
16 *Nature*, 365, 143–147, doi:10.1038/365143a0, 1993.

17 Bray, J. R. and Curtis, J. T.: An ordination of upland forest communities of southern
18 Wisconsin, *Ecol. Monogr.*, 27, 325–349, doi:10.2307/1942268, 1957.

19 Carpenter, R. S.: Spatial signatures of resilience, *Nature*, 496, 308–309,
20 doi:10.1038/nature12092, 2013.

21 Costa, A., Folch, A., Macedonio, G., Giaccio, B., Isaia, R., and Smith, V. C.: Quantifying
22 volcanic ash dispersal and impact of the Campanian Ignimbrite super-eruption, *Geophys. Res.*
23 *Lett.*, 39, L10310, doi:10.1029/2012GL051605, 2012.

24 Cruces, F., Urrutia, R., Parra, O., Araneda, A., Treutler, H., Bertrand, S., Fagel, N., Torres,
25 Le., Barra, R., and Chirinos, L.: Changes in diatom assemblages in an Andean lake in
26 response to a recent volcanic event, *Arch. Hydrobiol.*, 165, 23–35, doi:10.1127/0003-
27 9136/2006/0165-0023, 2006.

28 Cvetkoska, A., Reed, J. M., and Levkov, Z.: Diatoms as indicators of environmental change
29 in ancient Lake Ohrid during the last glacial–interglacial cycle (ca 140 ka), in: *Diatom*

- 1 Monographs, vol. 15, edited by: Witkowski, A., ARG Gartner Verlag, Ruggell, Liechtenstein,
2 220 pp., 2012.
- 3 Cvetkoska, A., Levkov, Z., [Reed, J. M.](#), and Wagner, B.: Late Glacial to Holocene climate
4 change and human impact in the Mediterranean: the last ca. 17 ka diatom record of Lake
5 Prespa (Macedonia/Albania/Greece), *Palaeogeogr. Palaeoclimatol.*, 406, 22–32,
6 doi:10.1016/j.palaeo.2014.04.010, 2014.
- 7 [Cvetkoska, A., Jovanovska, E., Francke, A., Tofilovska, S., Vogel, H., Levkov, Z., Donders,
8 T., Wagner, B., and Wagner-Cremer, F.: Ecosystem regimes and responses in a coupled
9 ancient lake system from MIS 5b to present: the diatom record of lakes Ohrid and Prespa,
10 *Biogeosciences Discuss.*, 12, 15051–15086, doi:10.5194/bgd-12-15051-2015, 2015a.](#)
- 11 Cvetkoska, A., Levkov, Z., [Reed, J. M.](#), Wagner, B., Panagiotopoulos, K., Leng, M., and
12 Lacey, J.: Quaternary climate change and Heinrich events in the southern Balkans: Lake
13 Prespa diatom palaeolimnology from the last interglacial to present, *J. Paleolimnol.*, 53, 215–
14 231, doi:10.1007/s10933-014-9821-3, [2015b](#).
- 15 D’Addabbo, M., Sulpizio, R., Guidi, M., Capitani, G., Mantecca, P., and Zanchetta, G.: Ash
16 leachates from some recent eruptions of Mount Etna (Italy) and Popocatépetl (Mexico)
17 volcanoes and their impact on amphibian living freshwater organisms, [Biogeosciences](#), 12,
18 [7087–7106](#), doi:10.5194/bg-12-7087-2015, 2015.
- 19 De Vivo, B., Rolandi, G., Gans, P. B., Calvert, A., Bohron, W. A., Spera, F. J., and Belkin,
20 H. E.: New constraints on the pyroclastic eruptive history of the Campanian volcanic Plain
21 (Italy), *Miner. Petrol.*, 73, 47–65, doi:10.1007/s007100170010, 2001.
- 22 Fedele, F. G., Giaccio, B., Isaia, R., and Orsi, G.: The Campanian Ignimbrite eruption,
23 Heinrich Event 4, and the Palaeolithic change in Europe: a high-resolution investigation, in:
24 *Volcanism and the Earth’s Atmosphere*, edited by: Robock, A. and Oppenheimer, C.,
25 *Geophys. Monogr. Ser.*, vol. 139, American Geophysical Union, Washington, DC, 301–325,
26 2003.
- 27 Fitzsimmons, K. E., Hambach, U., Veres, D., and Iovita, R.: The Campanian Ignimbrite
28 eruption: new data on volcanic ash dispersal and its potential impact on human evolution,
29 *PLoS ONE*, 8, e65839, doi:10.1371/journal.pone.0065839, 2013.
- 30 Francke, A., Wagner, B., Just, J., Leicher, N., Gromig, R., Baumgarten, H., Vogel, H., Lacey,
31 J. H., Sadori, L., Wonik, T., Leng, M. J., Zanchetta, G., Sulpizio, R., and Giaccio, B.:

- 1 Sedimentological processes and environmental variability at Lake Ohrid (Macedonia,
2 Albania) between 640 ka and present day, *Biogeosciences Discuss.*, 12, 15111–15156,
3 doi:10.5194/bgd-12-15111-2015, 2015.
- 4 Föller, K., Stelbrink, B., Hauße, T., Albrecht, C., and Wilke, T.: Constant diversification rates
5 of endemic gastropods in ancient Lake Ohrid: Ecosystem resilience likely buffers
6 environmental fluctuations, *Biogeosciences*, 12, 7209–7222, doi:10.5194/bg-12-7209-2015,
7 2015.
- 8 Grimm, E. C.: CONISS: a FORTRAN 77 program for stratigraphically constrained cluster
9 analysis by the method of incremental sum of squares, *Comput. Geosci.*, 13, 13–35, 1987.
- 10 Harper, M. A., Howorth, R., and Mcleod, M.: Late Holocene diatoms in Lake Poukawa:
11 effects of airfall tephra and changes in depth, *New Zeal. J. Mar. Fresh.*, 20, 107–118,
12 doi:10.1080/00288330.1986.9516135, 1986.
- 13 Holling, C.: Resilience and Stability of Ecological Systems, *Ann. Rev. Ecol. Syst.*, 4, 1–23,
14 doi:10.1146/annurev.es.04.110173.000245, 1973.
- 15 Holling, C.S.: The resilience of terrestrial ecosystems: local surprise and global change. In:
16 Sustainable Development of the Biosphere, edited by: Clark, W. C. and Munn, R. E.,
17 Cambridge University Press, London, 292–317, 1986.
- 18 Hoffmann, N., Reicherter, K., Fernández-Steeger, T., and Grützner, C.: Evolution of ancient
19 Lake Ohrid: a tectonic perspective, *Biogeosciences*, 7, 3377–3386, doi:10.5194/bg-7-3377-
20 2010, 2010.
- 21 Holm, N. P. and Armstrong, D. E.: Role of nutrient limitation and competition in controlling
22 the populations of *Asterionella formosa* and *Microcystis aeruginosa* in semicontinuous
23 culture, *Limnol. Oceanogr.*, 24, 622–634, doi:10.4319/lo.1981.26.4.0622, 1981.
- 24 Jovanovska, E., Nakov, T., and Levkov, Z.: Observations of the genus *Diploneis* from Lake
25 Ohrid, Macedonia, *Diatom Res.*, 28, 237–262, doi:10.1080/0269249X.2013.797219, 2013.
- 26 Juggins, S.: rioja: Analysis of quaternary science data. Available: [http://cran.r-](http://cran.r-project.org/web/packages/cluster/index.html)
27 [project.org/web/packages/cluster/index.html](http://cran.r-project.org/web/packages/cluster/index.html) (last access: 11 August 2015), 2013.
- 28 Kaufman, L. and Rousseeuw, P. J.: Finding Groups in Data: an Introduction to Cluster
29 Analysis, Wiley, New York, doi:10.1002/9780470316801, 1990.

- 1 Kilham, P., Kilham, S. S., and Hecky, R. E.: Hypothesized resource relationships among
2 African planktonic diatoms, *Limnol. Oceanogr.*, 31(6), 1169–1181,
3 doi:10.4319/lo.1986.31.6.1169, 1986.
- 4 Kostoski, G., Albrecht, C., Trajanovski, S., and Wilke, T.: A freshwater biodiversity hotspot
5 under pressure – assessing threats and identifying conservation needs for ancient Lake Ohrid,
6 *Biogeosciences*, 7, 3999–4015, doi:10.5194/bg-7-3999-2010, 2010.
- 7 Leicher, N., Zanchetta, G., Sulpizio, R., Giaccio, B., Wagner, B., Nomade, S., and Francke,
8 A.: First tephrostratigraphic results of the DEEP site record in Lake Ohrid, Macedonia,
9 *Biogeosciences Discuss.*, 12, 15411–15460, doi:10.5194/bgd-12-15411-2015, 2015.
- 10 Leng, M. J., Wagner, B., Aufgebauer, A., Panagiotopoulos, K., Vane, C., Snelling, A.,
11 Haidon, C., Woodley, E., Vogel, H., Zanchetta, G., Sulpizio, R., and Baneschi, I.:
12 Understanding past climatic and hydrological variability in the Mediterranean from Lake
13 Prespa sediment isotope and geochemical record over the last glacial cycle, *Quat. Sci. Rev.*,
14 66, 123–136, doi:10.1016/j.quascirev.2012.07.015, 2013.
- 15 Levkov, Z. and Williams, D. M.: Fifteen new diatom (Bacillariophyta) species from Lake
16 Ohrid, Macedonia, *Phytotaxa*, 30, 1–41, doi:10.11646/phytotaxa.30.1.1, 2011.
- 17 Levkov, Z. and Williams, D. M.: Checklist of diatoms (Bacillariophyta) from Lake Ohrid and
18 Lake Prespa (Macedonia), and their watersheds, *Phytotaxa*, 45, 1–76,
19 doi:10.11646/phytotaxa.45.1.1, 2012.
- 20 Levkov, Z., Krstic, S., Metzeltin, D., and Nakov, T.: Diatoms of Lakes Prespa and Ohrid.
21 About 500 taxa from ancient lake system, in: *Iconographia Diatomologica*, vol. 16, ARG
22 Gartner Verlag, Ruggell, Liechtenstein, 603 pp., 2007.
- 23 Lindhorst, K., Krastel, S., Papenberg, C., and Heidarzadeh, M.: Modeling submarine
24 landslide-generated waves in Lake Ohrid, Macedonia/Albania, *Adv. Nat. Technol. Haz.*, 37,
25 497–506, doi:10.1007/978-3-319-00972-8_44, 2014.
- 26 Lindhorst, K., Krastel, S., Reicherter, K., Stipp, M., Wagner, B., and Schwenk, T.:
27 Sedimentary and tectonic evolution of Lake Ohrid (Macedonia/Albania), *Basin Res.*, 27, 84–
28 101, doi:10.1111/bre.12063, 2015.

1 Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., and Hornik, K: Cluster Analysis
2 Extended Rousseeuw et al., available at: [http://cran.r-](http://cran.r-project.org/web/packages/cluster/index.html)
3 [project.org/web/packages/cluster/index.html](http://cran.r-project.org/web/packages/cluster/index.html) (last access: 11 August 2015), 2013.

4 Matzinger, A. and Schmid, M.: Eutrophication of ancient Lake Ohrid: global warming
5 amplifies detrimental effects of increased nutrient inputs, *Limnol. Oceanogr.*, 52, 338–353,
6 doi:10.4319/lo.2007.52.1.0338, 2007.

7 Matzinger, A., Jordanoski, M., Veljanoska-Sarafiloska, E., Sturm, M., Müller, B., and Wüest,
8 A.: Is Lake Prespa jeopardizing the ecosystem of Ancient Lake Ohrid?, *Hydrobiologia*, 553,
9 89–109, doi:10.1007/s10750-005-6427-9, 2006a.

10 Matzinger, A., Spirkovski, Z., Patceva, S., and Wüest, A.: Sensitivity of ancient Lake Ohrid
11 to local anthropogenic impacts and global warming, *J. Great Lakes Res.*, 32, 158–179,
12 doi:10.3394/0380-1330(2006)32[158:SOALOT]2.0.CO;2, 2006b.

13 Niemi, G. J., DeVore, P., Detenbeck, N., Taylor, D., Lima, A., Pastor, J., Yount, D. J., and
14 Naiman, R. J.: Overview of case studies on recovery of aquatic systems from disturbance,
15 *Environ. Manage.*, 14, 571–587, doi:10.1007/bf02394710, 1990.

16 Panagiotopoulos, K., Böhm, A., Leng, M., Wagner, B., and Schäbitz, F.: Climate variability
17 over the last 92 ka in SW Balkans from analysis of sediments from Lake Prespa, *Clim. Past*,
18 10, 643–660, doi:10.5194/cp-10-643-2014, 2014.

19 Pavlov, A., Levkov, Z., Williams, D. M., and Edlund, M. E.: Observations on *Hippodonta*
20 (Bacillariophyceae) in selected ancient lakes, *Phytotaxa*, 90, 1–53,
21 doi:10.11646/phytotaxa.90.1.1, 2013.

22 Reed, J. M., Cvetkoska, A., Levkov, Z., Vogel, H., and Wagner, B.: The last glacial-
23 interglacial cycle in Lake Ohrid (Macedonia/Albania): testing diatom response to climate,
24 *Biogeosciences*, 7, 3083–3094, doi:10.5194/bg-7-3083-2010, 2010.

25 Renberg, I.: A procedure for preparing large sets of diatom slides from sediment cores, *J.*
26 *Paleolimnol.*, 4, 87–90, doi:10.1007/BF00208301, 1990.

27 Scheffer, M. and Carpenter, S.: Catastrophic regime shifts in ecosystems: linking theory to
28 observation, *Trends Ecol. Evol.*, 18, 648–656, doi:10.1016/j.tree.2003.09.002, 2003.

- 1 [Schneider, S. C., Cara, M., Eriksen, T. E., Goreska, B. B., Imeri, A., Kupe, L., Lokoska, T.,](#)
2 [Patceva, S., Trajanovska, S., Trajanovski, S., Talevska, M., and Sarafiloska, E. V.:](#)
3 [Eutrophication impacts littoral biota in Lake Ohrid while water phosphorus concentrations are](#)
4 [low, *Limnologica*, 44, 90–97, doi:10.1016/j.limno.2013.09.002, 2014.](#)
- 5 [Spanbauer, T. L., Allen, C. R., Angeler, D. G., Eason, T., Fritz, S. C., Garmestani, A. S.,](#)
6 [Nash, K. L., and Stone, J. R.: Prolonged instability prior to a regime shift, *PLoS ONE*, 9\(10\),](#)
7 [e108936, doi:10.1371/journal.pone.0108936, 2014.](#)
- 8 Stanković, S.: The Balkan Lake Ohrid and its Living World, Monogr. Biol. IX, Uitgeverij Dr.
9 W. Junk, Den Haag, [The Netherlands](#), 1960.
- 10 Sulpizio, R., Zanchetta, G., D’Orazio, M., Vogel, H., and Wagner, B.: Tephrostratigraphy and
11 tephrochronology of lakes Ohrid and Prespa, *Balkans, Biogeosciences*, 7, 3273–3288,
12 doi:10.5194/bg-7-3273-2010, 2010.
- 13 Telford, R. J., Barkerb, P., Metcalfec, S., and Newtond, A.: Lacustrine responses to tephra
14 deposition: examples from Mexico, *Quaternary Sci. Rev.*, 23, 2337–2353,
15 doi:10.1016/j.quascirev.2004.03.014, 2004.
- 16 Urrutia, R., Araneda, A., Cruces, F., Torres, L., Chirinos, L., Treutler, H. C., Fagel, N.,
17 Bertrand, S., Alvial, I., Barra, R., and Chapron, E.: Changes in diatom, pollen, and
18 chironomid assemblages in response to a recent volcanic event in Lake Galletué (Chilean
19 Andes), *Limnologica*, 37, 49–62, doi:10.1016/j.limno.2006.09.003, 2007.
- 20 Vogel, H., Wagner, B., Zanchetta, G., Sulpizio, R., and Rosén, P.: A paleoclimate record with
21 tephrochronological age control for the last glacial–interglacial cycle from Lake Ohrid,
22 Albania and Macedonia, *J. Paleolimnol.*, 44, 295–310, doi:10.1007/s10933-009-9404-x,
23 [2010a.](#)
- 24 [Vogel, H., Wessels, M., Albrecht, C., Stich H.-B., and Wagner, B.: Spatial variability of](#)
25 [recent sedimentation in Lake Ohrid \(Albania/Macedonia\), *Biogeosciences*, 7, 3333–3342,](#)
26 [doi:10.5194/bg-7-3333-2010, 2010b.](#)
- 27 Wagner, B., Reicherter, K., Daut, G., Wessels, M., Matzinger, A., Schwalb, A., Spirkovski,
28 Z., and Sanxhaku, M.: The potential of Lake Ohrid for long-term palaeoenvironmental
29 reconstructions, *Palaeogeogr. Palaeocl.*, 259, 341–356, doi:10.1016/j.palaeo.2007.10.015,
30 2008.

- 1 Wagner, B., Vogel, H., Zanchetta, G., and Sulpizio R.: Environmental changes on the Balkans
2 recorded in the sediments from lakes Prespa and Ohrid, *Biogeosciences*, 7, 3365–3392,
3 doi:[10.5194/bg-7-3187-2010](https://doi.org/10.5194/bg-7-3187-2010), 2010.
- 4 Wagner, B., Aufgebauer, A., Vogel, H., Zanchetta, G., Sulpizio, R., and Damaschke, M.: Late
5 Pleistocene and Holocene contourite drift in Lake Prespa (Albania/F.Y.R. of Macedonia/
6 Greece), *Quatern. Int.*, 274, 112–121, doi:[10.1016/j.quaint.2012.02.016](https://doi.org/10.1016/j.quaint.2012.02.016), 2012a.
- 7 Wagner, B., Francke, A., Sulpizio, R., Zanchetta, G., Lindhorst, K., Krastel, S., Vogel, H.,
8 Rethemeyer, J., Daut, G., Grazhdani, A., Lushaj, B., and Trajanovski, S.: Possible earthquake
9 trigger for 6th century mass wasting deposit at Lake Ohrid (Macedonia/Albania), *Clim. Past*,
10 8, 2069–2078, doi:[10.5194/cp-8-2069-2012](https://doi.org/10.5194/cp-8-2069-2012), 2012b.
- 11 Wagner, B., Wilke, T., Krastel, S., Zanchetta, G., Sulpizio, R., Reicherter, K., Leng, M.,
12 Grazhdani, A., Trajanovski, S., Francke, A., Lindhorst, K., Levkov, Z., Cvetkoska, A., [Reed,](#)
13 [J. M.](#), Zhang, X., Lacey, J., Wonik, T., Baumgarten, H., and Vogel, H.: The SCOPSCO
14 drilling project recovers more than 1.2 million years of history from Lake Ohrid, *Sci. Dril.*,
15 17, 19–29, doi:[10.5194/sd-17-19-2014](https://doi.org/10.5194/sd-17-19-2014), 2014.
- 16 [Watzin, M. C., Puka, V., and Naumoski, T. B.: Lake Ohrid and its watershed: state of the](#)
17 [environment report, Lake Ohrid Conservation Project, Tirana, Albania and Ohrid, Macedonia,](#)
18 [2002.](#)
- 19 [Wutke, K., Wulf, S., Tomlinson, L. E., Hardiman, M., Dulski, P., Luterbacher, J., and Brauer,](#)
20 [A.: Geochemical properties and environmental impacts of seven Campanian tephra layers](#)
21 [deposited between 40 and 38 ka BP in the varved lake sediments of Lago Grande di](#)
22 [Monticchio, southern Italy, *Quat. Sci. Rev.*, 118, 67–83, doi:\[10.1016/j.quascirev.2014.05.017\]\(https://doi.org/10.1016/j.quascirev.2014.05.017\),](#)
23 [2015.](#)
- 24 Zhang, X., [Reed, J. M.](#), Lacey, J. H., Francke, A., Leng, M. J., Levkov, Z., and Wagner, B.:
25 [Complexity of diatom response to Lateglacial and Holocene climate and environmental](#)
26 [change in ancient, deep, and oligotrophic Lake Ohrid \(Macedonia/Albania\)](#), *Biogeosciences*
27 *Discuss.*, 12, 14343–14375, doi:[10.5194/bgd-12-14343-2015](https://doi.org/10.5194/bgd-12-14343-2015), 2015.

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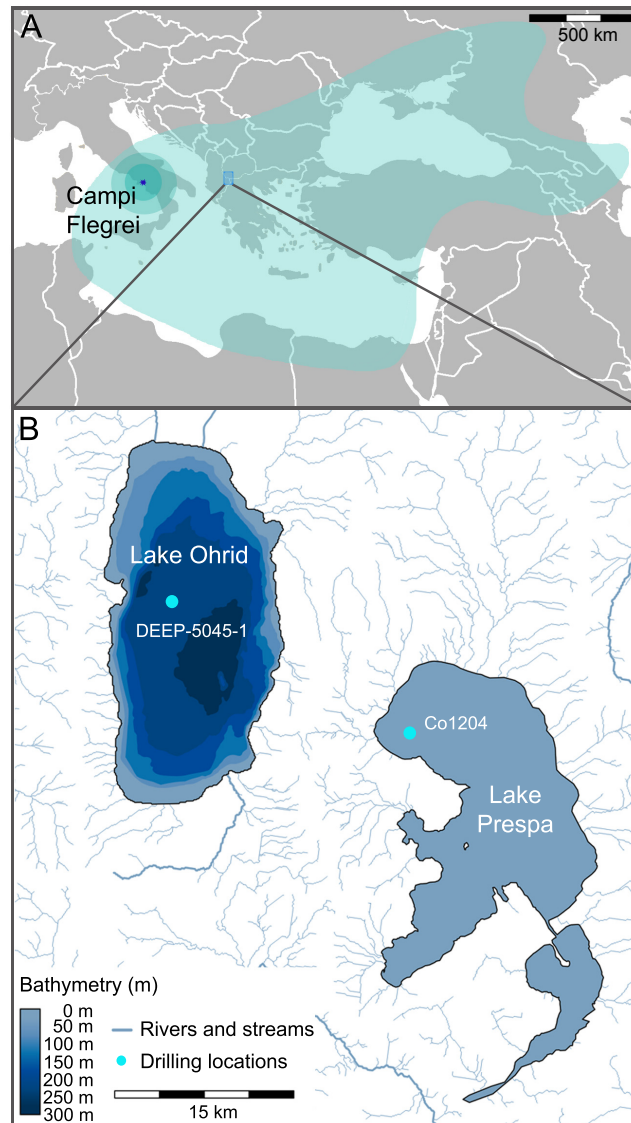


Figure 1. Maps showing (A) the Y-5 tephra distribution from the Campi Flegrei caldera in Europe (blueish-green shading, sensu Fitzsimmons et al., 2013) and (B) the drilling sites in lakes Ohrid (DEEP-5045-1) and Prespa (Co1204).

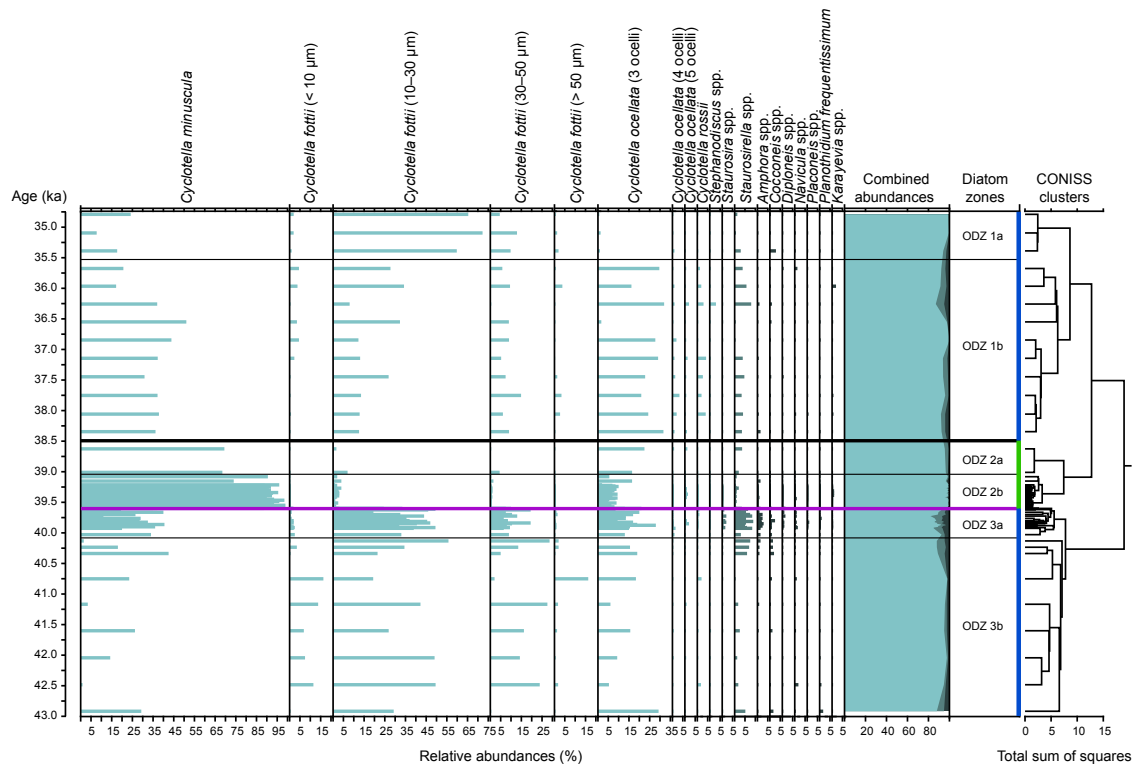


Figure 2. Summary diatom diagram for the Ohrid core (DEEP-5045-1). Only diatom taxa with relative abundances of > 2% are shown. Individual abundances are color-coded according to life style (light blue: planktonic, medium blue: facultative planktonic, dark blue: benthic). Diatom zones and subzones were 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.

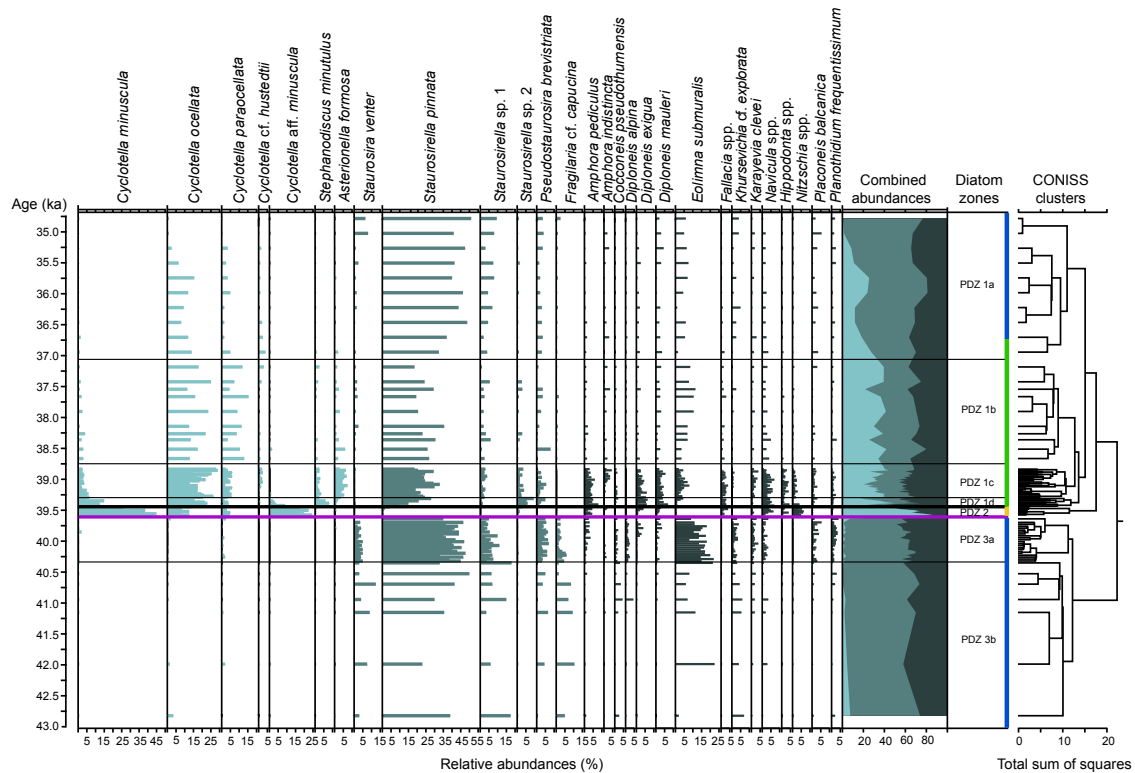


Figure 3. Summary diatom diagram for the Prespa core (Co1204). Only diatom taxa with relative abundances of > 4% are shown. Individual abundances are color-coded according to life style (light blue: planktonic, medium blue: facultative planktonic, dark blue: benthic). Diatom zones and subzones were defined 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.

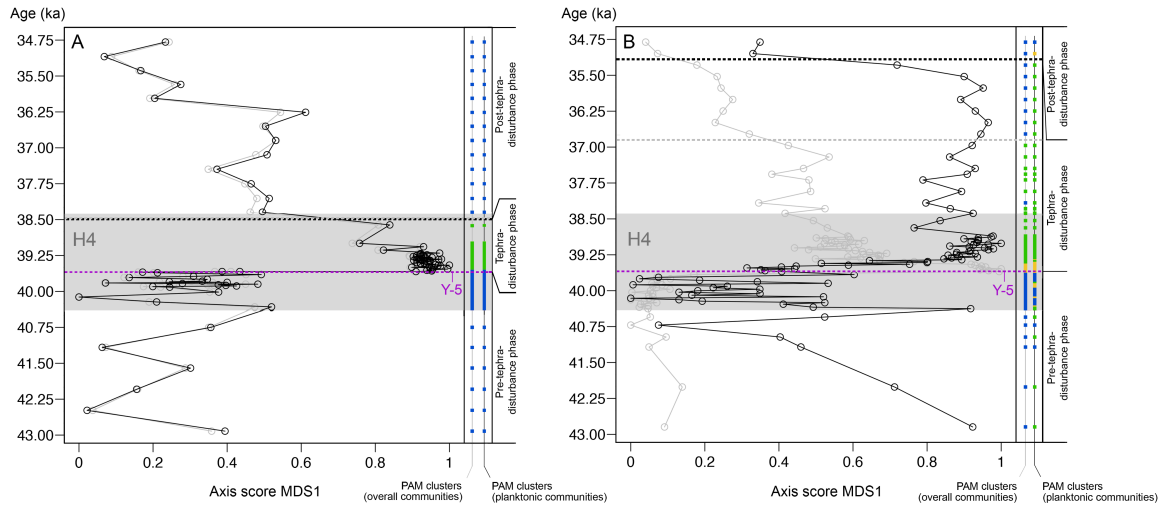


Figure 4. Diagrams showing changes in MDS diatom community compositions (black curves: planktonic communities; grey curves: overall communities) and respective PAM community assignments (colored rectangles) for lakes Ohrid (A) and Prespa (B). The purple dashed lines indicate the timing of the Y-5 eruption;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

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

3

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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±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±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 km², 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⁻³ (Matzinger et al., 2007) and total nitrogen (TN) concentration of
17 171–512 mg·m⁻³ (Watzin et al., 2002). The lake's silica (SI) concentration is < 200 mg·m⁻³ in
18 the trophogenic zone during summer (Stanković, 1960), the average water pH and water
19 conductivity are 8.48 and 208 µS cm⁻¹, 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 km², 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⁻³ (Wagner et al.,
27 2010), an average TN concentration of ca. 2000 mg·m⁻³, 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 ± 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% H₂O₂ 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% SiO₂, 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% SiO₂ 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 SiO₂ 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±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

25 **References**

26 Albrecht, C. and Wilke, T.: Ancient Lake Ohrid: biodiversity and evolution, *Hydrobiologia*,
27 615, 103–140, doi:10.1007/s10750-008-9558-y, 2008.

28 Albrecht, C., Wolff, C., Glöer, P., and Wilke, T: Concurrent evolution of ancient sister lakes
29 and sister species: the freshwater gastropod genus *Radix* in lakes Ohrid and Prespa,
30 *Hydrobiologia*, 615, 157–167, doi:10.1007/s10750-008-9555-1, 2008.

1 Allen, H. L. and Ocevski, B. T.: Limnological studies in a large, deep, oligotrophic lake (Lake
2 Ohrid, Yugoslavia). A summary of nutritional radiobioassay responses of the pelagial
3 phytoplankton, *Arch. Hydrobiol.*, 53, 1–21, doi:10.1007/BF00021231, 1977.

4 Baho, D. L., Drakare, S., Johnson, R. K., Allen, C. R., and Angeler, D. G.: Similar resilience
5 characteristics in lakes with different management practices, *PLoS ONE*, 9, e91881,
6 doi:10.1371/journal.pone.0091881, 2014.

7 Barker, P., Williamson, D., Gasse, F., and Gibert, E.: Climatic and volcanic forcing revealed
8 in a 50,000 year diatom record from Lake Massoko, Tanzania, *Quaternary Res.*, 60, 368–376,
9 doi:10.1016/S0033-5894(03)00114-5, 2003.

10 Baumgarten, H., Wonik, T., Tanner, D. C., Francke, A., Wagner, B., Zanchetta, G., Sulpizio,
11 R., Giaccio, B., and Nomade, S.: Age depth-model for the past 630 ka in Lake Ohrid
12 (Macedonia/Albania) based on cyclostratigraphic analysis of downhole gamma ray data,
13 [Biogeosciences, 12, 7453–7465, doi:10.5194/bg-12-7453-2015, 2015.](https://doi.org/10.5194/bg-12-7453-2015)

14 Bond, G., Broecker, W., Johnsen, S., McManus, J., Labeyrie, L., Jouzel, J., and Bonani, G.:
15 Correlations between climate records from North Atlantic sediments and Greenland ice,
16 *Nature*, 365, 143–147, doi:10.1038/365143a0, 1993.

17 Bray, J. R. and Curtis, J. T.: An ordination of upland forest communities of southern
18 Wisconsin, *Ecol. Monogr.*, 27, 325–349, doi:10.2307/1942268, 1957.

19 Carpenter, R. S.: Spatial signatures of resilience, *Nature*, 496, 308–309,
20 doi:10.1038/nature12092, 2013.

21 Costa, A., Folch, A., Macedonio, G., Giaccio, B., Isaia, R., and Smith, V. C.: Quantifying
22 volcanic ash dispersal and impact of the Campanian Ignimbrite super-eruption, *Geophys. Res.*
23 *Lett.*, 39, L10310, doi:10.1029/2012GL051605, 2012.

24 Cruces, F., Urrutia, R., Parra, O., Araneda, A., Treutler, H., Bertrand, S., Fagel, N., Torres,
25 Le., Barra, R., and Chirinos, L.: Changes in diatom assemblages in an Andean lake in
26 response to a recent volcanic event, *Arch. Hydrobiol.*, 165, 23–35, doi:10.1127/0003-
27 9136/2006/0165-0023, 2006.

28 Cvetkoska, A., Reed, J. M., and Levkov, Z.: Diatoms as indicators of environmental change
29 in ancient Lake Ohrid during the last glacial–interglacial cycle (ca 140 ka), in: *Diatom*

- 1 Monographs, vol. 15, edited by: Witkowski, A., ARG Gartner Verlag, Ruggell, Liechtenstein,
2 220 pp., 2012.
- 3 Cvetkoska, A., Levkov, Z., [Reed, J. M.](#), and Wagner, B.: Late Glacial to Holocene climate
4 change and human impact in the Mediterranean: the last ca. 17 ka diatom record of Lake
5 Prespa (Macedonia/Albania/Greece), *Palaeogeogr. Palaeoclimatol.*, 406, 22–32,
6 doi:10.1016/j.palaeo.2014.04.010, 2014.
- 7 [Cvetkoska, A., Jovanovska, E., Francke, A., Tofilovska, S., Vogel, H., Levkov, Z., Donders,
8 T., Wagner, B., and Wagner-Cremer, F.: Ecosystem regimes and responses in a coupled
9 ancient lake system from MIS 5b to present: the diatom record of lakes Ohrid and Prespa,
10 *Biogeosciences Discuss.*, 12, 15051–15086, doi:10.5194/bgd-12-15051-2015, 2015a.](#)
- 11 Cvetkoska, A., Levkov, Z., [Reed, J. M.](#), Wagner, B., Panagiotopoulos, K., Leng, M., and
12 Lacey, J.: Quaternary climate change and Heinrich events in the southern Balkans: Lake
13 Prespa diatom palaeolimnology from the last interglacial to present, *J. Paleolimnol.*, 53, 215–
14 231, doi:10.1007/s10933-014-9821-3, [2015b.](#)
- 15 D’Addabbo, M., Sulpizio, R., Guidi, M., Capitani, G., Mantecca, P., and Zanchetta, G.: Ash
16 leachates from some recent eruptions of Mount Etna (Italy) and Popocatepetl (Mexico)
17 volcanoes and their impact on amphibian living freshwater organisms, [Biogeosciences](#), 12,
18 [7087–7106, doi:10.5194/bg-12-7087-2015, 2015.](#)
- 19 De Vivo, B., Rolandi, G., Gans, P. B., Calvert, A., Bohron, W. A., Spera, F. J., and Belkin,
20 H. E.: New constraints on the pyroclastic eruptive history of the Campanian volcanic Plain
21 (Italy), *Miner. Petrol.*, 73, 47–65, doi:10.1007/s007100170010, 2001.
- 22 Fedele, F. G., Giaccio, B., Isaia, R., and Orsi, G.: The Campanian Ignimbrite eruption,
23 Heinrich Event 4, and the Palaeolithic change in Europe: a high-resolution investigation, in:
24 *Volcanism and the Earth’s Atmosphere*, edited by: Robock, A. and Oppenheimer, C.,
25 *Geophys. Monogr. Ser.*, vol. 139, American Geophysical Union, Washington, DC, 301–325,
26 2003.
- 27 Fitzsimmons, K. E., Hambach, U., Veres, D., and Iovita, R.: The Campanian Ignimbrite
28 eruption: new data on volcanic ash dispersal and its potential impact on human evolution,
29 *PLoS ONE*, 8, e65839, doi:10.1371/journal.pone.0065839, 2013.
- 30 Francke, A., Wagner, B., Just, J., Leicher, N., Gromig, R., Baumgarten, H., Vogel, H., Lacey,
31 J. H., Sadori, L., Wonik, T., Leng, M. J., Zanchetta, G., Sulpizio, R., and Giaccio, B.:

- 1 Sedimentological processes and environmental variability at Lake Ohrid (Macedonia,
2 Albania) between 640 ka and present day, *Biogeosciences Discuss.*, 12, 15111–15156,
3 doi:10.5194/bgd-12-15111-2015, 2015.
- 4 Föller, K., Stelbrink, B., Hauffe, T., Albrecht, C., and Wilke, T.: Constant diversification rates
5 of endemic gastropods in ancient Lake Ohrid: Ecosystem resilience likely buffers
6 environmental fluctuations, *Biogeosciences*, 12, 7209–7222, doi:10.5194/bg-12-7209-2015,
7 2015.
- 8 Grimm, E. C.: CONISS: a FORTRAN 77 program for stratigraphically constrained cluster
9 analysis by the method of incremental sum of squares, *Comput. Geosci.*, 13, 13–35, 1987.
- 10 Harper, M. A., Howorth, R., and Mcleod, M.: Late Holocene diatoms in Lake Poukawa:
11 effects of airfall tephra and changes in depth, *New Zeal. J. Mar. Fresh.*, 20, 107–118,
12 doi:10.1080/00288330.1986.9516135, 1986.
- 13 Holling, C.: Resilience and Stability of Ecological Systems, *Ann. Rev. Ecol. Syst.*, 4, 1–23,
14 doi:10.1146/annurev.es.04.110173.000245, 1973.
- 15 Holling, C.S.: The resilience of terrestrial ecosystems: local surprise and global change. In:
16 Sustainable Development of the Biosphere, edited by: Clark, W. C. and Munn, R. E.,
17 Cambridge University Press, London, 292–317, 1986.
- 18 Hoffmann, N., Reicherter, K., Fernández-Steeger, T., and Grützner, C.: Evolution of ancient
19 Lake Ohrid: a tectonic perspective, *Biogeosciences*, 7, 3377–3386, doi:10.5194/bg-7-3377-
20 2010, 2010.
- 21 Holm, N. P. and Armstrong, D. E.: Role of nutrient limitation and competition in controlling
22 the populations of *Asterionella formosa* and *Microcystis aeruginosa* in semicontinuous
23 culture, *Limnol. Oceanogr.*, 24, 622–634, doi:10.4319/lo.1981.26.4.0622, 1981.
- 24 Jovanovska, E., Nakov, T., and Levkov, Z.: Observations of the genus *Diploneis* from Lake
25 Ohrid, Macedonia, *Diatom Res.*, 28, 237–262, doi:10.1080/0269249X.2013.797219, 2013.
- 26 Juggins, S.: rioja: Analysis of quaternary science data. Available: [http://cran.r-](http://cran.r-project.org/web/packages/cluster/index.html)
27 [project.org/web/packages/cluster/index.html](http://cran.r-project.org/web/packages/cluster/index.html) (last access: 11 August 2015), 2013.
- 28 Kaufman, L. and Rousseeuw, P. J.: Finding Groups in Data: an Introduction to Cluster
29 Analysis, Wiley, New York, doi:10.1002/9780470316801, 1990.

- 1 Kilham, P., Kilham, S. S., and Hecky, R. E.: Hypothesized resource relationships among
2 African planktonic diatoms, *Limnol. Oceanogr.*, 31(6), 1169–1181,
3 doi:10.4319/lo.1986.31.6.1169, 1986.
- 4 Kostoski, G., Albrecht, C., Trajanovski, S., and Wilke, T.: A freshwater biodiversity hotspot
5 under pressure – assessing threats and identifying conservation needs for ancient Lake Ohrid,
6 *Biogeosciences*, 7, 3999–4015, doi:10.5194/bg-7-3999-2010, 2010.
- 7 Leicher, N., Zanchetta, G., Sulpizio, R., Giaccio, B., Wagner, B., Nomade, S., and Francke,
8 A.: First tephrostratigraphic results of the DEEP site record in Lake Ohrid, Macedonia,
9 *Biogeosciences Discuss.*, 12, 15411–15460, doi:10.5194/bgd-12-15411-2015, 2015.
- 10 Leng, M. J., Wagner, B., Aufgebauer, A., Panagiotopoulos, K., Vane, C., Snelling, A.,
11 Haidon, C., Woodley, E., Vogel, H., Zanchetta, G., Sulpizio, R., and Baneschi, I.:
12 Understanding past climatic and hydrological variability in the Mediterranean from Lake
13 Prespa sediment isotope and geochemical record over the last glacial cycle, *Quat. Sci. Rev.*,
14 66, 123–136, doi:10.1016/j.quascirev.2012.07.015, 2013.
- 15 Levkov, Z. and Williams, D. M.: Fifteen new diatom (Bacillariophyta) species from Lake
16 Ohrid, Macedonia, *Phytotaxa*, 30, 1–41, doi:10.11646/phytotaxa.30.1.1, 2011.
- 17 Levkov, Z. and Williams, D. M.: Checklist of diatoms (Bacillariophyta) from Lake Ohrid and
18 Lake Prespa (Macedonia), and their watersheds, *Phytotaxa*, 45, 1–76,
19 doi:10.11646/phytotaxa.45.1.1, 2012.
- 20 Levkov, Z., Krstic, S., Metzeltin, D., and Nakov, T.: Diatoms of Lakes Prespa and Ohrid.
21 About 500 taxa from ancient lake system, in: *Iconographia Diatomologica*, vol. 16, ARG
22 Gartner Verlag, Ruggell, Liechtenstein, 603 pp., 2007.
- 23 Lindhorst, K., Krastel, S., Papenberg, C., and Heidarzadeh, M.: Modeling submarine
24 landslide-generated waves in Lake Ohrid, Macedonia/Albania, *Adv. Nat. Technol. Haz.*, 37,
25 497–506, doi:10.1007/978-3-319-00972-8_44, 2014.
- 26 Lindhorst, K., Krastel, S., Reicherter, K., Stipp, M., Wagner, B., and Schwenk, T.:
27 Sedimentary and tectonic evolution of Lake Ohrid (Macedonia/Albania), *Basin Res.*, 27, 84–
28 101, doi:10.1111/bre.12063, 2015.

1 Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., and Hornik, K: Cluster Analysis
2 Extended Rousseeuw et al., available at: [http://cran.r-](http://cran.r-project.org/web/packages/cluster/index.html)
3 [project.org/web/packages/cluster/index.html](http://cran.r-project.org/web/packages/cluster/index.html) (last access: 11 August 2015), 2013.

4 Matzinger, A. and Schmid, M.: Eutrophication of ancient Lake Ohrid: global warming
5 amplifies detrimental effects of increased nutrient inputs, *Limnol. Oceanogr.*, 52, 338–353,
6 doi:10.4319/lo.2007.52.1.0338, 2007.

7 Matzinger, A., Jordanoski, M., Veljanoska-Sarafiloska, E., Sturm, M., Müller, B., and Wüest,
8 A.: Is Lake Prespa jeopardizing the ecosystem of Ancient Lake Ohrid?, *Hydrobiologia*, 553,
9 89–109, doi:10.1007/s10750-005-6427-9, 2006a.

10 Matzinger, A., Spirkovski, Z., Patceva, S., and Wüest, A.: Sensitivity of ancient Lake Ohrid
11 to local anthropogenic impacts and global warming, *J. Great Lakes Res.*, 32, 158–179,
12 doi:10.3394/0380-1330(2006)32[158:SOALOT]2.0.CO;2, 2006b.

13 Niemi, G. J., DeVore, P., Detenbeck, N., Taylor, D., Lima, A., Pastor, J., Yount, D. J., and
14 Naiman, R. J.: Overview of case studies on recovery of aquatic systems from disturbance,
15 *Environ. Manage.*, 14, 571–587, doi:10.1007/bf02394710, 1990.

16 Panagiotopoulos, K., Böhm, A., Leng, M., Wagner, B., and Schäbitz, F.: Climate variability
17 over the last 92 ka in SW Balkans from analysis of sediments from Lake Prespa, *Clim. Past*,
18 10, 643–660, doi:10.5194/cp-10-643-2014, 2014.

19 Pavlov, A., Levkov, Z., Williams, D. M., and Edlund, M. E.: Observations on *Hippodonta*
20 (Bacillariophyceae) in selected ancient lakes, *Phytotaxa*, 90, 1–53,
21 doi:10.11646/phytotaxa.90.1.1, 2013.

22 Reed, J. M., Cvetkoska, A., Levkov, Z., Vogel, H., and Wagner, B.: The last glacial-
23 interglacial cycle in Lake Ohrid (Macedonia/Albania): testing diatom response to climate,
24 *Biogeosciences*, 7, 3083–3094, doi:10.5194/bg-7-3083-2010, 2010.

25 Renberg, I.: A procedure for preparing large sets of diatom slides from sediment cores, *J.*
26 *Paleolimnol.*, 4, 87–90, doi:10.1007/BF00208301, 1990.

27 Scheffer, M. and Carpenter, S.: Catastrophic regime shifts in ecosystems: linking theory to
28 observation, *Trends Ecol. Evol.*, 18, 648–656, doi:10.1016/j.tree.2003.09.002, 2003.

- 1 [Schneider, S. C., Cara, M., Eriksen, T. E., Goreska, B. B., Imeri, A., Kupe, L., Lokoska, T.,](#)
2 [Patceva, S., Trajanovska, S., Trajanovski, S., Talevska, M., and Sarafiloska, E. V.:](#)
3 [Eutrophication impacts littoral biota in Lake Ohrid while water phosphorus concentrations are](#)
4 [low, *Limnologica*, 44, 90–97, doi:10.1016/j.limno.2013.09.002, 2014.](#)
- 5 [Spanbauer, T. L., Allen, C. R., Angeler, D. G., Eason, T., Fritz, S. C., Garmestani, A. S.,](#)
6 [Nash, K. L., and Stone, J. R.: Prolonged instability prior to a regime shift, *PLoS ONE*, 9\(10\),](#)
7 [e108936, doi:10.1371/journal.pone.0108936, 2014.](#)
- 8 Stanković, S.: The Balkan Lake Ohrid and its Living World, Monogr. Biol. IX, Uitgeverij Dr.
9 W. Junk, Den Haag, [The Netherlands](#), 1960.
- 10 Sulpizio, R., Zanchetta, G., D’Orazio, M., Vogel, H., and Wagner, B.: Tephrostratigraphy and
11 tephrochronology of lakes Ohrid and Prespa, *Balkans, Biogeosciences*, 7, 3273–3288,
12 doi:10.5194/bg-7-3273-2010, 2010.
- 13 Telford, R. J., Barkerb, P., Metcalfec, S., and Newtond, A.: Lacustrine responses to tephra
14 deposition: examples from Mexico, *Quaternary Sci. Rev.*, 23, 2337–2353,
15 doi:10.1016/j.quascirev.2004.03.014, 2004.
- 16 Urrutia, R., Araneda, A., Cruces, F., Torres, L., Chirinos, L., Treutler, H. C., Fagel, N.,
17 Bertrand, S., Alvial, I., Barra, R., and Chapron, E.: Changes in diatom, pollen, and
18 chironomid assemblages in response to a recent volcanic event in Lake Galletué (Chilean
19 Andes), *Limnologica*, 37, 49–62, doi:10.1016/j.limno.2006.09.003, 2007.
- 20 Vogel, H., Wagner, B., Zanchetta, G., Sulpizio, R., and Rosén, P.: A paleoclimate record with
21 tephrochronological age control for the last glacial–interglacial cycle from Lake Ohrid,
22 Albania and Macedonia, *J. Paleolimnol.*, 44, 295–310, doi:10.1007/s10933-009-9404-x,
23 [2010a.](#)
- 24 [Vogel, H., Wessels, M., Albrecht, C., Stich H.-B., and Wagner, B.: Spatial variability of](#)
25 [recent sedimentation in Lake Ohrid \(Albania/Macedonia\), *Biogeosciences*, 7, 3333–3342,](#)
26 [doi:10.5194/bg-7-3333-2010, 2010b.](#)
- 27 Wagner, B., Reicherter, K., Daut, G., Wessels, M., Matzinger, A., Schwalb, A., Spirkovski,
28 Z., and Sanxhaku, M.: The potential of Lake Ohrid for long-term palaeoenvironmental
29 reconstructions, *Palaeogeogr. Palaeocl.*, 259, 341–356, doi:10.1016/j.palaeo.2007.10.015,
30 2008.

- 1 Wagner, B., Vogel, H., Zanchetta, G., and Sulpizio R.: Environmental changes on the Balkans
2 recorded in the sediments from lakes Prespa and Ohrid, *Biogeosciences*, 7, 3365–3392,
3 doi:[10.5194/bg-7-3187-2010](https://doi.org/10.5194/bg-7-3187-2010), 2010.
- 4 Wagner, B., Aufgebauer, A., Vogel, H., Zanchetta, G., Sulpizio, R., and Damaschke, M.: Late
5 Pleistocene and Holocene contourite drift in Lake Prespa (Albania/F.Y.R. of Macedonia/
6 Greece), *Quatern. Int.*, 274, 112–121, doi:[10.1016/j.quaint.2012.02.016](https://doi.org/10.1016/j.quaint.2012.02.016), 2012a.
- 7 Wagner, B., Francke, A., Sulpizio, R., Zanchetta, G., Lindhorst, K., Krastel, S., Vogel, H.,
8 Rethemeyer, J., Daut, G., Grazhdani, A., Lushaj, B., and Trajanovski, S.: Possible earthquake
9 trigger for 6th century mass wasting deposit at Lake Ohrid (Macedonia/Albania), *Clim. Past*,
10 8, 2069–2078, doi:[10.5194/cp-8-2069-2012](https://doi.org/10.5194/cp-8-2069-2012), 2012b.
- 11 Wagner, B., Wilke, T., Krastel, S., Zanchetta, G., Sulpizio, R., Reicherter, K., Leng, M.,
12 Grazhdani, A., Trajanovski, S., Francke, A., Lindhorst, K., Levkov, Z., Cvetkoska, A., [Reed,](#)
13 [J. M.](#), Zhang, X., Lacey, J., Wonik, T., Baumgarten, H., and Vogel, H.: The SCOPSCO
14 drilling project recovers more than 1.2 million years of history from Lake Ohrid, *Sci. Dril.*,
15 17, 19–29, doi:[10.5194/sd-17-19-2014](https://doi.org/10.5194/sd-17-19-2014), 2014.
- 16 [Watzin, M. C., Puka, V., and Naumoski, T. B.: Lake Ohrid and its watershed: state of the](#)
17 [environment report, Lake Ohrid Conservation Project, Tirana, Albania and Ohrid, Macedonia,](#)
18 [2002.](#)
- 19 [Wutke, K., Wulf, S., Tomlinson, L. E., Hardiman, M., Dulski, P., Luterbacher, J., and Brauer,](#)
20 [A.: Geochemical properties and environmental impacts of seven Campanian tephra layers](#)
21 [deposited between 40 and 38 ka BP in the varved lake sediments of Lago Grande di](#)
22 [Monticchio, southern Italy, *Quat. Sci. Rev.*, 118, 67–83, doi:\[10.1016/j.quascirev.2014.05.017\]\(https://doi.org/10.1016/j.quascirev.2014.05.017\),](#)
23 [2015.](#)
- 24 Zhang, X., [Reed, J. M.](#), Lacey, J. H., Francke, A., Leng, M. J., Levkov, Z., and Wagner, B.:
25 [Complexity of diatom response to Lateglacial and Holocene climate and environmental](#)
26 [change in ancient, deep, and oligotrophic Lake Ohrid \(Macedonia/Albania\)](#), *Biogeosciences*
27 *Discuss.*, 12, 14343–14375, doi:[10.5194/bgd-12-14343-2015](https://doi.org/10.5194/bgd-12-14343-2015), 2015.

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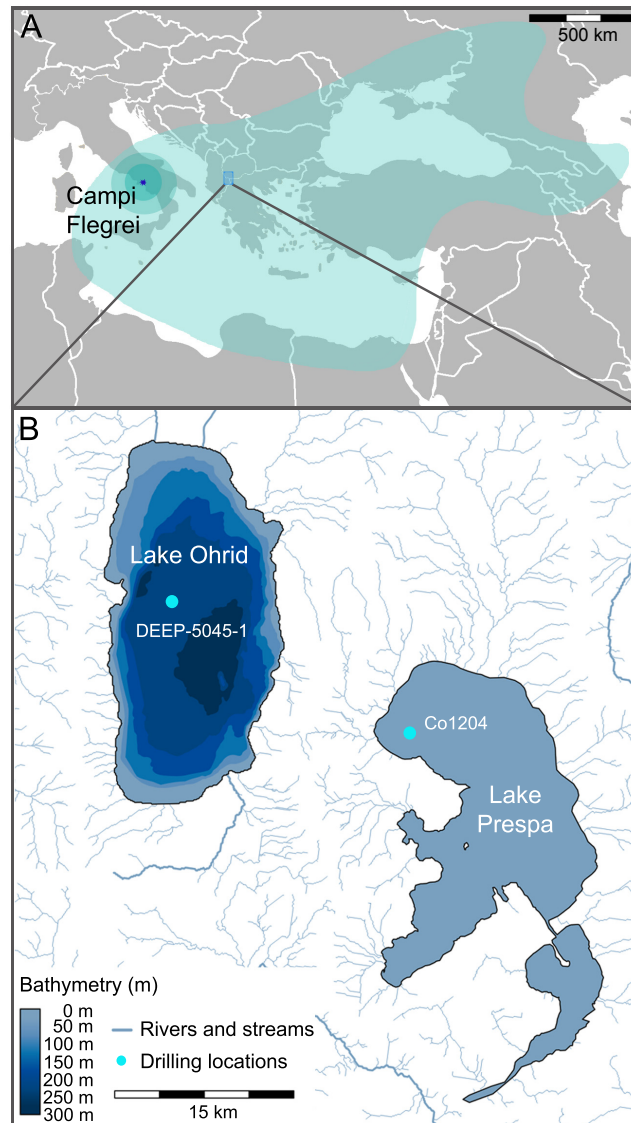


Figure 1. Maps showing (A) the Y-5 tephra distribution from the Campi Flegrei caldera in Europe (blueish-green shading, sensu Fitzsimmons et al., 2013) and (B) the drilling sites in lakes Ohrid (DEEP-5045-1) and Prespa (Co1204).

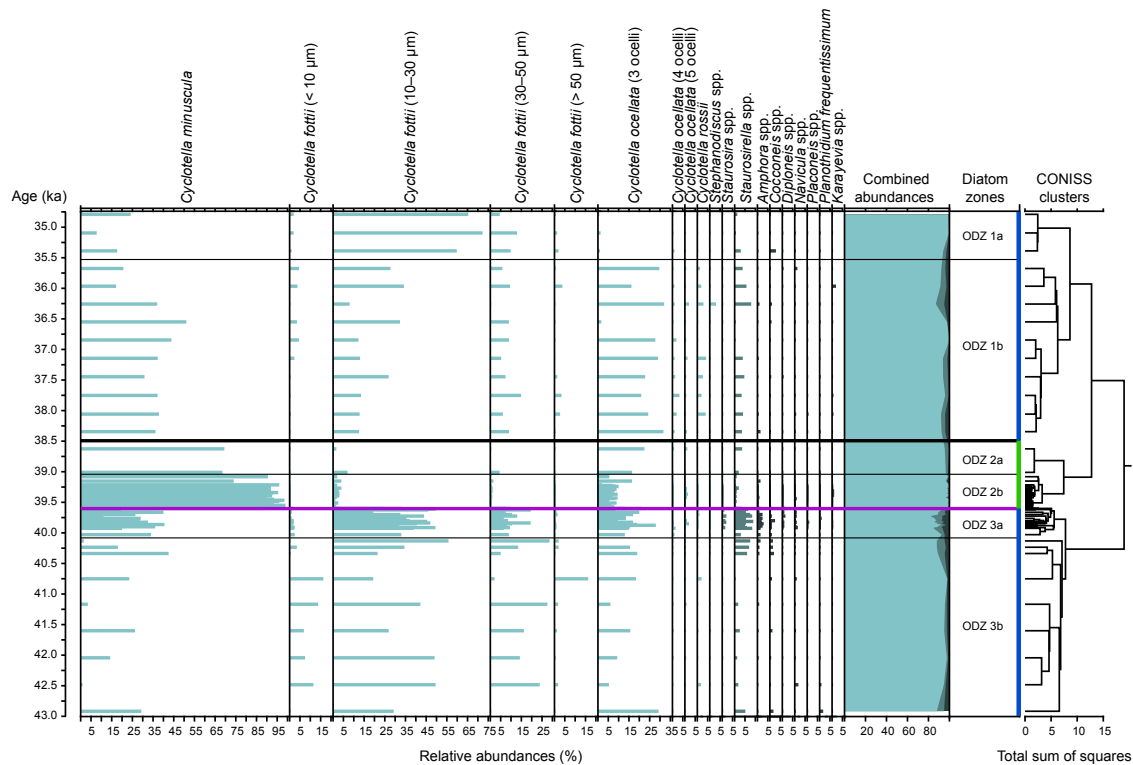


Figure 2. Summary diatom diagram for the Ohrid core (DEEP-5045-1). Only diatom taxa with relative abundances of > 2% are shown. Individual abundances are color-coded according to life style (light blue: planktonic, medium blue: facultative planktonic, dark blue: benthic). Diatom zones and subzones were 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.

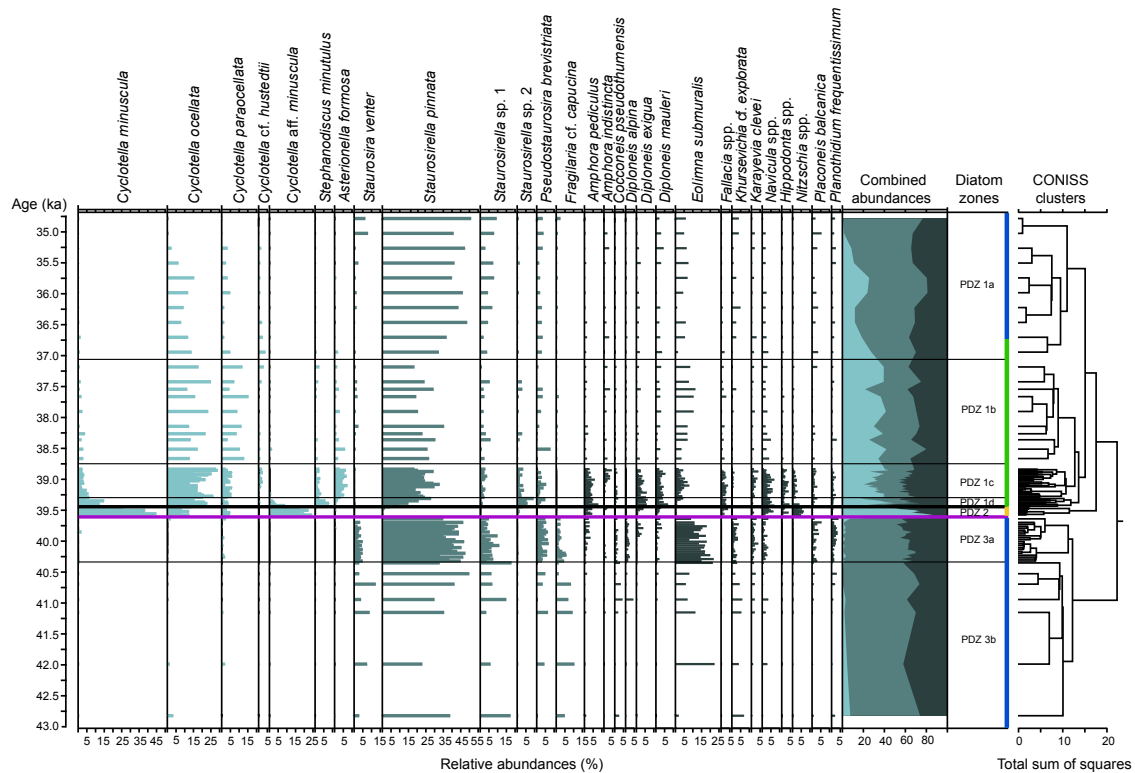


Figure 3. Summary diatom diagram for the Prespa core (Co1204). Only diatom taxa with relative abundances of > 4% are shown. Individual abundances are color-coded according to life style (light blue: planktonic, medium blue: facultative planktonic, dark blue: benthic). Diatom zones and subzones were defined 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.

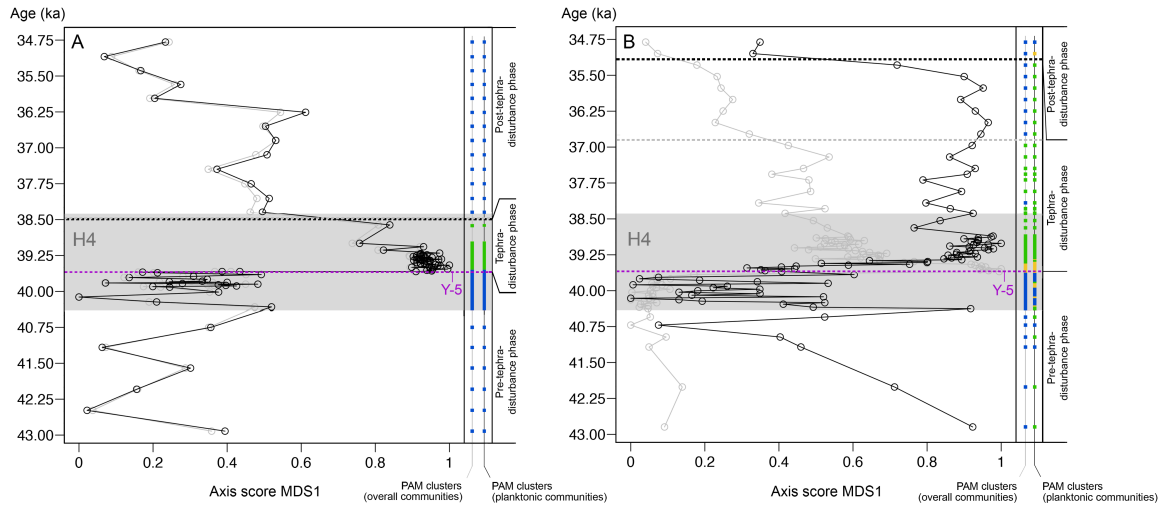


Figure 4. Diagrams showing changes in MDS diatom community compositions (black curves: planktonic communities; grey curves: overall communities) and respective PAM community assignments (colored rectangles) for lakes Ohrid (A) and Prespa (B). The purple dashed lines indicate the timing of the Y-5 eruption;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