



Neolithic human activity caused eutrophication in small central European lakes

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ABSTRACT

Human activities during the Early Neolithic have had major influences on central European terrestrial ecosystems through deforestation, burning, animal husbandry and agriculture. However, much less is known about how these landscape-scale changes affected aquatic ecosystems. In this study, we examined diatom assemblages preserved in radiocarbon dated and intermittently laminated sediment cores collected at Burgäschisee and Moossee, two small lakes on the Swiss Plateau, and compared the results with archaeological evidence for Neolithic lakeshore settlements and palaeobotanical records indicating distinct catchment scale phases of changing land use. The new diatom records were used to reconstruct changes to the lake ecosystem and of lake water nutrient concentrations from 6600 to 3800 calibrated radiocarbon years BP (cal yr BP). Blooms of small sized *Stephanodiscus* spp. together with algal remains (Cyanobacteria, Chlorophyta) indicate distinct phases of lake nutrient enrichment particularly during a land use and settlement phase associated with the Cortaillod culture (5800–5500 cal yr BP). In contrast, other land use phases were not associated with clear indications of water quality changes. Diatom response to human impact in the catchment was more pronounced at Burgäschisee relative to Moossee, notably for the phase corresponding to the Cortaillod culture.

The new results agree with previous studies that provided evidence of Neolithic human impact on lake ecosystems in central Europe. For small lakes, such as Moossee and Burgäschisee, the establishment of Neolithic lakeside settlements and land uses did not only lead to pronounced terrestrial ecosystem changes in the catchment but apparently influenced the lake ecosystems themselves. The different response of the diatom assemblages in the two lakes also suggests that the impact of land use on nutrient concentrations and algal communities varied between lakes during the Neolithic, presumably due to different intensities of human impact at different sites, but likely also due to differences in geographical and hydrological settings of the lakes (basin morphologies, stratification, and mixing regimes).

1. Introduction

Palynological and archaeological evidence show that agriculture expanded to the Swiss Plateau around 7500–7000 calibrated ¹⁴C year BP (cal yr BP) (Colombaroli et al., 2013; Hafner et al., 2020). From this period onwards, Neolithic farmers significantly changed the terrestrial surroundings through deforestation, settlement, agriculture, and animal husbandry (Kalis et al., 2003; Cubizolle et al., 2005; Wehrli et al., 2007).

Analysis of sediment from sequences obtained within a former lakeside settlement at the shorelines of Lake Zurich revealed evidence of elevated nutrient concentrations and decreased oxygen concentrations associated with the deposition of Neolithic cultural layers (Tóth et al., 2019). However, overall the impact of early prehistoric activities on aquatic communities is less well characterised than for terrestrial vegetation. In addition, aquatic environments in lowland Switzerland are spatially complex with large to small lakes, wetlands, and fluvial systems. This

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makes it difficult to generalize results from former lakeside settlements, such as those described by Tóth et al. (2019) to other types of aquatic environments or to entire lake basins.

Remains of Neolithic and Early Bronze Age pile-dwellings and lakeside settlements are found along the shores of Alpine region lakes and provide a unique record of long-term human-environment interactions. The UNESCO World Heritage Sites list 111 such sites around the Alps, including 56 Swiss sites (Hafner, 2012). Nearshore occupation of large lakes (e.g., Lakes Zurich, Constance, Neuchâtel, and Biel) occurred throughout the Neolithic and Early Bronze Age with short gaps of no known findings (Billamboz, 2014; Bleicher et al., 2017; Deak et al., 2018; Stöckli, 2016; Suter, 2017). Neolithic and Early Bronze Age pile-dwellings were also built on the shores of small lakes, such as Burgäschisee and Moossee, on the Swiss Plateau (Wey, 1999; Stöckli, 2004; Anliker et al., 2010; Hafner et al., 2012, 2020; Harb, 2018). Settlements at the shores and within the lake catchments likely influenced shoreline habitats and deepwater environments in these small lakes that are more sensitive to catchment and basin modifications than larger lake ecosystems. Anthropogenic activities around lakes can modify vegetation cover, increase soil erosion and nutrient transport to lakes. Human and livestock pressures augment nutrient release to lakes through land use and grazing as well as defecation, dung and other refuse that were often released in or at the settlements directly on the lake shore (Bleicher et al., 2017; Tóth et al., 2019; Gąsiorowski et al., 2021).

In order to gain a detailed picture of early human impact on the environment around Burgäschisee and Moossee, sediment cores were retrieved in 2009 and 2014. Initial analyses revealed that both lakes contain an exceptional geoarchive, covering > 18,700 years in Burgäschisee (Rey et al., 2017) and > 19,000 years in Moossee (Rey et al., 2020). Mid-Holocene sediments at both sites were intermittently annually layered (Rey et al., 2019a) and provided well-dated, high-precision, and high-resolution records (Rey et al., 2019a, 2019b). Palynological analyses revealed several intermittent, decadal-scale phases of impactful human activities near the lakes (Hafner et al., 2020) as evidenced by anthropogenic pollen indicators and coprophilous fungi spores (Rey et al., 2019a). Abundant akinetes of cyanobacteria were detected in pollen samples originating from some of these periods (Rey et al., 2019a), which agreed with increased deposition of cyanobacterial remains coinciding with cultural phases reported in some other Swiss lakes (e.g., Hillbrand et al., 2014). Since cyanobacteria thrive under high nutrient concentrations this suggested phases of nutrient enrichment due to local human activity. However, cyanobacteria blooms can also be promoted by other processes, such as high summer temperatures and strong lake stratification (Paerl et al., 2011; Winter et al., 2011; O’Niel et al., 2012; Smol, 2019) and the absence of cyanobacterial blooms does not necessarily indicate that lacustrine conditions were not influenced by Neolithic lakeside settlements. For Burgäschisee and Moossee, the extent that lake water quality was affected by land use phases and lakeside settlements during periods of high cyanobacteria abundance therefore remains uncertain. Similarly, it is unknown whether other phases of increased human activity detectable in the pollen record without corresponding increases in cyanobacteria were also accompanied by higher in-lake nutrient concentrations.

Diatoms are indicators of water quality that are highly sensitive to lake nutrient concentrations and are well preserved in lake sediments. For Burgäschisee and Moossee, a detailed interpretation of lake nutrient concentrations based on diatom indicators for the different Neolithic cultural phases would allow a detailed assessment of whether phases of higher human activity around the lakes, as detected in the pollen record, were associated with higher lake nutrient concentrations, even if they were not characterized by high cyanobacteria concentrations. Such nutrient increases and the associated water quality changes may have primarily derived from activities and settlements along the lake shore, and earlier studies from near-shore sediments (e.g., Toth et al., 2019) may therefore also have represented local changes in aquatic habitats

and conditions in shallow water. In contrast, analyses from sediment cores that were taken near the centre of the lakes, would allow an assessment of the effects of early Neolithic human impact on the water quality of the lake as whole and remote from lake shore settlements. The objectives of this study are (1) to present new diatom data as independent evidence of lake water quality changes from sediment cores from Burgäschisee and Moossee that were previously analysed for other paleoenvironmental data (Rey et al., 2017; Rey et al., 2019a, 2019b; Rey et al., 2020; Makri et al., 2020, 2021). (2) To find out if past aquatic ecosystem changes were associated with phases of human activities in the landscapes around the lakes, and (3) to determine the extent that the lakes recovered following Neolithic disturbance and water quality change.

2. Study sites

Burgäschisee and Moossee are small lowland lakes on the Swiss Plateau (Table 1), 25 km apart, and located on carbonate-rich molasse overlain with Quaternary glacial deposits. The lakes have comparable physical and hydrological conditions (Fig. 1; Schmid et al., 2004; Guthruf et al., 2015).

Initial archaeological finds were described during the mid-19th century (Harb, 2018; Hafner et al., 2020). Several major excavations of Neolithic settlements took place in the mid-20th century (Wey, 1999, 2001, 2012; Müller-Beck and Wey, 2008; Anliker et al., 2009, 2010; Harb, 2018). Burgäschisee and Moossee were repeatedly settled during the Neolithic (Harb, 2018; Hafner et al., 2020) and are situated between important Neolithic settlements in the Three Lakes Region (Seeland; Fig. 1 C) in the west and Lake Zurich (Fig. 1 C) in the east. The area was permanently occupied for more than 6000 years (Hafner et al., 2020). A total of five settlement sites, some multi-phased and considerable in size, are now known to have existed at Burgäschisee (Hafner et al., 2020), and two lake settlements at Moossee (Harb, 2018) during the Neolithic (Fig. 1 D, E).

3. Methods

3.1. Field work

In 2014, two parallel sediment cores at Burgäschisee and three parallel cores at Moossee were cored with a UWITEC piston corer with a tube diameter of 9 cm and a section length of 2 m in the deepest parts of the basins at a water depth of 30 m and 21 m, respectively. At both lakes

Table 1
Study site characteristics. TP, total phosphorus concentrations; Z_{max} , maximum water depth.

	Burgäschisee	Moossee
Coordinates	47°10'8.5"N, 7°40'5.9"E	47°11'17.0"N, 7°29'1.7"E
Elevation, m asl	465	521
Surface area, ha	20.65	30.35
Z_{max} , m	30	21.1
Volume, m ³	2,784,114	2,950,858
Catchment area, ha	382.73	2,081.24
TP, µg L ⁻¹ (Lotter et al., 1998)	99	31
TP, µg L ⁻¹ (TP measurements in the whole water column several times per year)	average: 30 median: 22 (Amt für Umwelt Kanton Solothurn, 2023)	average: 50 median: 26 (Guthruf et al., 2015)
Lithology of analysed sediment section	Fine detritus gyttja, partly laminated, organic content around 55 % (Rey et al., 2017)	Detritus gyttja, laminated (Rey et al., 2020), total organic carbon around 20 %, total inorganic carbon 4 % (Makri et al., 2021)

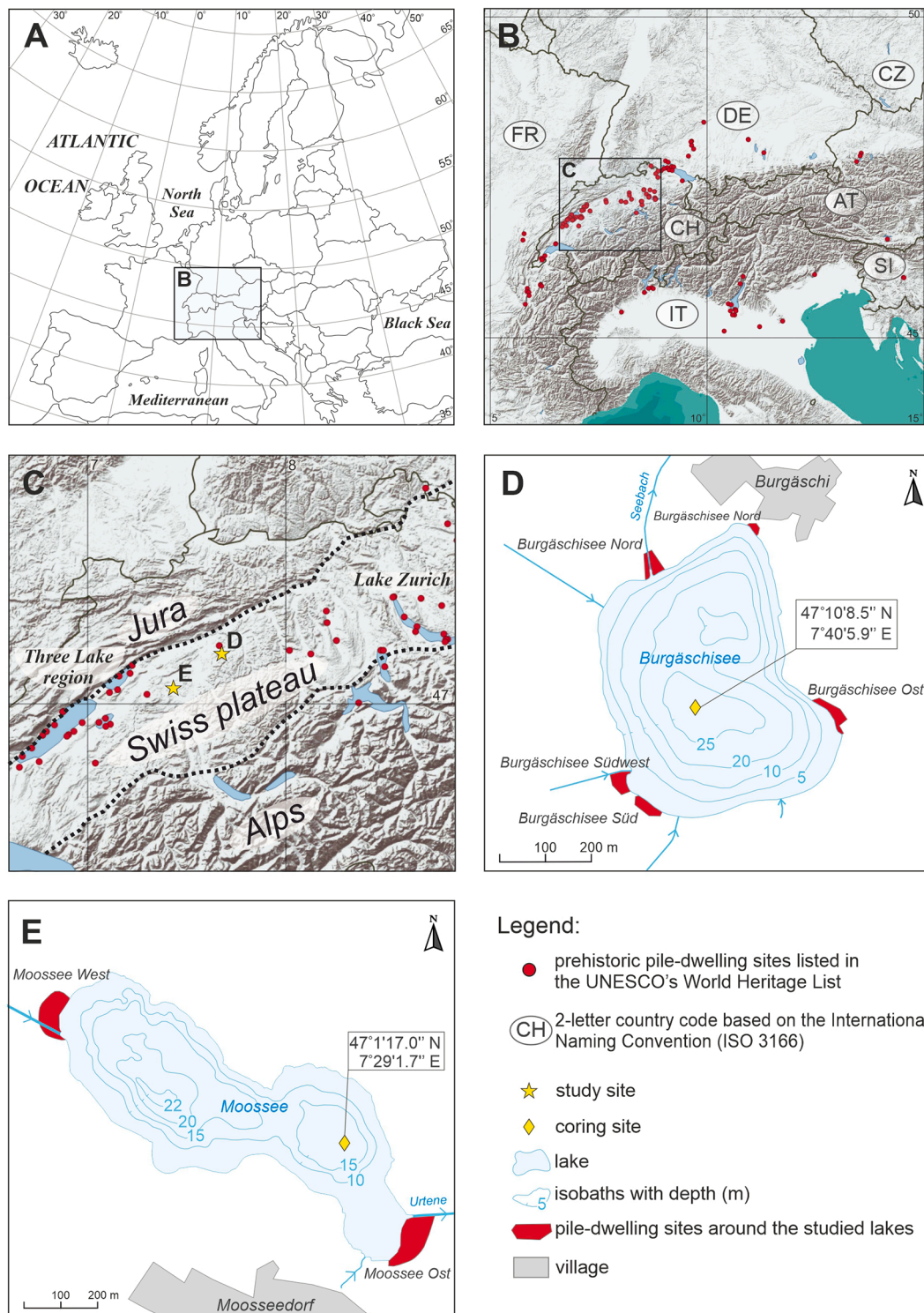


Fig. 1. Location of study sites: **A)** a map of Europe; **B)** an overview map of Alpine region with red dots indicating prehistoric pile-dwelling sites listed in the UNESCO's World Heritage List (CH – Switzerland, AT – Austria, DE – Germany, FR – France, IT – Italy, SI – Slovenia, CZ – the Czech Republic); **C)** central Switzerland with the two study sites (yellow stars); **D)** Burgäschisee, **E)** Moossee; **D)** a bathymetric map of Burgäschisee with a coring site marked with a yellow diamond; **E)** a bathymetric map of Moossee with a coring site marked with a yellow diamond. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the upper 7 m of sediments encompassed the past 9000 years (Rey et al., 2019a). Here, we further analyzed sections of the sediment sequences covering the Neolithic to Early Bronze Age (7000–3800 cal yr BP), where the sediments consisted of annual laminations that supported high-resolution analysis (Rey et al., 2019b).

3.2. Geochronologies and age-depth models

The chronologies of both sites were based on AMS ^{14}C dates and varve counts that used a total of 22 terrestrial plant macrofossils from Burgäschisee sediments (430–540 cm) and 27 terrestrial plant macrofossils from Moossee (520–690 cm) (Rey et al., 2019b). AMS ^{14}C dating

was done at the Laboratory for the Analysis of Radiocarbon, University of Bern. The original chronology of Rey et al., (2019b) was recalibrated with IntCal20 (Reimer et al., 2020). The age-depth models for both lakes were calculated in the program OxCal 4.3. In case of Burgäschisee a combination of two U-sequence models and a P-sequence model were used (Bronk Ramsey, 2001, 2008; Bronk Ramsey and Lee, 2013), and in Moossee only the V-sequence model (Bronk Ramsey, 2001; Bronk Ramsey et al., 2001) was applied.

3.3. Diatoms

Subsamples (0.25–0.5 cm³) of wet sediments for diatom analysis were taken from the same sediment cores used for the previously published pollen analysis (Rey et al., 2019a) and processed by sediment digestions (Battarbee et al., 2001a). Diatom accumulation rates (DAR) were calculated with a known quantity of synthetic microspheres added to the diatom suspensions. A few drops of the cleaned subsample were spread over a coverslip, dried overnight at room temperature, and mounted with Naphrax™ (1.73 refractive index) onto a microscope slide. Diatoms were identified under a Leica DMR light microscope by using oil immersion differential interface contrast illumination at 1000 × magnification. Between 400 and 500 diatom valves (Burgäschisee: mean = 482, sd = 125; Moossee: mean = 484, sd = 51) were counted and identified to species level to estimate relative abundance of taxa for most of the samples with a few exceptions. Six samples of Burgäschisee had less than 300 diatom valves counted due to poor preservation and low diatom concentration. Eight samples from Moossee had no diatoms detected. Additionally, chrysophyte (golden algae) cysts, scales, phytoliths and sponge spicules were counted alongside diatoms. Chrysophyte cysts were expressed relative to the total number of diatom valves because this ratio represents an index of the relative importance of these two algal groups (Smol, 1995).

The diatom taxonomy was based on diatom floras (Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b; Houk et al., 2010, 2014; Lange-Bertalot et al., 2017) and the updated nomenclature of diatoms from the AlgaeBase data was adopted (Guiry and Guiry, 2022). Diatom taxa were grouped into planktonic and periphytic according to preferred habitat tendencies. Small fragilarioid taxa, a large taxonomically complex and morphologically variable group of benthic and tychoplanktonic diatoms that includes *Staurosira* (Ehrenberg) Williams and Round, *Staurosirella* Williams and Round, *Pseudostaurosira* (Grunow) Williams and Round, were separated from periphytic taxa, as these taxa can also live in the water column up to depths of 6–8 m (Brugam et al., 1998) and on sand grains (Round, 1965). Diatom diagrams were created with Tilia v.1.7.16 software (Grimm, 2011) and CorelDRAW 2019 (Corel Corporation, 2019)

3.4. Statistical analyses

Diatom assemblage zones (DAZ) were delineated with stratigraphically constrained incremental sum of squares cluster analysis (CONISS) performed on the full percentage diatom data with Tilia (Grimm, 2011). The statistical significance of the diatom assemblage zones was assessed by a broken-stick model (Bennett, 1996) in the program R version 4.2.2 using the package rojia (Juggins, 2020). Diatom productivity was estimated using accumulation rates of diatom valves (DAR). The compositional changes in the diatom assemblages over time were assessed with detrended correspondence analysis (DCA; Hill and Gauch, 1980). The gradient length along DCA axis 1 was 2.34 standard deviations (SD) in Burgäschisee, and 2.21 SD in Moossee diatom data, indicating that methods based on unimodal species response models, such as DCA, were applicable to the data (ter Braak, 1995). DCA with detrending by segments was performed using CANOCO 5.1 (ter Braak and Šmilauer, 2018) with downweighting of rare species. All taxa were square root transformed in order to stabilise the variances and to reduce the effects of predominant taxa (Birks, 1995).

The diatom abundances were used to generate quantitative reconstruction of total phosphorus (TP; Juggins & Birks, 2012) as an indication of plant nutrient change in the study lakes. Phosphorus is typically the limiting nutrient for plant growth in Central European lakes (Wetzel, 2001). Diatom-inferred TP (DI-TP) reconstructions were generated based on the European Diatom Database (EDDI) training-set (Battarbee et al., 2001b), which includes 345 sites from Switzerland, Germany, Austria, Italy, France, Denmark, the United Kingdom, and Sweden. The TP gradient in the EDDI training-set ranges from 2 (ultra-oligotrophic) to 1189 (hypertrophic) µg L⁻¹. The trophic condition was classified as ultra-oligotrophic (TP < 4 µg L⁻¹), oligotrophic (TP = 4–10 µg L⁻¹), mesotrophic (TP = 10–35 µg L⁻¹), eutrophic (TP = 35–100 µg L⁻¹), or hypertrophic (TP > 100 µg L⁻¹) according to the OECD Fixed Boundary Trophic Classification System (OECD, 1982). Weighted averaging partial least squares (WA-PLS) with 2 components was used to estimate DI-TP based on log transformed TP values and square root transformed percentage diatom data since it provided the best statistical characteristics (highest r² between bootstrap predicted and observed values of 0.76; lowest root mean squared error of prediction (RMSEP) of 0.28) compared with other evaluated models (WA-PLS with different number of components, MAT and WA). The calculations were performed in C2 version 1.8.0. (Juggins, 2022).

4. Results

4.1. Chronology and previously published data

Tables with radiocarbon dates and IntCal20 (Reimer et al., 2020) recalibrated ages are provided in the supplementary material (Tables A1 and B1) with varve counts and wiggle-matching techniques presented in Rey et al., (2019b). Details of the cultural periods as reconstructed based on archaeological data are published in Rey et al., (2019a) and in this study were used as basis for the discussion of the diatom data in the context of previously published pollen, non-pollen palynomorphs (NPPs) and charcoal data. Average sedimentation rates during the Neolithic in the sediment sequences were 18.7 years cm⁻¹ at Burgäschisee and 26 years cm⁻¹ at Moossee (Rey et al., 2019b).

4.2. Diatoms

A total of 157 diatom taxa belonging to 44 genera were found in the Burgäschisee sediments and 237 taxa from 59 genera at Moossee. Only diatom taxa accounting for ≥ 2 % of the diatom abundances in ≥ 2 samples are presented in the diatom diagram of Burgäschisee (Fig. 2 A). For Moossee (Fig. 2 B), due to high periphytic taxa diversity and low relative abundances, we included some diatom taxa with abundances ≥ 2 % in ≥ 1 sample. Diatom preservation was variable at both sites, but in the Moossee sequence eight samples (seven samples from 656 to 635 cm and one at 626 cm) were completely barren of diatoms. In some slides with poor preservation due to chemical erosion only heavily silicified central areas of valves of cyclotelloid taxa were preserved. Related diatom taxa with similar ecological preferences were therefore grouped in one group, as done in previous diatom records from Alpine and pre-Alpine lakes (Wunsam et al., 1995). *Lindavia radiosa*, *L. balatonis* and *L. praetermissa* were combined as *Lindavia radiosa* group. Small cyclotelloids, characterized by similar but variable valve morphologies, such as *Pantocsekiella comensis* and *P. pseudocomensis*, were combined into *Pantocsekiella comensis* group (Scheffler and Morabito, 2003). *Stephanodiscus binatus* was grouped together with *S. parvus* s.l. as both are difficult to distinguish under optical microscopy.

4.2.1. Burgäschisee diatom assemblages (Fig. 2 A, 3 A)

The Burgäschisee diatom record covers 2670 years (6440–3770 cal yr BP) and includes the Neolithic and beginning of the Bronze Age. Dominant diatom taxa throughout the sequence are planktonic *Asterionella formosa* and *Fragilaria crotonensis*, whereas planktonic

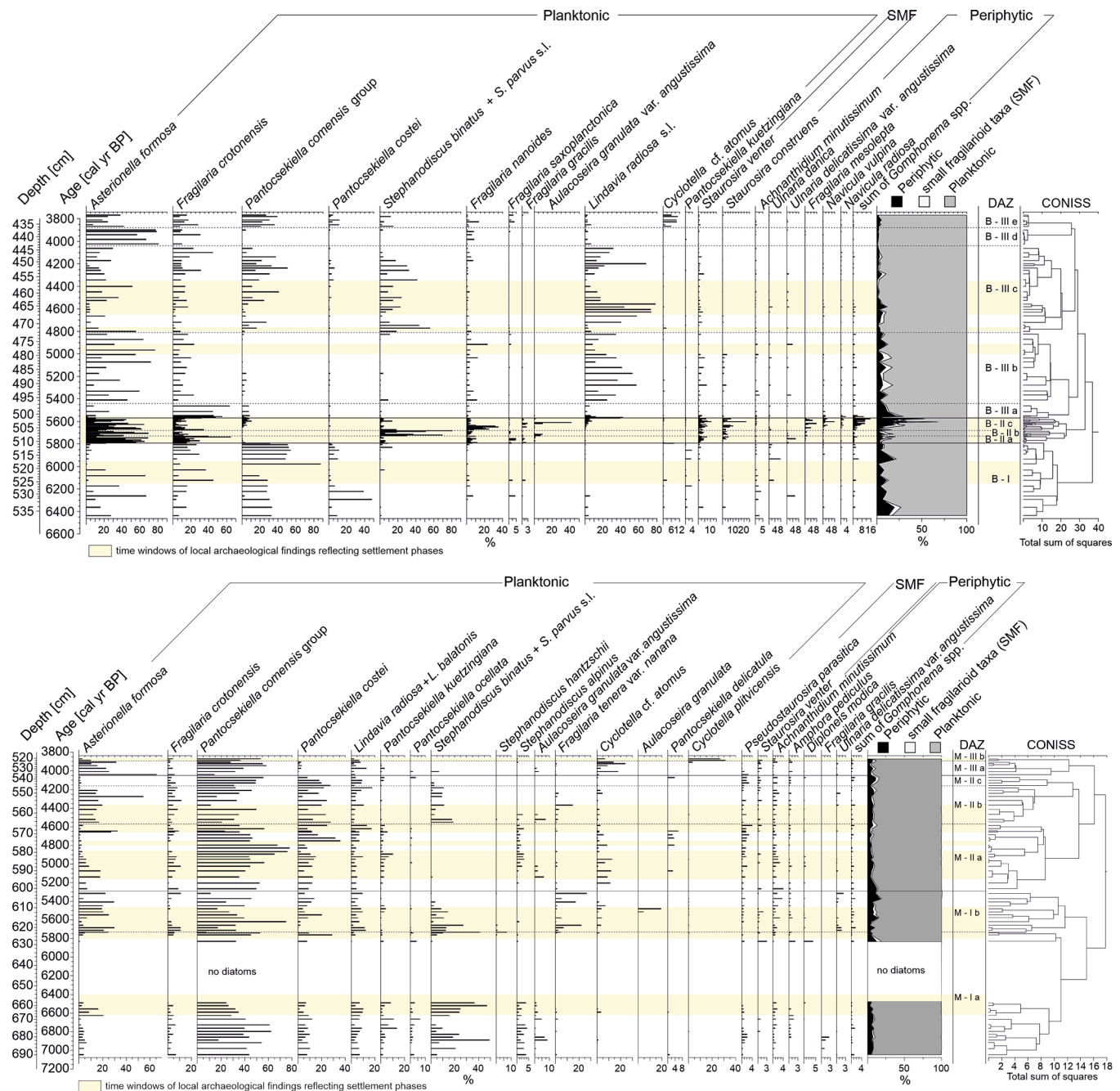


Fig. 2. Diatom diagrams of **A)** Burgäschisee and **B)** Moossee. Only diatom taxa accounting for $\geq 2\%$ of the diatom abundances in ≥ 2 samples are presented for Burgäschisee (**2 A**), whereas diatom taxa accounting for $\geq 2\%$ of the diatom abundances at least in 1 sample are presented for Moossee (**2B**). Light yellow bars throughout the diagram indicate the time windows of local archaeological findings reflecting settlement phases (Rey et al., 2019a). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Pantocsekiella comensis group, *Lindavia radiosa* group, *Stephanodiscus binatus* and *S. parvus* s.l. dominate alternately in the Burgäschisee record.

Three significant diatom assemblage zones (DAZ B – I; B – II and B – III) were defined by CONISS. DAZ B II was also separated into three insignificant subzones (DAZ B – II (a–c)) and DAZ B – III included five subzones (DAZ B – III (a–e)) to further facilitate the discussion of changes in diatom assemblages.

In DAZ B – I (532.9–510.5 cm; 6440–5790 cal yr BP) the two lowermost samples (534.15 and 535.95 cm; 6360 and 6440 cal yr BP) have a high concentration of chrysophyte cysts (308–468 %) and very poor preservation of diatom frustules, indicating limnological conditions overall less favorable for diatom production and preservation

(Bradbury et al., 2002). Diatom valve dissolution might occur under high pH, potentially as evidenced by increased carbonate content (loss-on-ignition 950 °C ca. 10 %) at the same depth (Rey et al., 2017). Planktonic *P. comensis* group dominates in this zone varying from 19 to 88 %, but in some samples, other planktonic diatoms dominated, such as *Pantocsekiella costei* (39–48 %), *A. formosa* (66–67 %), and *F. crotonensis* (37–45 %).

DAZ B – II (510.5–501.5 cm; 5790–5570 cal yr BP) lasts ca. 220 years and is characterized by conspicuous changes in dominant diatom assemblages, as well as varying diatom valve preservation and DAR, periphytic/planktonic ratio, and increased chrysophyte abundances. Pollen data indicates a distinct landscape opening and increased

anthropogenic activities around the lake from ca. 5790 to 5570 cal yr BP (Rey et al., 2019a).

The first diatom assemblage subzone **B – II a** (510.5–508 cm; 5790–5730 cal yr BP) covers ca. 60 years. Planktonic *A. formosa* increases up to 69 %, *F. crotonensis* varies around 28 % and reaches its peak of percentage abundance of 64 %, *Fragilaria saxoplanctonica* increases up to 5 %. Compared to the preceding zone, *P. comensis* group decreases significantly and *P. costei* disappears completely. Gradual increases of small fragilarioid taxa, such as *Staurosira venter*, *S. construens*, and *Staurosirella pinnata* are apparent. In the second subzone **B – II b** (508–505.9 cm; 5730–5680 cal yr BP), which covers 50 years of the record, DAR increase to unprecedented peaks ($647\text{--}745 \times 10^6$ valves $\text{cm}^{-2} \text{yr}^{-1}$; Fig. 3 A) at 5720 and 5680 cal yr BP. 70–80 % of both peaks are formed by small *Stephanodiscus* spp. (*Stephanodiscus binatus* and *S. parvus* s.l.), which are indicators of enhanced nutrient concentrations in the lake (Houk et al., 2014). In the middle of **B – II b**, at ca. 5700 cal yr BP, *A. formosa* reaches maximum values around 54–70 %. The third subzone **B – II c** (505.9–501.5 cm; 5680–5570 cal yr BP) is twice as long as the previous two subzones, ca. 110 years, and is distinguished from the preceding subzones by a remarkable rise in the percentages of benthic diatoms, which gradually increase up to 45 % at 5580 cal yr BP. The main proportion of benthic diatoms are *Fragilaria mesolepta*, *Navicula vulpina*, *N. radiosa*, *Stauroneis gracilis*, and different taxa from *Gomphonema* spp. (e.g. *Gomphonema auritum*, *G. hebridense*, *G. parvulum*). A distinct increase in small fragilarioid taxa (up to 34 % at ca. 5600 cal yr BP) is observed in this zone, a group that are considered indicators of disturbed environment (Lotter and Bigler, 2000). Compared to **B – II b**, DAR abruptly decline reaching their lowest values ($1\text{--}9 \times 10^6$ valves $\text{cm}^{-2} \text{yr}^{-1}$) in the record from 5640 to 5575 cal yr BP, whereas chrysophyte cyst concentrations increase from 1 to 36 %, which coincides with increases of periphytic diatoms.

The boundary between DAZ **B – II** and **B – III** (501.5–431.35 cm; 5570–3770 cal yr BP) is defined by an abrupt decrease in the abundance of *A. formosa* and a considerable increase in the abundance of *F. crotonensis* (32–63 %). DAZ **B – III** is characterized by high abundances of planktonic diatoms, such as *A. formosa*, *F. crotonensis*, *L. radiosa*, small *Pantocsekiella* and *Stephanodiscus* spp., as well as by gradually decreasing relative percentages of periphytic diatoms. The subzones differ mainly in which planktonic taxon is predominant. DAR in **B – III** are very low (ca. 3×10^6 valves $\text{cm}^{-2} \text{yr}^{-1}$) at the beginning, followed by a modest and gradual increase reaching peak values (381×10^6 valves $\text{cm}^{-2} \text{yr}^{-1}$) in subzone **B – III d** at ca. 3900 cal yr BP.

In subzone **B – III a** (501.5–496.7 cm; 5570–5440 cal yr BP), planktonic *F. crotonensis* dominates, subzone **B – III b** (496.7–472.2 cm; 5440–4810 cal yr BP) is characterized by high abundances of *A. formosa* and *L. radiosa*, while in subzone **B – III c** (472.2–443.5 cm; 4810–4040 cal yr BP) a simultaneous increase of small *Pantocsekiella* spp. and small *Stephanodiscus* spp. can be observed together with high values of *L. radiosa*. Diatom assemblage subzone **B – III d** (443.5–436.6 cm; 4040–3880 cal yr BP) is dominated by long shaped planktonic diatoms, such as *A. formosa* (57–81 %) and *F. crotonensis* (up to 30 %), and shows an increase of planktonic *F. nanoides* (6–8 %). In **B – III e** (436.6–431.3 cm; 3880–3770 cal yr BP) small round shaped planktonic taxa prevail, such as *P. comensis* group and *Cyclotella* cf. *atomus*. Small sized *Stephanodiscus* spp. appear again but they do not reach such high percentages as in **B – II b** and **B – III c**.

4.2.2. Diatom ordination of the Burgäschisee record

DCA axis 1 and 2 scores (Fig. 3 A) summarize compositional change of diatom assemblages through time and show major shifts in the diatom dataset, indicating a distinct change in diatom assemblages at ca. 5790 cal yr BP. The highest DCA axis 1 SD scores (1.5–2) are observed in the DAZ **B – II** from 5790 to 5570 cal yr BP, while the maximal DCA axis 2 SD values (1.4–1.9) are detected in the transition from **B – II c** to **B – III a** from 5610 to 5550 cal yr BP.

4.2.2.1. *Burgäschisee DI-TP reconstructions.* The occurrence of Burgäschisee fossil diatoms in the modern training-set varied from 83.8 to 100 %. The DI-TP values throughout the analysed sediment section alternate between 6.5 and 68.9 $\mu\text{g L}^{-1}$ (ranging within errors from 3.3 to 131.6 $\mu\text{g L}^{-1}$), with a median value of 18.2 $\mu\text{g L}^{-1}$ (Fig. 3 A). In general, Burgäschisee can be characterised as a mesotrophic lake during the Neolithic with an exception at 5740–5680 cal yr BP and 5620–5610 cal yr BP, when reconstructed DI-TP crossed the 35 $\mu\text{g L}^{-1}$ line (Fig. 3 A) reaching up to 68.9 $\mu\text{g L}^{-1}$. This indicates remarkable enrichment in nutrients in the Burgäschisee water column compared with reconstructed DI-TP values before the Cortaillod culture, when DI-TP values were close to oligotrophic conditions (6.5 and 28.1 $\mu\text{g L}^{-1}$, mean value 14.3 $\mu\text{g L}^{-1}$). Around 5510 cal yr BP a drop in DI-TP suggests recovery of nutrient concentrations in Burgäschisee to lower values.

4.2.3. Moossee diatom assemblages (Fig. 2 B, 3B)

The analysed Moossee diatom record focusses on 7050–3860 cal yr BP (ca. 3190 years) and similar to Burgäschisee it covers the Neolithic, as well as the beginning of the Bronze Age.

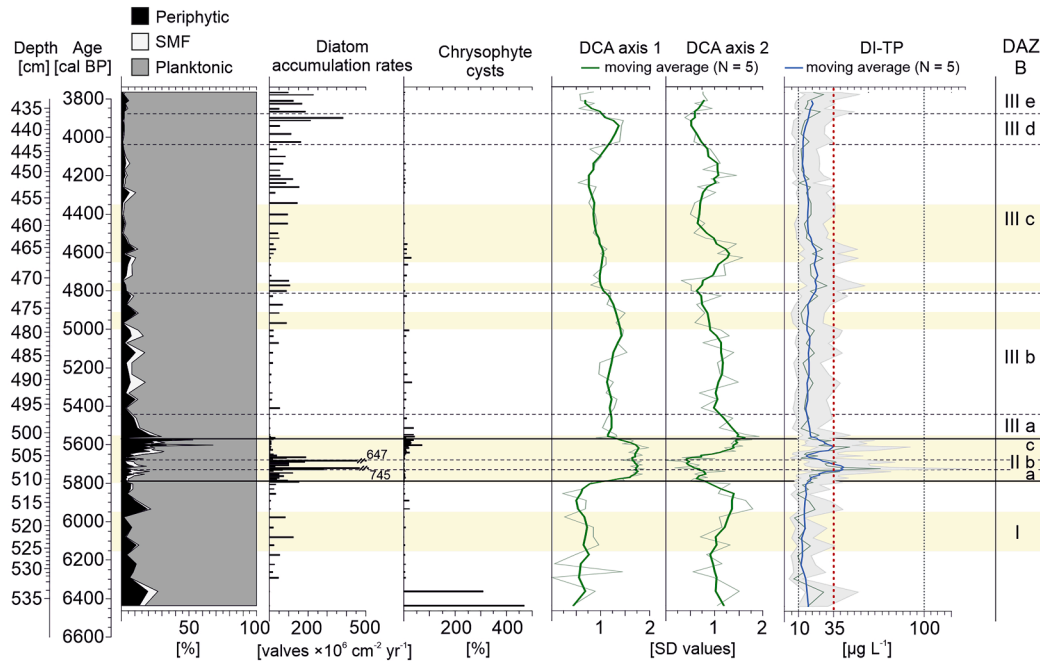
Throughout the studied sediment sequence the most abundant diatoms were planktonic small cyclotelloids, which were grouped under *P. comensis*. Other planktonic diatoms, such as *S. binatus* and *S. parvus* s.l., *P. costei*, *A. formosa*, *Fragilaria tenera* var. *nanana*, *Cyclotella plitvicensis* and *Aulacoseira granulata* var. *angustissima* exhibit sporadic dominance or sub-dominance in some DAZ. Small cyclotelloids alternate in approximate opposition to long fragilarioids, such as *A. formosa* and *F. crotonensis*, reflecting specific environmental conditions associated with stratification and nutrient cycling (Lotter, 1989). Periphytic diatoms constitute a minor proportion (on average 6 %) of the diatom assemblage throughout the Moossee sediment sequence, with a few exceptions at some intervals where they collectively reach abundances up to 12–16 %. A modest gradual increase of small fragilarioids (e.g. *Pseudostaurosira parasitica*, *S. venter*) from ca. 1 % at the bottom to ca. 3 % in the upper part of the sediment sequence were observed through time.

Similar to the Burgäschisee diatom record, three significant diatom assemblage zones (DAZ **M – I**; **M – II** and **M – III**) were identified based on CONISS and again these zones were further divided into not statistically significant subzones to facilitate the discussion of the results: two in DAZ **M – I** (a–b), three in DAZ **M – II** (a–c) and two in DAZ **M – III** (a–b).

Overall, in DAZ **M – I** (690–601.5 cm; 7050–5290 cal yr BP) minor changes in species composition were observed. Small planktonic *P. comensis* group, *S. binatus* and *S. parvus* s.l. were the most abundant taxa indicating nutrient-rich environment. In the subzone DAZ **M – I a** (690–623.7 cm; 7050–5730 cal yr BP) samples from ca. 6460–5780 cal yr BP were barren of diatoms due to dissolution of diatom valves. The subzone **M – I b** (623.7–601.5 cm; 5730–5290 cal yr BP) differs from the preceding subzone due to an abrupt increase of *A. formosa* up to 30 %, higher abundance of *F. tenera* var. *nanana* (in some samples reaching 22–26 %) and gradual decrease in small *Stephanodiscus* spp.

DAZ **M – II** (601.5–537.5 cm; 5290–4050 cal yr BP) is distinguished from **M – I** by a marked decrease in the abundance of long planktonic fragilarioids – *F. tenera* var. *nanana* and *A. formosa*. The small cyclotelloids predominate, with the most abundant taxa being *P. comensis* group and *P. costei*. The relative abundances of species grouped in *P. comensis* as well as *P. costei* vary within a large range between 11 and 78 % and 2–39 %, respectively. *P. comensis* group reaches its maximum (65–78 %) in the middle of subzone **M – II a** (601.5–565 cm; 5290–4570 cal yr BP) that covers around 100 years from 4890 to 4790 cal yr BP, followed by a peak of another small cyclotelloid *P. costei* (32–36 %) and by a rapid increase of *A. formosa* for a very short time (4660–4640 cal yr BP). An abrupt change in the composition of some dominant diatom species was observed on the boundary between the subzone **M – II a** and **M – II b** (565–546 cm; 4570–4160 cal yr BP). The latter zone was marked the sudden appearance of small *Stephanodiscus* spp. (19 %), increase of *A. formosa* (17 %) and a sharp decline in the abundance of *L. radiosa* and *Pantocsekiella kuetzingiana*. Subzone **M – II c** (546–537.5

A - Burgäschisee



B - Moossee

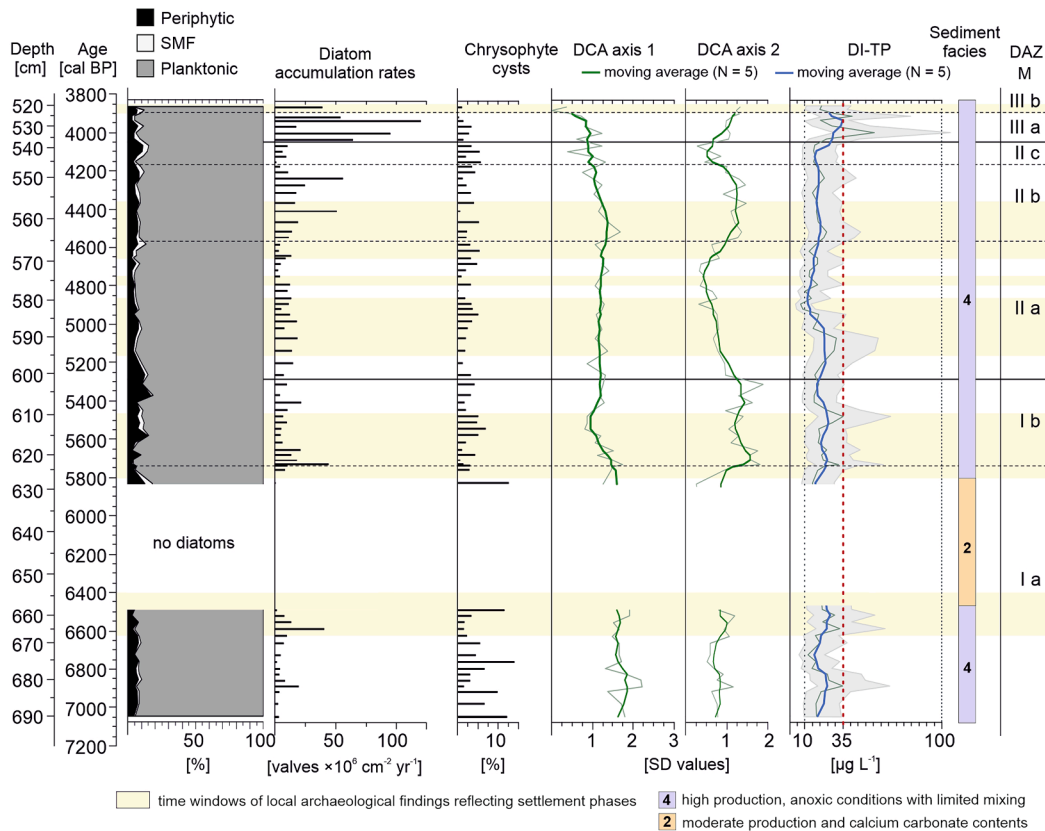


Fig. 3. Summary diagrams of **A)** Burgäschisee and **B)** Moossee presenting: relative abundance of periphytic, small fragiliroid taxa (SMF) and planktonic diatoms, diatom accumulation rates, chrysophyte cysts and scales, two first axis of detrended correspondence analysis (DCA axis 1 and 2) with smoothing (moving average of 5, green line), reconstructed DI-TP values (moving average of 5, blue line), where the red dotted line indicates the border between mesotrophic to eutrophic conditions ($35 \mu\text{g L}^{-1}$), and diatom assemblage zones defined by CONISS. Light yellow bars throughout the diagram indicate the time windows of local archaeological findings reflecting settlement phases (Rey et al., 2019a). A summary of Moossee sediment facies changes (Makri et al., 2020) is also shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

cm; 4160–4050 cal yr BP) represents a short interval (ca. 110 years) characterized by a very low percentage contribution of *A. formosa* (1–2 %). Mean values of DAR in the first part of the Moossee sequence (M – I and M – II a) were 10×10^6 valves $\text{cm}^{-2} \text{yr}^{-1}$ with some exceptional peaks (21 and 43×10^6 valves $\text{cm}^{-2} \text{yr}^{-1}$).

The boundary between DAZ M – II and M – III (537.5–520.2 cm; 4050–3860 cal yr BP) is defined by an abrupt reduction in the abundance of *P. costei* and *P. comensis* group and substantial increase in the abundance of *A. formosa*, peaking at 65 % and a gradual decrease to 3 %. In subzone M – III a (537.5–523 cm; 4050–3890 cal yr BP), *Cyclotella* cf. *atomus* reaches a maximum abundance of 18–24 %. DAR reach maximal values of 95 and 120×10^6 valves $\text{cm}^{-2} \text{yr}^{-1}$ (Fig. 3 B) at 4000 and 3940 cal yr BP, respectively. The subzone M – III b (523–520.2 cm; 3890–3860 cal yr BP) is characterized by the appearance of well-preserved planktonic *C. plitvicensis* making up 27–31 % of the total assemblage, concurrent with a considerable decrease in *A. formosa* and *C. cf. atomus*.

4.2.4. Diatom ordination of the Moossee record

DCA axis 1 varies little in the core except for DAZ III – b (Fig. 3 B), where SD values decrease rapidly, while DCA axis 2 features more distinct variation. The highest SD scores of DCA axis 2 are at the beginning of the subzone M – I b 1.6 – 1.8 SD (5730–5660 cal yr BP) and the maximum value is reached in the last sample of this subzone (ca. 5310 cal yr BP). In the M – II a subzone, DCA axis 2 scores decrease down to 0.3–0.5 SD at the same depth where planktonic diatoms have the highest percentage contribution (95–96 %). A similar pattern in DCA axis 2 scores were observed in the Burgäschisee diatom record and suggests DCA axis 2 relates to higher periphytic diatoms abundances.

4.2.5. Moossee DI-TP reconstructions

The occurrence of Moossee fossil diatoms in the modern training-set varied from 68.1 to 99.8 %. The reconstructed DI-TP values varied from 7.3 to $55.6 \mu\text{g L}^{-1}$ (ranging within errors from 3.8 to $105.6 \mu\text{g L}^{-1}$), with a median value of $19 \mu\text{g L}^{-1}$. Before the Cortaillod culture, DI-TP values alternate between 11.9 and $34.7 \mu\text{g L}^{-1}$ (mean value $21.4 \mu\text{g L}^{-1}$), during the Cortaillod culture (5760–5450 cal yr BP) the DI-TP slightly increase up to $35.2 \mu\text{g L}^{-1}$ (mean value $23.9 \mu\text{g L}^{-1}$). Afterwards the reconstructed DI-TP values decreased till the Early Bronze Age, when at ca. 4040 cal yr BP a rapid increase in DI-TP values was observed with highest values reaching up to $55.6 \mu\text{g L}^{-1}$ indicating eutrophic state in Moossee.

5. Discussion

5.1. Subfossil algal evidence of lake ecosystem variability

Burgäschisee and Moossee are located 25 km apart and have comparable physical characteristics (Table 1). Diatom assemblages were similar, although differences amongst dominant species were observed. Chrysophyte-rich intervals and concomitantly low DAR were observed in both lakes in the lowest intervals.

Pronounced chrysophyte dominance (>300–450 %) occurred in Burgäschisee at 6360–6440 cal yr BP while in Moossee chrysophyte abundances > 10 % were detected in some samples at 7050–5830 cal yr BP. Chrysophytes compete favourably with diatoms under oligotrophic conditions and short growing seasons (Jong and Kamenik, 2011). In temperate lakes, chrysophytes generally dominate or co-dominate in nutrient-poor lakes with low productivity, low pH, low alkalinity, and low conductivity (Smol, 1995; Sandgren, 1991; Zeeb and Smol, 2001). Extremely high values of chrysophytes might indicate pH values lower than 7.5, as the maximum relative abundance occurs in lakes with mean annual pH values in the range of pH 5–7.5 (Sandgren, 1991). However, the local bedrock buffers lake water at Moossee and Burgäschisee and this suggests that phases with high chrysophyte concentrations were caused by chrysophytes outcompeting diatoms for growth-limiting nutrients (Sandgren, 1991) as opposed to pH changes. Very low sediment

accumulation rates of ca. 0.25 mm yr^{-1} indicate low autochthonous productivity in Burgäschisee at 6520–6290 cal yr BP. High values of the green alga *Botryococcus* were observed during pollen analyses in both lakes, which synchronously declined before 6450 cal yr BP. *Botryococcus* is commonly found in temperate oligotrophic lakes in large floating masses (Hutchinson, 1967; Borowitzka, 2018). Distinct diatom assemblage changes were first observed after 5800 cal yr BP in both records (Fig. 4 A, 4B). Burgäschisee diatom assemblage changes were clearly more pronounced relative to Moossee. A rapid increase in DI-TP and changes of DCA axis 1 and 2 values (Fig. 3 A) are observed in Burgäschisee data, while in Moossee rapid changes are only evident along DCA axis 2 (Fig. 3 B).

5.1.1. Burgäschisee disturbances and recoveries (Fig. 2A, 3A)

Predominant diatom taxa before 5800 cal yr BP in Burgäschisee were planktonic *A. formosa*, *F. crotonensis*, *P. comensis* group, and *P. costei* (Fig. 2 A), commonly found in mesotrophic, deep lakes on carbonate bedrock (Houk et al., 2010; Talling, 2012). Often planktonic, araphid *A. formosa* and *F. crotonensis* appear together in mesotrophic, temperate waters where they depend on hypolimnetic nutrients delivered to the epilimnion during water column mixing (Talling, 2012; Bradbury et al., 2002). Due to the dependence on turbulence, they have been observed in spring blooms, when temperature and light are increasing and the Si:P is near the maximum (Neale et al., 1991; Kienel et al., 2017), as well as in autumn blooms during circulation (Brown and Austin, 1973). *A. formosa* is a better competitor for silica than *F. crotonensis*, and *F. crotonensis* a better competitor for phosphorus (Kilham, 1986), hence variations between *A. formosa* and *F. crotonensis* are considered as an indicator of phosphorus- or silica-limited conditions. Once lakes stratify and Si:P ratios decrease, long araphid *A. formosa* and *F. crotonensis* abundances decline (Reynolds, 1983) and are replaced by small centric diatoms such as *Stephanodiscus* and *Cyclotella* (Kilham, 1986). *Stephanodiscus* spp. is considered to bloom during early spring or winter in lakes when ice cover does not form, while cycloteloid species usually thrive in summer.

In Burgäschisee at ca. 6000 cal yr BP, long araphid planktonic diatoms were substituted by small cycloteloids (Fig. 2 A), such as *P. comensis* group and *P. costei*. *P. comensis* is small pancake-shaped cycloteloid taxon that is more buoyant (Rühland et al., 2015) than *A. formosa* and *F. crotonensis*, and thrives in thermally stratified water columns during summer. Commonly cycloteloid taxa occur in oligotrophic to moderate eutrophic lakes (Houk et al., 2010). In general, *A. formosa* and *F. crotonensis* together with cycloteloids collectively indicate stable summer and early autumn temperature stratification with weak circulation (Bradbury et al., 2002). The increase in elongated planktonic diatom taxa, such as *A. formosa*, indicate increased deposition of nitrogen and phosphorus as well as mixing of the water column, because of anthropogenic land use and land cover changes (Bradshaw et al., 2005; Hundey et al., 2014).

The sharpest shifts in diatom composition with a strong variability (DCA axis 1 SD varies between 1.24 and 2.34 and DCA axis 2 varies 0.00–1.89 SD) in diatom assemblages and DAR (Fig. 3 A) occurred at 5790–5570 cal yr BP, in an interval associated with Cortaillod culture. These changes mark a 220-year interval of eutrophication divided into three phases: a) 5790–5730, b) 5730–5680, and c) 5680–5570 cal yr BP. The first interval lasted 60 years, characterized by small fragilarioid taxa, such as *S. construens* and *S. venter* (Fig. 2 A), which are r-strategists, adapted to rapid shifts in environmental conditions (Lotter and Bigler, 2000). Small fragilarioid taxa are promoted by increasing turbidity in the water column (Anderson, 2000; Grudzińska et al., 2017) possibly caused by early forest clearance and agricultural activities in the watershed. *F. saxoplanctonica*, with peak-to-high abundances in this interval, is an additional indicator commonly found in eutrophic artificial ponds (Lange-Bertalot et al., 2017) and may have been promoted by intensified soil erosion and nutrient release that led to high nutrient loading in the lake.

The second eutrophication interval (5730–5680 cal yr BP) at

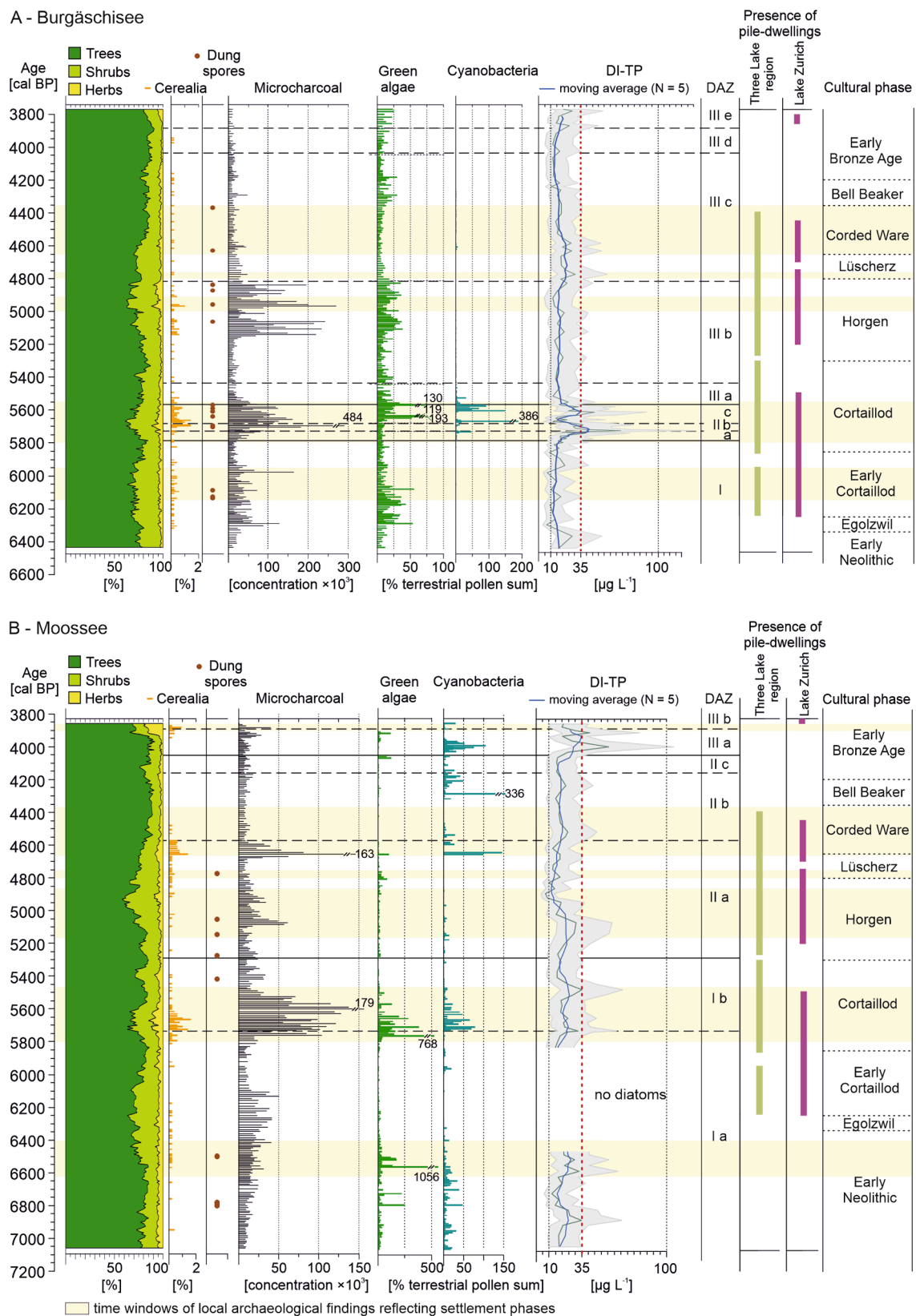


Fig. 4. Composite figure of A) Burgäschisee and B) Moossee data. Relative abundance of trees, shrubs and herbs pollen, *Cerealia* pollen, presence of dung spores, concentration of microscopic charcoal, percentages of green algae and cyanobacteria calculated from terrestrial pollen sum, reconstructed DI-TP values (moving average of 5, blue line), where the red dotted line indicates the border between mesotrophic to eutrophic conditions ($35 \mu\text{g L}^{-1}$), diatom assemblage zones defined by CONISS, summarised archaeological settlement phases within Three Lake Region and Lake Zurich (Stöckli, 2016), cultural phases in western Switzerland (Schibler, 2013). Light yellow horizontal zones throughout the diagram indicate the time windows of local archaeological findings reflecting settlement phases at the two lakes (Rey et al., 2019a). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Burgäschisee was indicated by extremely high DAR, mainly of *S. binatus* and *S. parvus* s.l. The small *Stephanodiscus* taxa have an advantage in nutrient competition and proliferate during spring turnover when nutrients, such as silica and phosphorus, are brought up from the lake bottom. The maximum peaks of small *Stephanodiscus*, both in percentages and DAR, most likely represent substantial diatom blooms from individual years, due to increased nutrient loading in the lake (Gibson, 1981). Evidence of increased erosion and nutrient transport into the lakes included the appearance of meroplanktonic *A. granulata* var. *angustissima* that requires high concentrations of accessible dissolved silica (Kilham and Kilham, 1975; Stone et al., 2011). As *Aulacoseira* spp. have heavy chain forming frustules, this species is dependent on turbulence to remain in the water column (Bradbury et al., 2002; Rühland et al., 2015). Therefore, it is considered as an indicator of intense mixing in late summer or autumn caused by increased precipitation or windiness (Kilham et al., 1996).

The third eutrophication interval at Burgäschisee was characterized by poor diatom preservation, very low DAR (Fig. 3 A) and high relative abundances of periphytic diatoms that suggests dissolution of planktonic diatoms or impeded development under poor environmental conditions. These environmental conditions lasted for around 110 years (5680–5570 cal yr BP). Diatom dissolution is often found under high alkalinity or salinity (Flower, 1993; Ryves et al., 2006), but in the case of Burgäschisee both factors seem unlikely. Possibly dissolution of planktonic diatom frustules was caused by water column silica deficiency. Due to a very low Si:P ratio planktonic diatoms were outcompeted by cyanobacteria (*Aphanizomenon*, *Gloetrichia*) and green algae (*Tetraedron*) as indicated by high abundances of remains (Rey et al., 2019a; Fig. 4 A). When silica concentrations are low, other algae, such as green algae and cyanobacteria, are superior competitors for phosphorus (Kilham, 1986). Massive cyanobacteria and green algae blooms overshadow and reduce the light quality and quantity for planktonic diatoms (Paerl and Paul, 2012). Periphytic diatoms can cope with turbid conditions, are not strictly reliant on nutrients dispersed in a water column, and have access to alternative silica sources; such as terrestrial in-wash, sediments, and recycled diatom remains (Anderson, 1989, 2000). Increased sedimentation of periphytic diatoms into the middle of the lake, as is observed in this phase, can be caused by a deterioration of planktonic ecosystem conditions and littoral and lakeshore disturbances followed by transport to deepwater sediments via currents and sediment focusing (Lotter and Bigler, 2000). The observed increase of epiphytic *Gomphonema* spp. is favoured by high nutrient concentrations. Together with recorded higher relative abundances of *Typha latifolia* and other aquatic macrophyte pollen (*Myriophyllum spicatum*, *Potamogeton*, *Juncus*; Supplement Fig. C1, Rey et al., 2019a; NEOTOMA, 2022) this may indicate high abundances of littoral plants and nutrient-rich conditions.

During this third eutrophication interval at Burgäschisee, green algae were replaced by nitrogen fixing cyanobacteria *Anabaena*, *Aphanizomenon*, and *Gloetrichia* (Supplement Fig. C1), when nitrogen-limiting conditions arose in the lake (Howarth et al., 1988; Bradbury et al., 2002). In contrast to diatoms, which form large populations during strong mixing, cyanobacteria and green algae bloom during phases of high thermal stability. Cyanobacteria data from Burgäschisee show that *Anabaena*, which dominated in earlier phases, was later outcompeted by *Aphanizomenon* (Rey et al., 2019a), a taxon that successfully competes with other species under phosphorus- or light-limiting conditions (van Geel et al., 1994). Both cyanobacteria can be toxic to very toxic to animals and humans in or around the lake and may have had serious implications. The replacement of *Anabaena* with *Aphanizomenon* emphasizes the unsuitable environmental conditions for diatom development and indicates limitations of silica in the lake water combined with strong thermal stratification, the latter possibly promoted by hotter and drier summers. Nevertheless, thermal stability in late summer or early autumn was apparently reduced between 5615 and 5610 cal yr BP. This is evidenced by a high abundance of meroplanktonic *A. granulata* var. *angustissima* (41 %), which is favoured during turbulent periods in

summer (Kilham and Kilham, 1975).

More than a hundred years (5570–5460 cal yr BP) after the strongest eutrophication, there was low phosphorus in the water column, indicated by the dominance of planktonic *F. crotonensis*, which is a better phosphorus competitor under these conditions than other common diatoms in Burgäschisee (Kilham, 1986). The recurrence of planktonic diatoms and gradual decrease of the relative abundance of periphytic diatoms indicates some ecosystem recovery, but, as DAR remained extremely low, this pattern was apparent only at decadal-to-centennial scales. DI-TP values showed a relatively fast drop from 48.8 $\mu\text{g L}^{-1}$ (eutrophic conditions) at ca. 5600 cal yr BP to 11.6 $\mu\text{g L}^{-1}$ (close to oligotrophic state) at ca. 5500 cal yr BP. The presence of *Anabaena* indicates continued strong thermal stratification during the warmest months, whereas increases in *F. crotonensis* suggest weak spring or autumn circulation - conditions that prevent biogenic silica entering the epilimnion and limit diatom blooms.

After 5460 cal yr BP several species from the *L. radiosa*-complex became abundant. Increases in *L. radiosa* have been reported as a sign of lake recovery after eutrophication (Horn et al., 2011; Saros et al., 2014) and abundances of *L. radiosa* positively correlate with water temperatures and water column stability and negatively with dissolved nutrient concentration. *L. radiosa* may be a good competitor at low nutrient concentrations that requires thermal stratification (Saros et al., 2014; García et al., 2022), whereas others claim that it is an indicator of high phosphorus concentrations (Wolfram et al., 2015) or a meso-eutrophic species (Rimet et al., 2015). This inconsistency might be explained by different *L. radiosa* morphotypes covering different environmental conditions (Krammer and Lange-Bertalot, 1991a; Wunsam et al., 1995). In general, *L. radiosa* is more abundant in moderately warm, low nutrient conditions (Saros et al., 2014). Appearance of small *Stephanodiscus* taxa (4830–4100 cal yr BP) suggests more intense spring circulation with higher nutrient input to the lake.

5.1.2. Moossee disturbances and recoveries (Fig. 2 B, 3B)

In Moossee, diatom assemblages appear to have been more stable, dominated by small centric diatoms, such as *P. comensis* group, *P. costei*, and small *Stephanodiscus* (*S. binatus* and *S. parvus* s.l.), and elongated araphid *A. formosa*. Based on the dominating planktonic diatom types, it appears that silica was a limiting nutrient in Moossee during the Neolithic (with a few exceptions, when *Aulacoseira* spp. appeared), as small centric diatoms typically have lower silica requirements than pennate taxa (van Donk and Kilham, 1990; Interlandi et al., 1999). Wunsam et al. (1995) concluded that phosphorus is the most important factor influencing distribution of different cyclotelloids and the group as a whole is abundant in a wide range of trophic conditions, from oligotrophic to eutrophic lakes (Lotter et al., 1998; Houk et al., 2010). However, cyclotelloids thrive usually in late summer or early autumn when nutrients are low and when there is strong water column stratification in lakes because the frustules are less dense than many other diatom taxa allowing them to remain suspended in the epilimnion.

Alongside *P. comensis* group and *P. costei*, relative high abundances were recorded for *S. binatus* and *S. parvus* s.l. at 7050–5290 cal yr BP. The presence of both diatom groups, small cyclotelloids and small *Stephanodiscus* spp., in the same samples may indicate strong seasonal and interannual variability in the trophic status (Marchetto et al., 2008) and light availability (Saros et al., 2014) determined by turbidity and water column stability. *Stephanodiscus* (in contrast to cyclotelloid taxa) commonly prefers very low temperatures and blooms in late winter and early spring (Rühland et al., 2015). *Stephanodiscus alpinus* is a typical cold-water diatom and an indicator of deeper mixing (Houk et al., 2014). Higher relative abundance of *S. alpinus* was observed at 7050–6460 and 5050–4550 cal yr BP. Another indicator for intense circulation is *A. granulata* var. *angustissima*. Episodic resurgence of this taxon, indicate more turbulent water conditions during late summer and early autumn (Kilham and Kilham, 1975; Rühland et al., 2015), as well as availability of additional nutrients (e.g., silica and phosphorus) brought up from the

hypolimnion to the photic zone.

Overall, the regular presence of marked blooms of cyanobacteria and green algae during the Neolithic (Fig. 4 B) suggest that Moossee was characterized by a stable summer stratification with effects on water quality. DCA axis 1 values remain relatively stable with some significant changes only in the Early Bronze Age (Fig. 3 B). This low variability in DCA axis 1 values indicates that Moossee has been comparatively stable regarding diatom flora and limnology during the Neolithic (ca. 7000–4000 cal yr BP), except with one slight drop in SD values to 0.80–0.87 during 5550–5480 cal yr BP, most likely related to the appearance of *Aulacoseira granulata*. Meroplanktonic *A. granulata* occurs relatively late in summer, as the result of turbulent mixing and the temporary breakdown of stratification (Kilham and Kilham, 1975; Simola et al., 1990; Anderson, 2000). Similar to previously discussed *A. granulata* var. *angustissima*, the presence of *A. granulata* indicates nutrient-rich conditions (Kilham and Kilham, 1975). The first distinct shift in DCA axis 2 values at ca. 5730 cal yr BP is caused by a rapid increase in *Stephanodiscus* spp. (Fig. 2 B, 3B).

Stephanodiscus hantzschii is a strong indicator of nutrient enrichment, which is frequently observed in eutrophic (Houk et al., 2014) and hypereutrophic (Wolfram et al., 2015) lakes along with periphytic *Ulnaria delicatissima* var. *angustissima*, another eutrophic indicator *Ulnaria* spp. grow in the littoral zone attached to different surfaces with a competitive advantage under high Si:P (Tilman et al., 1982; Smith and Kalf, 1983). The presence of both taxa might be linked to increased erosion, potentially due to land clearance and agricultural activities that raised in-lake nutrient concentrations, particularly of silica (Bradshaw et al., 2005). As soon as increased growth of diatoms reduced available biogenic silica in the water column, green algae, and cyanobacteria, which thrive at low Si:P ratios (Sommer, 1983; Tilman and Kiesling, 1984), dominated in the lake, as indicated by cyanobacteria remains observed during pollen analysis, such as *Anabaena*, *Aphanizomenon* and *Gloetrichia*, as well as green algal remains of *Tetraedron* (Rey et al., 2019a). Cyanobacteria and green algae have no requirement for silica but demands for phosphorus are an order of magnitude higher than those of the diatoms (Kilham, 1986). The reconstructed TP values are mesotrophic with the uncertainty reaching eutrophic values in Moossee (Fig. 4 B). Around 5460–5400 cal yr BP small *Stephanodiscus* spp. gradually decreases, while *U. delicatissima* var. *angustissima* increases again, which suggests that phosphorus concentrations decreased while silica was still available enough for *Ulnaria* to develop its large frustules during late spring and early summer (Ryves et al., 2003). Gradual decrease of small *Stephanodiscus* spp. and the subsequent temporary disappearance from the record between 5300 and 4550 cal yr BP coincides with low values of akinetes of cyanobacteria, indicating ecosystem recovery. Changes in diatom assemblages affected reconstructed DI-TP values that decreased from 30.6 to 15.3 $\mu\text{g L}^{-1}$ between 5070 and 5020 cal yr BP.

5.2. Comparison of lake ecosystem response to prehistoric human disturbance

Changes in diatom assemblages and composition at Burgäschisee and Moossee, together with variations in DAR, reconstructed DI-TP values, and the abundance of algal remains (cyanobacteria, green algae) in the pollen record reflect lake hydrological and nutrient regimes during the Neolithic. Previous research on palynological records from both sites suggested synchronous land use and deforestation patterns at Burgäschisee and Moossee for more than 2000 years during the Neolithic (Rey et al., 2019a). By combining diatom data with pollen and archaeological information about landscape development, we can compare the responses of in-lake conditions at the two small lakes to prehistoric human settlements and disturbance and examine ecosystem recovery after the pile-dwellers abandoned the settlements.

Previous studies (Tinner et al., 2005; Colombaroli et al., 2013; Makri et al., 2020) report that the pre-Alpine region was affected by

anthropogenic disturbance since the onset of the Neolithic at ca. 7500 cal yr BP. At our study sites, the earliest indicators of anthropogenic impact appeared centuries later. These included intermittent pollen grains of *Cerealia*-type and dung fungi spores, *Podospora* and *Sporormiella*, that were observed in Moossee by ca. 6950 cal yr BP. Continuous anthropogenic activity in the lake catchment, such as landscape opening and gradual increase of biomass burning were recorded ca. 6550 cal yr BP in Moossee (Fig. 4 B) and ca. 6300 cal yr BP, in Burgäschisee (Fig. 4 A). The first changes in aquatic ecosystems were observed around this time, such as the increase of *Tetraedron* (Supplement Fig. C1, D1; Rey et al., 2019a). However, according to diatom data (DCA axis 1 and 2 and DI-TP), these first human impacts seem to have played a minor role for both lakes. Possibly, the degree of human disturbance was relatively low because of limitations due to still relatively small populations and limited by technologies for land management. Although a rapid decrease of *P. costei* and higher values of *F. crotonensis* were observed during the first pile-dwelling settlement at Burgäschisee (6150–5950 cal yr BP), which might indicate a slight shift in nutrient regime, nutrient concentrations as indicated by reconstructed DI-TP stayed stable at low values. In the case of Moossee, the dissolution of diatom valves in the period ca. 6460 to 5780 cal yr BP makes it difficult to draw conclusions about whether anthropogenic activities had an impact on the lake ecosystem during or after the first lakeshore settlement phase. However, green algae and cyanobacteria also show low values during this time (Fig. 4 B). Moossee might have had a higher buffering capacity for nutrients for zone DAZ 1a (Fig. 3 B) because of a higher lake level (Magny, 2004, 2013). Interestingly, elevated abundances of cyanobacteria akinetes were observed before the earliest lake shore settlement and reconstructed DI-TP values became slightly higher with the uncertainties reaching values typical for eutrophic conditions (Fig. 4 B). This suggests that Moossee was initially more nutrient rich relative to Burgäschisee during the Mid Holocene.

The best studied lake shore settlements from both lakes are from Cortaillod culture (Harb, 2018; Hafner et al., 2020), an archaeologically defined material culture from the Neolithic (5850–5450 cal yr BP) that populated the western and central Swiss Plateau (Stöckli, 2016). Archaeological pile-dwellings around Burgäschisee dated from 5800 to 5550 cal yr BP (Hafner et al., 2020). The similar development of lake shore settlements lasted ca. 90 years longer around Moossee (5800–5460 cal yr BP; Harb, 2018). Palynological data show major changes in vegetation and increased human impact on the landscape associated with Cortaillod period. Synchronous afforestation and reduced agricultural intensity are interpreted towards the end of these cultural phases around 5550 cal yr BP at both sites (Rey et al., 2019a; Fig. 4 A, 4B).

Along with lake shore settlements established at ca. 5800 cal yr BP major shifts in the diatom assemblages are apparent at both lakes (Fig. 4 A, 4B), suggesting significant alterations of the nutrient regime associated with Cortaillod phase. The diatom composition changes were more pronounced at Burgäschisee, as indicated by major changes in DCA axis 1, whereas at Moossee compositional shifts were subtler and mainly expressed along DCA axis 2. Diatom assemblage changes coincided with the beginning of excessive anthropogenic burning, forest clearance and agriculture (Rey et al., 2019a). This period also agrees with the peaks of total chlorophylls analysed in the sediments of Moossee (Makri et al., 2020) indicating high aquatic primary production (Leavitt and Hodgson, 2001). Additional nutrient loading into the lake could have been caused by deforestation and burning in the areas rich in fertile luvisols (Hafner et al., 2020) as well as due to the presence of human settlements and animal husbandry directly along the lakeshores. Spores from coprophilous fungi (dung spores), such as *Sporormiella* and *Cercophora*-type, have been found in several Burgäschisee pollen slides (Fig. 4 A, Rey et al., 2017), indicative of herbivore presence.

Palynological records from both sites contained relatively high concentrations of green algae and cyanobacteria that reflect enhanced nutrient conditions (van Geel et al., 1994) during Cortaillod settlements.

At Burgäschisee DI-TP values exceeded $35 \mu\text{g L}^{-1}$ (the threshold between mesotrophic to eutrophic conditions) and cyanobacteria were particularly abundant during the main eutrophication interval coinciding with the Cortaillod culture and rare or absent in other sections. In contrast, in Moossee cyanobacteria were generally more frequent, yet intermittent, notably with high values during the Cortaillod culture, although DI-TP values did not increase above $35 \mu\text{g L}^{-1}$. Diatoms are superior competitors for phosphorus compared to green algae (Kilham, 1986) and more successful under lower nutrient concentrations as long as sufficient silica is available in the water column. Cyanobacteria blooms often occur during hot summers in nutrient-rich lakes and form heavy growth at the water surface (O'Neil et al., 2012), although several studies show that algal and cyanobacterial blooms may also appear in oligotrophic lakes with no apparent nutrient enrichment, and even in waters with declining nutrient concentration (Winter et al., 2011; Smol, 2019). Strong thermal stratification, which is supported by previous studies (Makri et al., 2020), in combination with the higher Mid Holocene summer temperatures might have promoted frequent cyanobacterial blooms in Moossee. Considerable amount of akinetes of *Anabaena* and *Aphanizomenon* in the examined records, particularly for Moossee, point either to very high phosphorus loading in the lake (van Geel et al., 1994; Hillbrand et al., 2014), which is not supported by DI-TP reconstructions, or to stable thermal stratification during warm summers.

In the Burgäschisee diatom record there was a partial lake recovery (Fig. 4 A; changes in DCA axis 1 SD) immediately after abandonment of the shore settlement towards the end of the Cortaillod phase. A similarly rapid lake recovery after abandonment of lakeside dwellings was reported for Nussbaumersee, Eastern Switzerland, as indicated by a pronounced reduction of cyanobacteria akinetes and *Tetraedron* at ca. 5640 cal yr BP (Hillbrand et al., 2014). In Moossee and Burgäschisee, decreases in cyanobacteria and *Tetraedron* occurred later, abruptly at ca. 5550 cal yr BP, showing a rapid lake recovery. Interestingly, Moossee diatom assemblages (Fig. 3 B; DCA axis 1 and 2) recovered slower than Burgäschisee, which could be due to minor differences in the geographic and hydrological conditions, as is also reflected by the slightly higher nutrient concentrations at Moossee before the Cortaillod settlements.

The next phases of intensification of fires and landscape opening around Burgäschisee began at 5150 cal yr BP during the Horgen culture (Fig. 4A). Changes in diatom assemblages (DCA axis 1 SD values) and DI-TP values were not as pronounced as during the onset of Cortaillod settlement phase. This suggests that prehistoric resource-use pressures on the lake were lower or the lake was less sensitive to these as it still had not been returned completely to its ecological state prior to Cortaillod impacts. At Moossee, similar to Burgäschisee, the next phase of fire and forest clearance also appeared with the Horgen culture at 5100 cal yr BP (Fig. 4B; Harb, 2018; Rey et al., 2019a). However, diatom composition did not change to indicate more eutrophic conditions (in contrast DCA axis 2 scores continued to recover from the earlier eutrophication phase and DI-TP values decreased from 22 to $13 \mu\text{g L}^{-1}$). There was also no increase in cyanobacteria or green algae in the record. Possibly, human activity was less pronounced along the lakeshore or led to less nutrient input into the lake during this phase. Later changes in diatom assemblages (associated with higher DCA axis 2 values, as well as slightly higher DI-TP) and increases of *Anabaena* (Rey et al., 2019a) were observed at 4650 cal yr BP along with the arrival of Corded Ware culture. Small *Stephanodiscus* spp., indicators of high phosphorus appeared in diatom assemblages after the known pile-dwelling abandonment.

Diatom assemblage changes, together with variations of cyanobacteria and green algae remains, suggest that variations in lake nutrient regimes in Moossee in the absence of lakeside settlements may have been of similar amplitude as those observed during phases of increased human activity in the landscape when lakeside settlements were established. At this site, diatom assemblage shifts during the Cortaillod culture are apparent but only slightly more pronounced than during other phases. In contrast, at Burgäschisee at least the settlement phase during the Cortaillod culture had a much more pronounced impact on the lake

with changes in diatom assemblages exceeding the variations during previous intervals.

Both Burgäschisee and Moossee suggest that anthropogenic land use pressure on aquatic ecosystems of small lakes in Switzerland occurred earlier than presumed and was related to catchment deforestation, land use, and lakeside dwellings. Previous off-site records from larger lakes, for example, from Lake Morat on the Swiss Plateau, showed little evidence for Neolithic lake impacts. Particularly, detectable impacts began during the Early Iron Age and Roman period (Haas et al., 2019). Neolithic human impact on water quality was also detected locally around known archaeological sites of settlement areas of Lake Zurich (Tóth et al., 2019). However, these results were from shallow-water sediments within or very close to Neolithic settlements and not from deeper sediments that represent off-site conditions within the lake basin. Burgäschisee and Moossee were apparently more sensitive to local human activity around the lake shores than some of the larger lake ecosystems. The results from off-site cores in the lake centre indicated that water quality, and more specifically lake nutrient concentrations, were influenced within the entire lake basin during the Cortaillod culture, affecting the littoral environments and open-water diatom assemblages. This finding agrees with earlier studies of aquatic non-pollen palynomorphs in the sediments of small lakes (Hillbrand et al., 2014; Rey et al., 2019a). However, based on the limited information presently available, Neolithic land use and lakeside settlements have not always led to detectable impacts on Swiss lakes even when the settlements were in close vicinity of the lake shores, and the impact of activities associated with lakeside settlements (e.g., clearcutting, agriculture, pasturing) can differ amongst small lakes. This is exemplified in our study by the cultural phases in the pollen records that are not associated with significant changes in diatom assemblages of Burgäschisee and Moossee, and by the observation that Moossee was less susceptible to human induced eutrophication during the Cortaillod phase than Burgäschisee. This suggests that the Neolithic impacts on aquatic ecosystems are spatio-temporally complex, with some phases showing human impact, and others characterized by limited impacts, or apparent insensitivity. This may be due to varying sensitivity of aquatic ecosystems to disturbance due to local geological, geographic and hydrological conditions, but almost certainly also due to varying locations, intensities and forms of cultural activities and land use practices around Swiss lakes during the Neolithic.

6. Conclusions

Burgäschisee and Moossee diatom assemblages show that the Early Neolithic human settlement and land use led to phases of increased nutrient loading, eutrophication, and turbidity, particularly during the Cortaillod culture, in small central European lakes. Each record showed different degrees of lake ecosystem responses to Neolithic activities, even though the archaeological and palaeovegetation evidence from both lakes suggested that Neolithic land cover and agricultural changes were similar (Rey et al., 2019a). However, diatom response to settlement phases of increased human impact were much more pronounced at Burgäschisee, notably corresponding to Cortaillod culture. The spatio-temporal patterns in the algal records suggest different specific anthropogenic land use pressures and differences in lake water hydrology at small lakes on the Swiss Plateau.

Our results and other published data suggest that the effects of local Neolithic human activity may have been more pronounced in small oligo- to mesotrophic lakes compared to large Swiss Plateau lakes. Neolithic anthropogenic activities had a disproportionate impact on algal response in lakes with lower nutrient concentrations and lower tendency to support cyanobacterial populations under pre-impact conditions (Burgäschisee). In such ecosystems, nutrient release associated with prehistoric human activities led to unprecedented cyanobacteria blooms, potentially with toxic effects, with implications for animals and humans. In contrast, Moossee showed that in other lake ecosystems such

blooms occurred prior to known Neolithic settlements, although at Moossee they were further promoted during the Cortaillod phase. Small central European lakes may be particularly susceptible to local land and near-shore use impacts since the Early Neolithic. As our results show, many small lakes may have a long and complex history of human impacts and recoveries during the millennia before the wide-ranging water quality and ecosystem changes observed in recent centuries.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Author contributions.

IGE and OH conceived and designed the study, EG, WT and FR planned and conducted the field work, sedimentological analyses and dating, IGE performed diatom analysis, AM contributed to the classification and ecological interpretation of diatom data, IGE, OH and CCM wrote the initial draft version of the manuscript, and all the authors contributed to the submitted version.

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Data availability.

Research data will be available in a data repository DRYAD.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.catena.2023.107738>.

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