**Climate-related soil saturation and peatland development may have conditioned surface water brownification at a central European lake for millennia**

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# Abstract

Water brownification has long altered freshwater ecosystems across the northern hemisphere. The intensive surface water brownification of the last 30 years was however preceded by previous long-lasting more humic browning episodes in many catchments. To disentangle a cascade of browning-induced environmental stressors this longer temporal perspective is essential and can be reconstructed using paleolimnological investigations. Here we present a Holocene duration multi-proxy paleolimnological record from a small forest mountain lake in the Bohemian Forest (Czechia) and show that climate-related soil saturation and peatland development has driven surface water brownification for millennia there. A long core retrieved from the central part of the lake was dated using 14C and 210Pb, subsampled and analyzed for diatoms and zoological indicator (chironomids, planktonic cladocerans) remains. X-ray fluorescence (XRF) provided a record of elements sensitive to biogeochemical processes connected to browning and catchment development (P, Ti, Al/Rb, Fe/Ti, Mn/Ti, Si/Ti). Three threshold shifts related to the processes of water browning were detected in both diatom and chironomid successions at ~10.7, ~5.5 and ~4.2 cal. ky BP. Since, postglacial afforestation of the catchment ~10.7 cal. ky BP the lake experienced strong thermal stratification of the waters, but after ~6.8 cal. ky BP soil saturation and expansion of peatlands led to effective shading and probable nutrient limitation within the lake ecosystem. The more intensive in-wash of dissolved organic matter appears to decline after ~4.2 cal. ky BP, when the paludified catchment soils became permanently anoxic. Two temporary negative and positive anomalies of browning progress occur at the same time and may be connected with the “8.2 ka event” and the “4.2 ka event”, respectively. The key role of peatlands presence in the catchment was manifested in millennial-scaled browning process and a climatic forcing of long-lasting browning is evidenced by coincidence with the moistening of climate across the northern hemisphere after ~6 cal. ky BP.

Key words: natural acidification, dystrophication, paludification, humic substances, Mid-Holocene climate transition, Bohemian Forest

# Introduction

Water brownification, i. e. increased brown coloration, stems mainly from heightened terrestrial input of humic substances measured as dissolved organic carbon (DOC) (Roulet and Moore, 2006; but see Kritzberg and Ekström, 2012). Brownification has gripped an attention of the scientific community, as fresh waters across the northern hemisphere have been getting browner for the last 30 years (Kritzberg, 2017; Meyer-Jacob et al., 2019). Proposed factors driving higher levels of DOC in surface waters involve recent climate change (Creed et al., 2018; Fee et al., 1996), land-use (Mattsson et al., 2009; Meyer-Jacob et al., 2015; Sankar et al., 2020) and/or recovery from anthropogenic acid deposition from the atmosphere (Hruška et al., 2009; Monteith et al., 2007). Although recovery from acid deposition cannot explain the hemispherical extent of recent surface water brownification (Clark et al., 2010; Kritzberg, 2017), the recovery-based hypothesis builds on the important point that many freshwater bodies were probably brown naturally before the period of anthropogenic surface water acidification. Lacustrine sedimentary records offer the potential to study the progress of water brownification over these millennial time-scales. Such long-term records are needed to disentangle the differing mechanisms attributed to brownification, since recovery from anthropogenic acidification can bias correlation between spatial and decadal-scaled studies (Gavin et al., 2018; Stetler et al., 2021).

In low productivity (oligotrophic) lakes, the heightened concentration of DOC triggers a series of interconnected environmental shifts with direct impact such as (i) lower pH caused by the dominant proportion of humic acids in DOC (Thurman, 1985) and (ii) effective light attenuation (Vincent and Pienitz, 1996; Wetzel, 2001). Those direct impacts can result in further indirect changes producing (iii) water column thermal stratification by enhanced heating of surface layer (Fee et al., 1996; Snucins and Gunn, 2000), (iv) anoxic bottom conditions sustained by thermal stratification limiting oxygen replenishment (Brothers et al., 2014; Nürnberg and Shaw, 1999) and (v) altered nutrient availability (Corman et al., 2018; Nürnberg and Shaw, 1999; Sanders et al., 2015). Through this complex suite of stressors, water brownification can produce severe impacts on aquatic organisms (Karlsson et al., 2009; Solomon et al., 2015; Vasconcelos et al., 2016), which can amplify the effects of brownification by biotic processes (Brothers et al., 2014). Conversely, promotion of growth of aquatic biota by allochthonous input of humic compounds has also been documented (Daggett et al., 2015; Kissman et al., 2013; Pienitz and Vincent, 2000). A hypothesis of a unimodal relationship between primary production and DOC links these contradicting observations and depicts the responses to brownification as a trade-off between positive response to input of nutrients from dissolved organic matter (DOM) and limitation by reduced light availability (Jones, 1992; Kelly et al., 2018). The degree of fertilizing ability of DOM varies with differences in the stoichiometry between nutrients contained in the organic matter (Tipping et al., 2016) or change in co-export mechanism of DOM and soil-bounded nutrients during leaching (Kopáček et al., 2011). The capacity of soils to bound DOM alters substantially with redox changes on the gradient of soil saturation (Olivie-Lauquet et al., 2001; Possinger et al., 2020). Spatial scales appear to also matter, with positive correlations observed between concentrations of DOC in fresh waters and extent of wetlands in catchments (Kortelainen, 1993; Laudon et al., 2011; Rantala et al., 2016) and rainfall/run-off (Brothers et al., 2014; Ejarque et al., 2018).

The inter-linked impacts of precipitation dynamics and the processes of soil development, e.g., podzolization and paludification, could be traced on the millennial scale and further elucidate mechanisms of natural brownification. In the Post-glacial, vegetational succession mediated the effects of climate on brownification by providing sources of organic matter and interacting with soil biogeochemistry and hydrology (Engstrom et al., 2000; Huvane and Whitehead, 1996; Korsman et al., 1994; Pienitz et al., 1999). Soil formation and subsequent hardening of soil horizons during podzolization made dissolved organic matter (DOM) available for a transport into lakes (Engstrom et al., 2000; Steinberg, 1991). Humic acids potentially played an important role in acidification on deglaciated base-poor bedrocks (Ampel et al., 2015; Ford, 1990), besides the prominence of depletion of base cations in the initial phases of glacial lake ontogeny (Boyle, 2007; Boyle et al., 2013a, 2013b). Steps in the progress of millenial-scale brownification often occurred in phase with pulses of climate humidity (Brodin, 1986). Whereas the cold and dry Younger Dryas stadial (~12.9–11.7 ky BP) interrupted water brownification in some lakes due to temperatures limiting vegetation growth and freezing soil waters (Ampel et al., 2015; Norton et al., 2011), a lack of leaching water locally during the dry Mid-Holocene “thermal maximum“ (~8–5 cal. ky BP) may have reduced brownification for some catchments (Huvane and Whitehead, 1996; Itkonen et al., 1999).

A regional shift to a wetter climate after ~6 cal. ky BP, known as Mid-Holocene Climate Transition (Magny et al., 2006; Wanner et al., 2008), appears to have accelerated brownification in many boreal catchments (Myrstener et al., 2021; Pienitz et al., 1999; Solovieva and Jones, 2002). This pronounced climatic threshold has been linked to the inception and expansion of peatlands (paludification) (Bauer et al., 2003; Le Stum-Boivin et al., 2019; Myrstener et al., 2021), that further supplied headwaters with DOC (Belyea and Malmer, 2004). The extent to which the formation of impermeable soil horizons (podzolization) conditioned this regional paludification remains the subject of debate (Payette et al., 2012; Schaffhauser et al., 2017). Similarly, uncertainties accompany understanding of the progress of brownification outside the well-studied boreal regions of northern Europe and the North America in the Holocene. In particular, new paleolimnological records from mid-latitude Europe could alter the picture of Holocene brownification, given both the differences in the Holocene trajectory of climate humidity compared to northern Europe (Florescu et al., 2019; Mauri et al., 2015) and the acidic base-line of these catchments prior to anthropogenic acidification (Jüttner et al., 1997; Sienkiewicz, 2016). Unfortunately, studies from central Europe tracking the progress and possible controls over brownification in mountain lakes through the Holocene are rare (e.g., Steinberg, 1991).

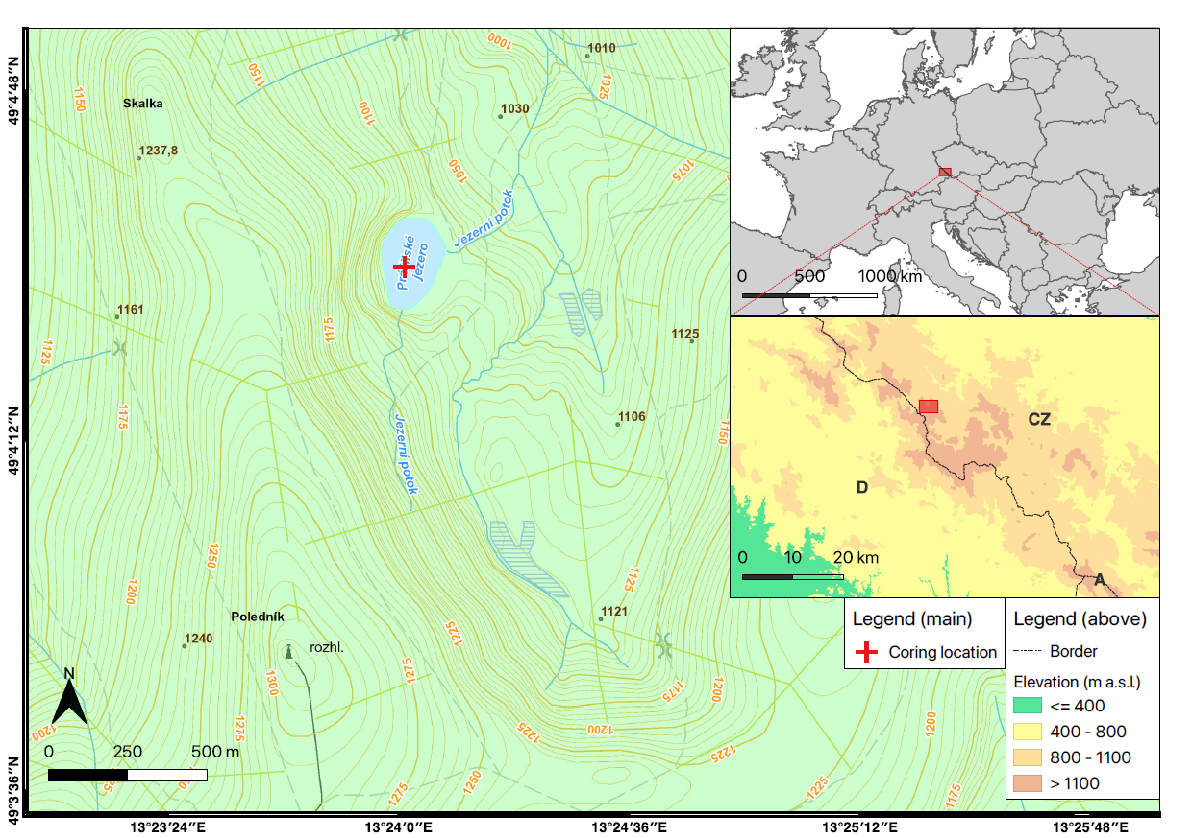
DOC levels in prehistory can be reconstructed for lake sediments through diatom-based transfer functions (Pienitz and Vincent, 2000) or by measuring total organic carbon concentration in sediments (Meyer-Jacob et al., 2017; Russell et al., 2019). However, an increase of humic content in boreal lakes during the Holocene was most often detected indirectly in paleorecords as a decrease in ecosystem productivity or water pH, hence the terms “dystrophication” and “natural acidification” remain rooted in paleolimnological studies. The various scale and complexity of feedback mechanisms during brownification invite the application of a multi-proxy approach (Birks and Birks, 2006) to reveal particular driving factors behind and impacts on aquatic biota during millennial-scaled brownification. Paleolimnological studies can employ numerous complementary geochemical and biological indicators that can disentangle sensitive and interwoven responses to the impacts of brownification, including:

1. acidification by humic acids can be detected using changes in diatom communities (Battarbee et al., 2010; Birks and Simpson, 2013; Curtis et al., 2009),
2. shading of the water column creates imbalance in primary production between planktonic and benthic communities (Karlsson et al., 2009),
3. thermal stratification imprints on dynamics of floating-dependent diatom species (Reynolds, 2006; Rühland et al., 2015) and possibly to some extent on changes in the ratio between chrysophycean cysts and diatom valves - C:D ratio (Werner and Smol, 2005),
4. anoxic bottom water conditions affect chironomid indicators and concentrations of their remains (e.g., Quinlan and Smol, 2001; Ursenbacher et al., 2020) and can be reflected in redox-sensitive element ratios such as Mn/Fe, Mn/Ti and Fe/Ti (Davison, 1993; Kylander et al., 2013; Makri et al., 2021),
5. altered nutrient availability affects the taxonomic composition of both diatom (Hall and Smol, 2010; Rivera-Rondón and Catalan, 2020) and chironomid communities (Brodersen and Quinlan, 2006; Lindegaard, 1995) and the C:D ratio (Smol, 1985).

Here, we assess the evidence and explore the range of causal factors for lake water brownification using the sediments of a small mountain lake (Prášilské jezero) located in the Bohemian Forest of central Europe. This type of lake, with poorly-buffered soils and boreal-type vegetation, holds the catchment properties constant providing the opportunity to compare brownification in central Europe with that encountered in the more widely studied boreal regions. The data generated facilitate inferring trends in pH using diatom-based transfer functions, estimating the intensity of light limitation of algal life-forms in the water by separate assessment of periphytic and euplanktonic diatoms, using chironomid assemblage composition and trends redox-sensitive elements (e.g., Mn/Ti and Fe/Ti) to reveal phases of anoxia, and exploring the nutrient dynamics during brownification episodes using changes in diatom-based transfer functions (e.g., total phosphorus) and sediment geochemistry (e.g., Al, Si, P). Specifically, we: (i) track the onset and extent of brownification in what appears to be a naturally humic and small catchment lake, (ii) reconstruct the impacts of brownification on the lacustrine ecosystem using remains of aquatic organisms (i.e., diatoms and chironomids) and sediment geochemistry, and (iii) explore the main factors causing brownification during the Holocene and contrast the ecosystem functioning of this central European lake with those across wider boreal regions.

# Material and methods

## Study site

Fig. 1: Map of the Prášilské jezero catchment, the location of the study site in the Bohemian Forest mountain range (red rectangular section in the lower inset), and the location of the Bohemian Forest in Europe (red rectangular section in the upper inset).

Eight glacial lakes are situated along the Czechia-Germany-Austria border in the Bohemian Forest (central Europe, Fig. 1) and analyses of their sediments document the last phases of the deglaciation in this low mountain range (Mentlík et al., 2013; Vondrák et al., 2019a; Vondrák et al., 2021). Shallow soils, siliceous bedrock (gneiss, mica-schist, granite, quartzite) and presence of Norway spruce (*Picea abies*) as the dominant tree taxon, have enhanced the sensitivity of lake waters to acidifying effects, thereby both pre-industrial acidification by humic substances (Moravcová et al., 2021; Pražáková et al., 2006; Steinberg et al., 1991; Vondrák et al., 2019b) and anthropogenic acidification by mineral acids (Fott et al., 1994; Schmidt et al., 1993; Steinberg et al., 1988; Vesely et al., 1993; Vrba et al., 2003) were documented in the Bohemian Forest lakes. All lakes in the Bohemian Forest were reported as brown-water prior to anthropogenic acidification (see Vrba et al., 2000 for review), thereupon atmospheric acid deposition (1960’s–1990’s) increased their water-transparency by in-lake precipitation of humic substances (Steinberg, 1991). During a recent recovery from anthropogenic acidification (Nedbalová et al., 2006; Vrba et al., 2016, 2003a), water colour has become darker in most of the lakes in the area (Vrba et al., 2000).

Prášilské jezero (49°05´N, 13°24´E; Fig. 1) is the smallest dimictic lake in the region (Šobr and Janský, 2016; Vrba et al., 2003b), with higher DOC and TP concentrations displayed compared to the other Bohemian Forest’s lakes (Tab. 1; see Vrba et al., 2000). Six small inlets and one outlet drain the semicircular cirque that contains Prášilské jezero (Dočkalová et al., 2022). Owing to moderate anthropogenic acidification of the lake leading to low concentrations of toxic aluminium, crustacean zooplankton survived there (Fott et al., 1994) and Prášilské jezero´s biota has undergone an earlier recovery from acidification compared to larger lakes (Vrba et al., 2016, 2006). Prášilské jezero is considered as naturally fishless given the absence of any historical observations of fish populations and the steepness of the outlet prohibiting immigration (Kubečka et al., 2000; Veselý, 1994).

Tab. 1: Parameters of Prášilské jezero. ANC – acid neutralizing capacity, TP – total phosphorus, DOC – dissolved organic carbon, AlT – total reactive aluminium. Parameters after Soldán et al. (2012) and Šobr and Janský (2016), chemical variables measured in September 2007.

| Altitude | 1079 | m a.s.l. |
| --- | --- | --- |
| Surface lake area | 0.042 | km2 |
| Max. depth | 17.2 | m |
| Lake volume | 0.35 | 106 m3 |
| Catchment area | 0.65 | km2 |
| Lake retention time\* | 0.54 | years |
| pH | 4.96 |  |
| ANC | -10 | mmol l-1 |
| TP | 5.8 | µg l-1 |
| DOC | 5.5 | mg l-1 |
| AlT | 167 | µg l-1 |
| \*rough estimate of lake retention time given by ratio of lake volume/catchment area [m3 m-2] (Vrba et al., 2000) | | |

## Sampling and chronology

The profile retrieved from the central part of Prášilské jezero (total thickness 2.21 m) consisted of three parallel drives sampled from a stable floating platform (Pra-15-2-1, Pra-15-1-2 and Pra-15-2-2) as 1.5 x 0.07 m half-cylinder Russian-style cores, and the intact sediment water interface taken by a 0.1m diameter gravity core (Pra-15-GC2) (Boyle, 1995) during a fieldwork in August 2015. All drives were correlated using matching of core scan data collected using the Liverpool Geotek Multi-sensor Core Logger (MSCL), and an age-depth model generated for the sediment record using 14C and 210Pb age measurements (for details on dating see Carter et al. (2018a) and age-depth model in Fig. A.1).

## Geochemistry

For correlation of the cores and interpretation of sediment characteristics, all long-cores were photographed at 15 μm pixel resolution using the Line-scan camera fitted to the Liverpool GeotekMulti-Sensor Core Logger (MSCL), and then they were covered with 6μm thickness polypropylene film and measured at 5mm intervals on a wet sediment basis using an Olympus Delta energy dispersive μXRF mounted on the Liverpool Geotek MSCL (Boyle et al., 2015; Schillereff et al., 2015). For the gravity core and a suite of subsamples at ~0.05 m intervals from the longer record were measured for major and trace element concentrations on a dry mass basis using XEPOS 3 Energy-dispersive XRF. This suite of subsamples was selected to recover P concentrations, as signal attenuation precludes recovery of P data from wet sediments. All dry mass samples were lightly hand ground, pressed and then measured under a He atmosphere under combined Pd and Co excitation radiation and using a high resolution, low spectral interference silicon drift detector. Both the Olympus Delta and XEPOS 3 XRFs undergo daily standardization procedures and have accuracies verified routinely using 18 certified reference materials (Boyle et al., 2015). Organic content, by loss-on-ignition (LOI) values, was used to correct light element concentrations. LOI values were measured by heating the samples at 105°C overnight to evaporate all moisture content and then igniting them in a furnace at 450°C for 4.5 hours to combust all organic matter (Boyle, 2001).

Near Infrared Spectroscopy (NIRS) results have been shown to correlate with loss-on-ignition (LOI) measurements (Martin et al., 2004; Pearson et al., 2014; Russell et al., 2019). NIRS reflectance has been measured on samples through the PRA core using the Liverpool BRUKER MPA FT-NIR spectrometer (Russell et al., 2019). In this, lightly-ground samples were scanned at 4 nm intervals across 3598 -12493 nm. The Liverpool NIRS and LOI (550°C) training set of lake and peat sediments (n = 456 samples) shows a strong correlation (r2 = 88%) between the first derivative of the entire NIR spectra and the measured LOI. The LOI was predicted from the NIRS data and provides robust, rapid and non-destructive estimates for LOI and C concentrations (Fig. A.7).

## Diatom and chrysophyte analyses

Remains of siliceous algae were isolated from 36 samples at 10 cm intervals through the profile (with higher resolution of 2–5 cm intervals in sections of interest: depth in core 1630–1620 cm, 1570–1478.5 cm) using standard procedures (Battarbee et al., 2001). Dry sediment (~0.1 g) was boiled in 30% hydrogen peroxide. After the solution cooled, a drop of 35 % hydrochloric acid was added. Solutions were rinsed with distilled water five times. Precise volume of diluted sample solution (50 μl) and distilled water (550 μl) together with a specific concentration of divinylbenzene microspheres (100 μl, 30.65×104 particles/ml) and drop of ammonia were permanently mounted onto cover slides using Naphrax mounting resin. The only exception represents the most basal sample concentration (1698–1698.5 cm) with the 20 μl of sample solution with 580 μl of distilled water.

Using a light microscope, at least 400 diatom valves were counted under 1000× magnification. To retain sufficient resolution of diatom periphyton for further quantitative analyses, euplanktonic dominant *Asterionella ralfsii* was suppressed. In samples where *A*. *ralfsii* dominated (1567–1500.5 cm), only 100 valves of *A*. *ralfsii* were counted concurrently to periphytic diatoms, then its counting was stopped and at least additional 400 valves of periphytic diatoms were counted in the sample. We use broadly accepted term “periphyton” (Wetzel, 2001) for any other diatom life-form than euplanktonic following the definition that periphyton includes “all the microscopic algae, bacteria, and fungi on (or associated with) substrata” (Stevenson et al., 1996). Diatom periphyton was classified into guilds designed by Passy (2007) regarding supplementary suggestions and species database in Rimet and Bouchez (2012). We separated four guilds: low-profile (firmly attached to substrate), high-profile (loosely attached to substrate), motile (actively moving on substrate) and facultatively planktonic (= tychoplanktonic).

Chrysophyte to diatom ratio (C:D ratio) was estimated by concurrent counting of chrysophyte stomatocysts and diatom valves. C:D ratio was expressed as a percentage of chrysophyte cysts while total count of diatom valves represented 100%. Diatom and chrysophyte accumulation rates were estimated using the divinylbenzene microspheres as reference particles.

Diatoms were identified using Krammer and Lange-Bertalot (1986, 1988, 1991a, b), Lange-Bertalot and Metzeltin (1996), Lange-Bertalot (2001), Krammer (2000, 2002, 2003), Houk (2003), Houk and Klee (2007) and Lange-Bertalot et al. (2011, 2017). Diatom nomenclature was updated and unified according to AlgaeBase (Guiry and Guiry, 2022). Our specimens of *Asterionella ralfsii* W. Smith (Fig. A.8) show distinctly heteropolar narrow valves with capitate headpole and rostrate rounded footpole. Headpole ending is not rounded as in *A*. *formosa* Hassall but only slightly truncated in comparison with *A*. *ralfsii* var. *americana* Körner (Spaulding and Edlund, 2009). Striae are almost invisible in LM.

## Chironomid and planktonic cladoceran analyses

In total, 123 sediment samples with average wet volume of 3.2 ml were processed. The samples were sieved over 100 μm mesh size using distilled water. Chironomid head capsules (HCs) were picked from a Sedgwick-Rafter counting cell using a stereoscopic microscope at 40–50× magnification, fine forceps, and steel needles, then dehydrated in 90% ethanol, and mounted in Euparal mounting medium to prepare permanent slides. Due to very low average head capsule abundances in the studied material, samples with less than 50 identified HCs were merged with adjacent samples to exceed the minimum count level. This approach allowed plotting of relative abundance data (%) and more robust ecological interpretation of the subfossil assemblages (Heiri and Lotter, 2001). The taxonomic identification of HCs and related ecological preferences of the individual taxa followed mostly Wiederholm (1983) and Brooks et al. (2007). Finally, we distinguished four chironomid ecological groups – (i) taxa of oxygenated profundal, (ii) other lake taxa inhabiting bottom substrates, (iii) semi-terrestrial and rheophilic taxa (including taxa associated with seepages, moss, and small streams), and (iv) lake taxa associated with aquatic macrophytes.

The same samples were also used for the identification of remains of planktonic cladocerans (families Daphniidae and Bosminiidae). Resting eggs of genus *Daphnia* and g. *Ceriodaphnia* were concurrently observed and counted during the HCs picking, whereas head shields and shells of g. *Bosmina* were analyzed qualitatively, i.e., *Bosmina* remains very abundant or common (1) versus rare or absent (0). Identification of the selected cladoceran remains followed the atlas by Szeroczyńska and Sarmaja-Korjonen (2007).

## Numerical analyses

Zonation of the sediment profile was guided by three different cluster analyses using Hellinger transformed relative abundances of diatom and chironomid taxa. Two types of species data were entered for cluster analysis of the diatom data: (i) using the whole diatom assemblage and (ii) using the periphytic assemblage but excluding the euplanktonic *A. ralfsii*. Constrained Incremental Sums of Squares (CONISS) (Grimm, 1987) (Fig. A.2) tested by Broken-stick model (MacArthur, 1957; Legendre and Legendre, 1998) identified significant assemblage zones and was conducted using packages “analogue”, “rioja” and “vegan” (Juggins, 2012; Oksanen et al., 2008; Simpson and Oksanen, 2013) in R 4.1.2 software (R Core Team, 2021). Hill’s N2 (Hill, 1973) was calculated using C2 software version 1.5 (Juggins, 2007) in order to assess “effective number of taxa” (Jost, 2006) for every total diatom assemblage, diatom non-planktonic assemblage, diatom facultatively planktonic assemblage, and total chironomid assemblage.

Diatom-inferred pH and total phosphorus (DI-pH, DI-TP) were calculated using combined modern training sets and weighted-averaging with inverse (for pH) and classical (for TP) deshrinking available at the European Diatom Database (EDDi) (Juggins, 2001). Relative abundances of periphytic diatom taxa were used in the DI-pH and DI-TP reconstructions, excluding the euplanktonic *A*. *ralfsii* given the questionable indicator value (discussed in Section 4.2). The periphytic-based estimations can provide a relevant signal of chemical changes in lakes (DeNicola and Kelly, 2014; Philibert and Prairie, 2002; Werner and Smol, 2005), if we consider their potential bias towards littoral habitats (Pla-Rabés and Catalan, 2018). The combined training sets and two regional training sets for pH (ALPE) and TP (NW Europe dataset) proved sufficient overlap with our periphytic diatom assemblages when the squared chi-squared distance to the closest analogue obtained by MAT (Modern Analogue Technique, five nearest analogues) served as a measure of analogy for the training sets (Juggins, 2001). Finally, the combined training sets for both pH and TP were favoured for the reconstruction (Tab. 2), because of the absence of *A*. *ralfsii* in the “ALPE” and “NW Europe” regional datasets. Even though we excluded this species from the weighted averaging, we preserved its influence at least in the MAT step. The inferred environmental variables derived using the combined and regional datasets are compared in Fig. A.3.

Tab. 2: Parameters of training sets used for reconstruction of past variables provided by Juggins (2001). TP – total phosphorus, RMSE – root mean square error, r2 – coefficient of determination.

|  | Combined pH training set  (inverse deshrinking) | Combined TP training set  (classical deshrinking) |
| --- | --- | --- |
| RMSE | 0.46114 | 0.38594 |
| r2 | 0.75623 | 0.63857 |
| Average bias | 0.0042676 | 0.0038784 |
| Maximum bias | 0.54009 | 0.49712 |

# Results

## Zonation

In total, four zones were determined based on the cluster analyses for diatom and chironomid relative abundances: Zone 1a, Zone 1b, Zone 2, and Zone 3 (see Fig. 2, 3 and A.2). Zones 1, 2 and 3 were supported by significant clustering of diatom assemblages, based on the whole diatom assemblage (Zone 2/Zone 3; depth of 1566.25 cm) and periphytic diatom assemblage (Zone 1/Zone 2; depth of 1585.25 cm). Zone 1 was subdivided further based on the first non-significant chironomid splitting accompanied by the second diatom non-significant splitting (Zone 1a/ Zone 1b; depth of 1675.25 cm).

## Zone 1a (11.4–10.7 cal. ky BP)

Diatom and chironomid assemblages were dominated strongly by few taxa producing a low Hill’s N2 (Fig. 2, Fig. 3). Facultatively planktonic *Aulacoseira pfaffiana* and *A*. *alpigena* proliferated considerably (Fig. 2, A.4, A.5), so that the total influx of diatom valve concentrations peaked in this zone (~16.5\*109 valve particles cm-2 y-1; Fig. 4) and outnumbered chrysophyte stomatocysts resulting in the lowest C:Dratio (10.5%) within the record (Fig. 4). Si/Ti ratios reflect this trend of siliceous algae influx with excess biogenic Si relative to lithogenic elements (Fig. 4; Fig. A.7). Chironomid assemblages were dominated by taxa that inhabit bottom substrates in well-oxygenated profundal waters (31–57%; Fig. 3), namely *Heterotrissocladius grimshawi*-type, *Micropsectra insignilobus*/*contracta*-type, and *Tanytarsus lugens*-type (Fig. A.6). Concentrations of chironomid head capsules (HCs) reached values higher by order of magnitude than in the rest of the core, with up to 131 HCs cm-3 compared with values 0–38 HCs cm-3 in Zones 1b–3 (Fig. 4). Concentrations of *Daphnia longispina*-type ephippia increased during the zone and *Bosmina longispina* remains were abundant (Fig. 3). Average DI-pH values of 5.82 were affected by a low value 5.54 in a sample with maximal *A*. *pfaffiana* dominance (Fig. 4). This sample showed the very high standard error in estimation of DI-TP, which averaged ~1.5 µg l-1 through the zone. Ti concentrations decreased sharply from ~680 to ~260 µg g-1 reflecting a decline in supply of lithogenic elements to the lake (Fig. 4). Trends in Mn/Ti and Fe/Ti broadly corresponded in the first half of the zone reflecting the gradual decline of Mn, Fe and Ti since the Holocene onset, but then diverged as Fe increases in concentration (Fig. 4, A.7).

## Zone 1b (10.7–5.5 cal. ky BP)

Here, diatom assemblage reached the highest effective number of diatom taxa (Hill’s N2 ~22, ~9 cal. ky BP; Fig. 2). Increasing relative abundances of the low-profile guild were disrupted by a bloom of facultatively planktonic diatoms and a dominant *Aulacoseira lirata* between ~8.1 and ~7.6 cal. ky BP (Fig. 2). This event is evidenced by increased Ti concentrations and the synchronous trends in Mn/Ti and Fe/Ti that harmonize from the previous distinct excess of Fe relative to Ti contrasting the patterns Mn/Ti (Fig. 4). Also, concentrations of other biotic remains responded sensitively around 8.1 cal. ky BP, with an increase in chironomid HCs concentrations, a distinct peak of other lake taxa inhabiting bottom substrates; especially *Heterotrissocladius marcidus*-type (Fig. 3, Fig. 4, A.6), and decrease in the siliceous algae remains (Fig. 4) and *Daphnia longispina*-type ephippia (Fig. 3). Substantial fall in the influx of chrysophyte stomatocysts reduced the C:D ratio (Fig. 4). Simultaneous decrease in Si/Ti ratio was preceded by an oscillation to higher values ~8.2 cal. ky BP (Fig. 4). DI-pH shifted from the values averaging 6.04 before the event to slightly higher values averaging 6.16 after the event to the end of the zone (Fig. 4). DI-TP increased up to ~7.5 µg l-1 simultaneously with the peak of low-profile diatoms ~9 cal. ky BP, afterwards decreased during the event (~8.1–7.6 cal. ky BP) and these trends are mirrored in the concentrations of sedimentary P. Then the average DI-TP value reduced to ~3.1 µg l-1 until the end of the zone ~7.5–5.8 cal. ky BP (Fig. 4) whereas the sedimentary P increased to its highest values (max ~9.8 mg g-1) during this period (Fig. 4). In the immediate aftermath of the ~8.1–7.6 cal. ky BP event, there was a return to the distinct excess of Fe relative to Ti contrasting the patterns in Mn/Ti ratios which reflect elevated Fe concentrations.

Apart from the ~8.1–7.6 cal. ky BP event, the chironomid concentrations were very low (2–18 HCs cm-3) and the assemblages were characterized by increased proportions of semi-terrestrial and rheophilic taxa (e.g., *Georthocladius luteicornis*-type) and taxa associated with aquatic macrophytes (e.g., *Corynoneura edwardsi*-type) (Fig. 3, A.6). Bottom substrate species were dominated by *Procladius* (5–38% of the total assemblage), a taxon tolerant to oxygen depletion that did not reach such high relative abundances in the other zones (Fig. 3). Trends of Mn/Ti and Fe/Ti harmonized with reduced Fe and elevated Mn concentrations, and Al/Rb and Al/Ti started to fluctuate to their highest values after ~6.8 cal. ky BP (Fig. 4). At the very end of the zone, influx of chrysophyte stomatocysts (~9.3\*109 particles cm-2 y-1; Fig. 4) and the effective number of chironomid taxa (~18; Fig.3) peaked. At the same time, effective number of diatom taxa decreased, mainly because of *A*. *alpigena* dominance (max. ~46%; Fig. 2). *Bosmina longispina* remains were numerous in all samples of the Zone 1b, but *Ceriodaphnia* ephippia were still absent, except for a one isolated occurrence (Fig. 3).

## Zone 2 (5.5–4.2 cal. ky BP)

A decline in planktonic species characterizes Zone 2 and involves decreases in the relative abundance of facultatively planktonic diatoms (Fig. 2), concentrations of *D*. *longispina*-type ephippia (Fig. 3) and influxes of chrysophyte stomatocysts (Fig. 4). Euplanktonic diatom *Asterionella ralfsii* and a cladoceran of genus *Ceriodaphnia* became established at low concentrations (Fig. 2, 3). *Bosmina longispina* remains continued to be very abundant (Fig. 3). Effective numbers of chironomid taxa decreased (Fig.3), whereas the effective number of taxa in the total diatom assemblage increased (Fig. 2), which coincides with lack of dominant planktonic diatoms. Relative abundances of non-planktonic diatom periphyton increased together with the proportion of non-planktonic Hill’s N2 as the dominants within assemblages (Fig. 2). The influx of siliceous algae decreased towards the Zone 2/3 border, but Si/Ti and C:D both peaked ~4.2 cal. ky BP on the Zone 2/3 boundary (Fig. 4). Chironomid concentrations became almost negligible (max. ~8, average ~3 HC cm-3; Fig. 4) and the assemblages comprised high portions of semi-terrestrial and rheophilic taxa (9–27%, dominated by *G. luteicornis*-type) and taxa associated with aquatic macrophytes (29–35%; dominated by *P. sordidellus*/*psilopterus*-type) (Fig. A.6). DI-pH showed a distinct decreasing trend (Fig. 4) and DI-TP remained low values averaging ~2.5 µg l-1, sedimentary P started to decline from previously high values (Fig. 4). Ti concentrations declined to ~100 µg g-1 pattern that is mirrored in other conservative lithogenic elements (e.g., Rb) towards the top of Zone 2 except for a distinct peak (~4.7 cal. ky BP; Fig. 4, A.7). The apparent synchrony of Mn/Ti and Fe/Ti ratios was disrupted at the mineral inwash peak in Ti at ~4.7 cal. ky BP, with excess Fe concentrations relative to Ti contrasting the Mn/Ti ratio (Fig. 4). Al/Rb and Al/Ti ratios continued to fluctuate in synchrony, with the peaks reaching their highest values particularly at the Zone 2/3 boundary.

## Zone 3 (4.2 cal. ky BP–recent)

A bloom of *Asterionella ralfsii* dominates the diatom relative abundances and minimizes the effective number of diatom taxa taken from the total assemblage (Fig. 2). However, the effective number of diatom taxa from non-planktonic and facultatively planktonic periphytic assemblages has increased from those in Zone 2. Non-planktonic diatom periphyton prevail over facultatively planktonic periphyton throughout the Zone 3, particularly the relative abundances of motile, high-profile, and low-profile guilds that peaked successively through ~1.7–0.2 cal. ky BP (Fig. 2). Relative abundances of semi-terrestrial and rheophilic chironomids peaked (max. of 36.5%; ~3.2 cal. ky BP; mainly *Limnophyes* and *G. luteicornis-type*) followed by a peak of chironomids associated with aquatic macrophytes (max. of 47.1%; ~1.2 cal. ky BP; mainly morphotypes of genus *Corynoneura*) (Fig. 3, A.6). Chironomid concentrations further decreased to the average of ~2 HC cm-3 until a further increase towards the top of Zone 3 (Fig. 4), where taxa associated to bottom substrates rise due to a peak of *Tanytarsus pallidicornis*-type 2 (Fig. 3). *Ceriodaphnia* ephippia increase in concentrations and were present in all merged samples between ~4.2 and ~1.3 cal. ky BP, whereas *Bosmina longispina* remains suddenly disappear from the record ~3.5 cal. ky BP (Fig. 3). While influxes of chrysophyte stomatocysts and periphytic diatoms decrease, the high influx of euplanktonic diatom *A*. *ralfsii* reduces C:D ratio. C:D ratio reaches its maximum only after decline of *A*. *ralfsii* (max. ~474%; ~0.4 cal. ky BP) (Fig. 4). Si/Ti ratios gradually decreased from maxima at the Zone 2/3 boundary ~4.2 cal. ky BP reaching minimum values ~1.4 cal. ky BP (Fig. 4). DI-pH decreased to 5.51 ~4.1 cal. ky BP, remained <6 through Zone 3, and finally decreasing to its minimum (5.06) in the uppermost sample representing (sub)recent conditions (Fig. 4). DI-TP increased from the base of Zone 3 averaging ~5 µg l-1 through the zone and peaking in the uppermost sample at 11 µg l-1 admittedly with large uncertainties (Fig. 4, A.3). Sedimentary P followed the trends of DI-TP except the peak in the uppermost sample. Al/Rb and Al/Ti ratios declined from ~3.9 cal. ky BP and Ti remained at low concentrations except for minor peaks ~0.35 cal. ky BP and ~0.28 cal. ky BP (Fig. 4). Mn/Ti and Fe/Ti retained opposite trends through Zone 3 reflecting excess Fe concentrations relative to Ti, which contrasts the Mn/Ti ratio except for ~0.5–0.3 cal. ky BP with the highest Mn/Ti values (Fig. 4).

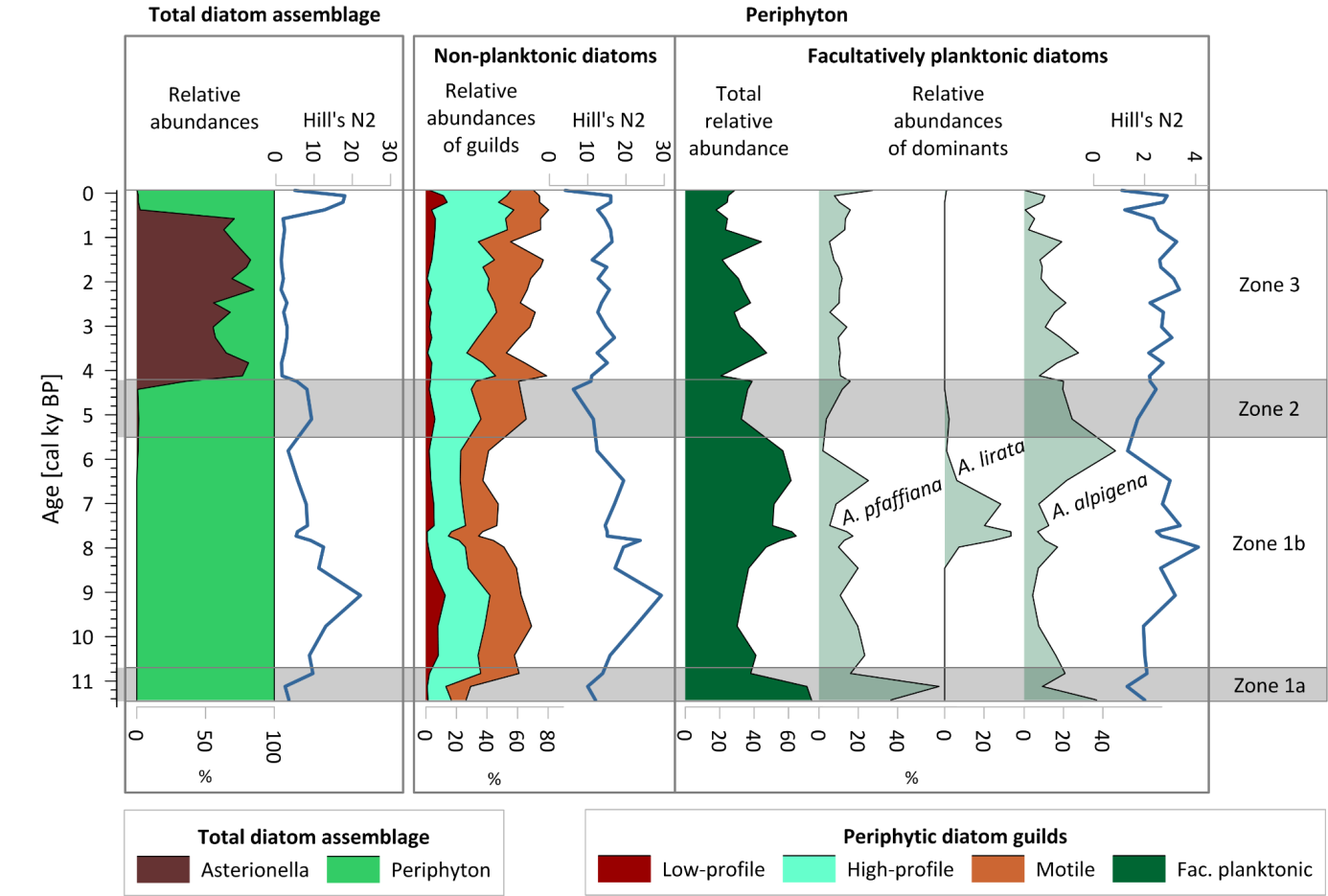
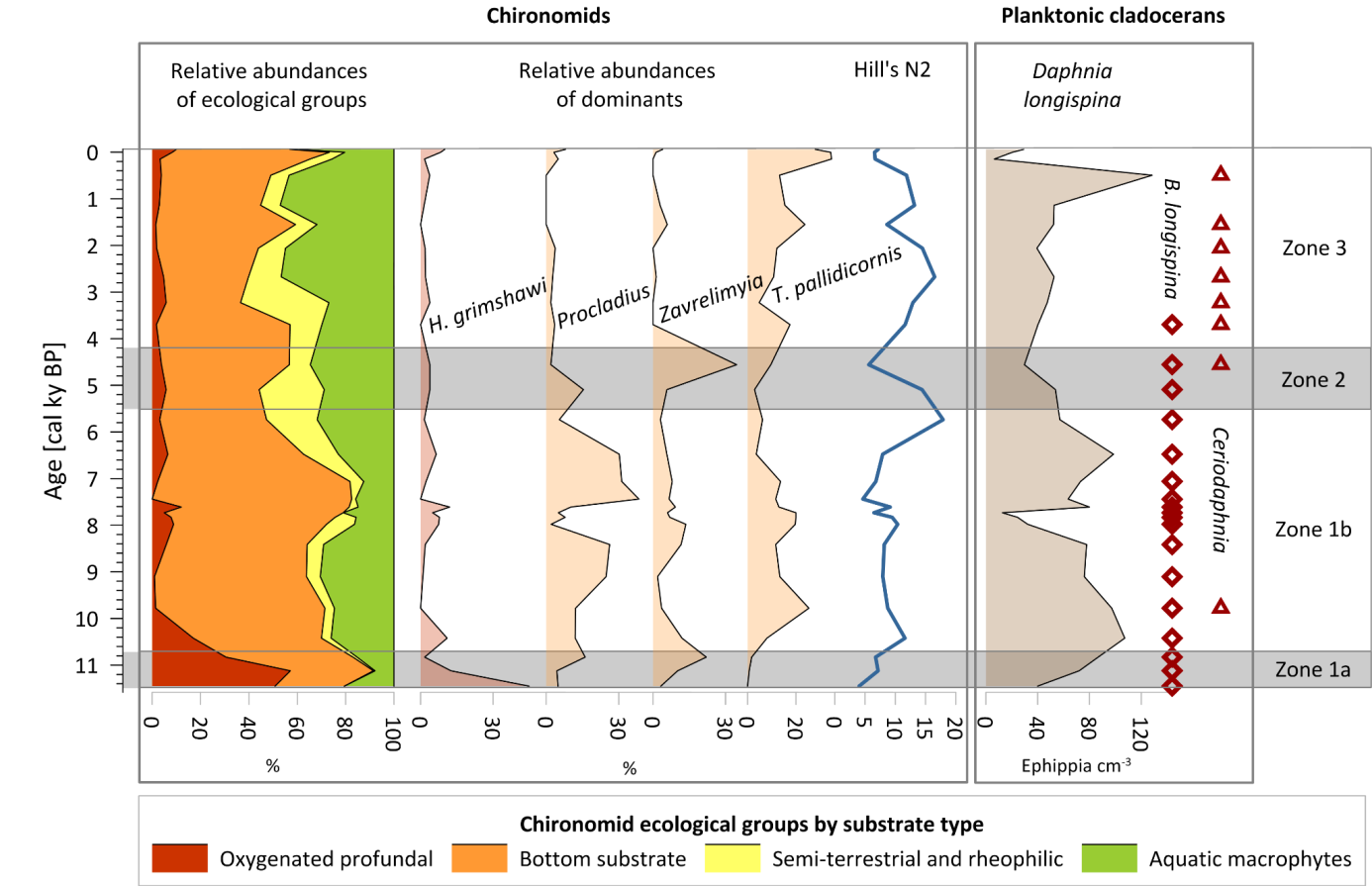
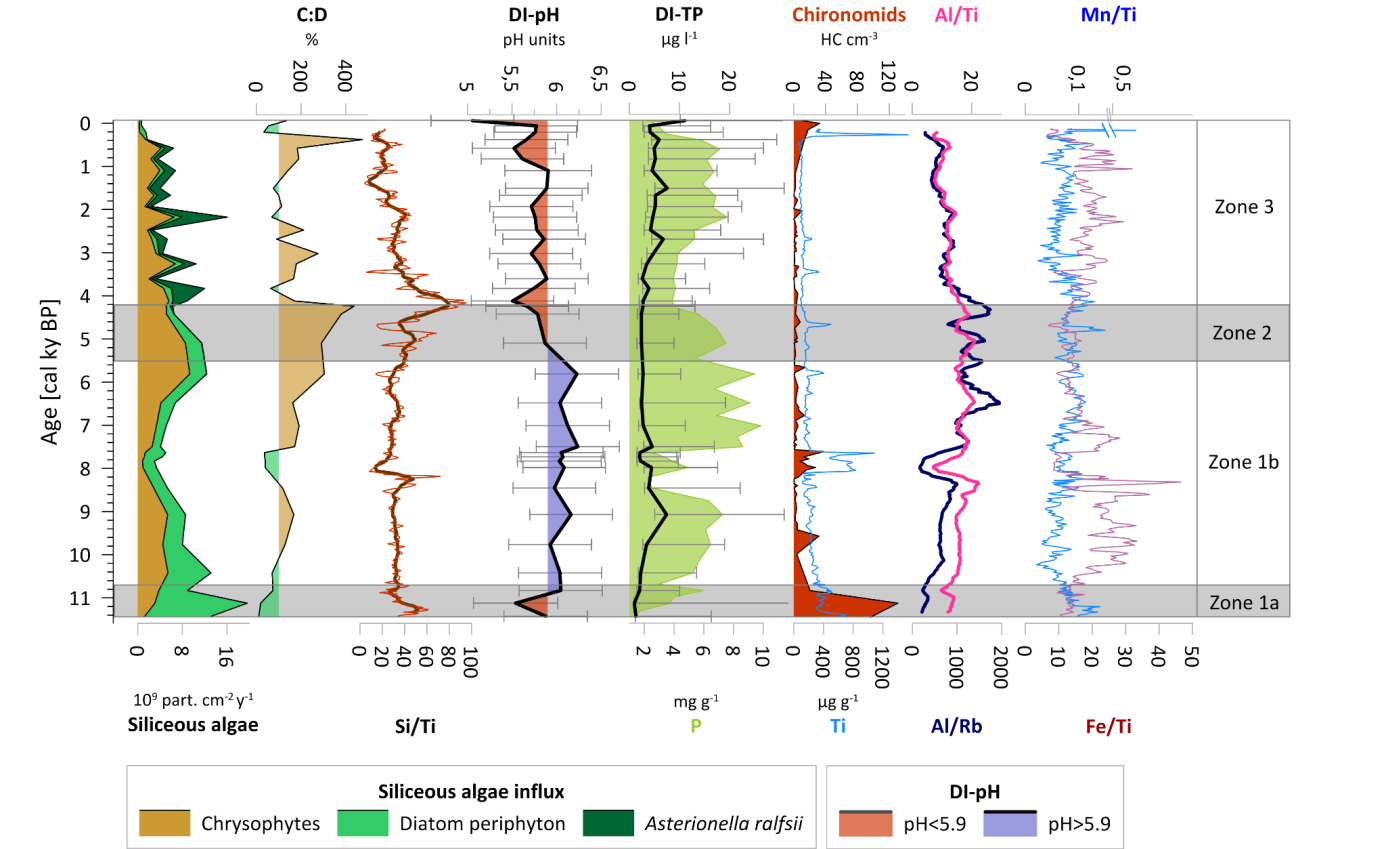


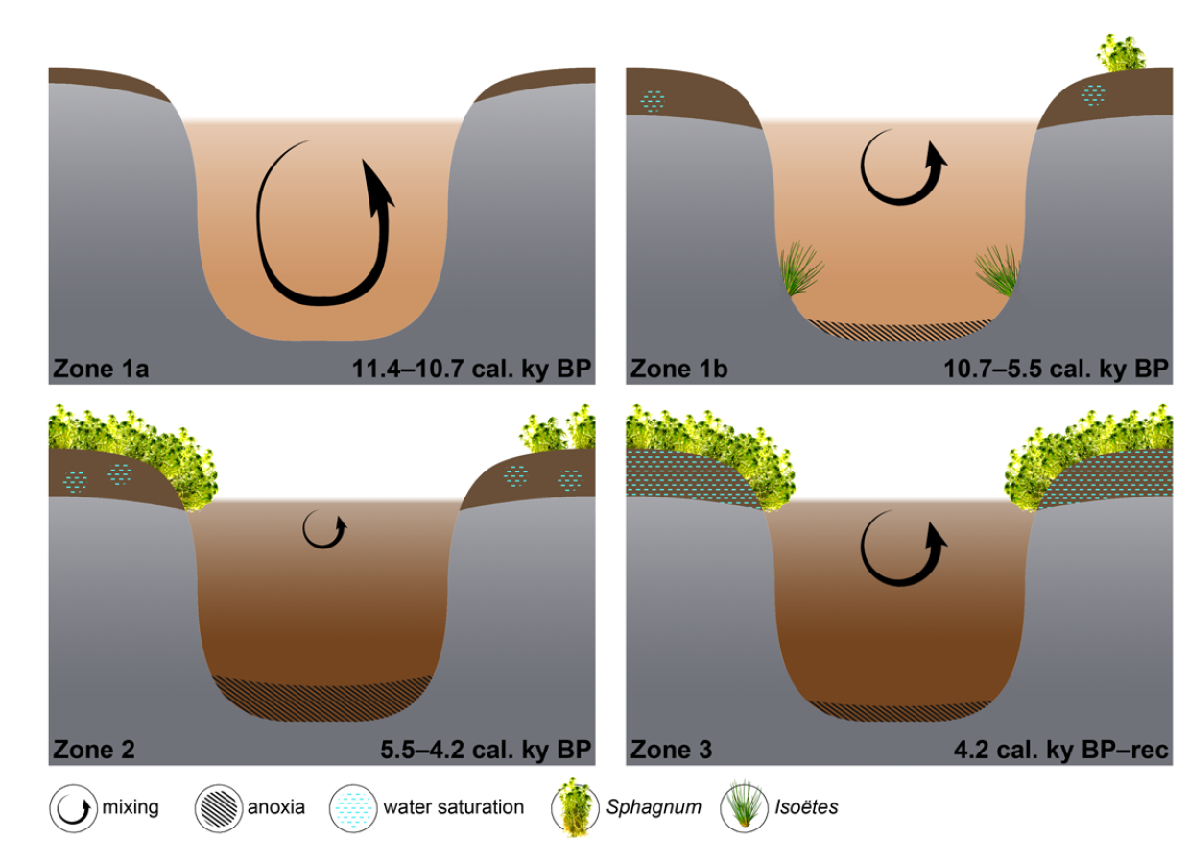
Fig. 2: Diatom stratigraphical diagram showing proportion (%) of euplanktonic *Asterionella ralfsii* (dark brown silhouette) against diatom periphyton (light green s.) and relative abundances of particular guilds of the diatom periphyton: low-profile (dark red s.), high-profile (turquoise s.), motile (ginger s.), facultatively planktonic (=tychoplanktonic) (dark green s.). All three most abundant periphytic species originate from facultatively planktonic guild (dark greenish silhouettes): *Aulacoseira alpigena*, *Aulacoseira lirata*, *Aulacoseira pfaffiana*. “Effective number of diatom taxa” (Hill’s N2) (dark blues lines) is plotted for each group. Zonation (Zone 1a, Zone 1b, Zone 2, and Zone 3) is defined by clustering of diatom and chironomid assemblages using CONISS (stratigraphically constrained cluster analysis) and Broken-Stick model.

Fig. 3: Freshwater invertebrate stratigraphical diagram. Relative abundances of chironomid ecological groups (left): taxa of oxygenated profundal (red silhouette), other lake taxa inhabiting bottom substrate (orange s.), semi-terrestrial and rheophilic taxa (including taxa associated with seepages, moss, and small streams) (yellow s.), and lake taxa associated with aquatic macrophytes (green s.) (for details see Section 2.5). Four most abundant chironomid species: *Heterotrissocladius grimshawi*-type (light red s.), *Procladius*, *Zavrelimyia* type A, *Tanytarsus pallidicornis*-type 2 (light orange silhouettes). “Effective number of chironomid taxa” (Hill’s N2) is plotted in dark blue line. Planktonic cladoceran taxa remains (right) are plotted in volumetric concentrations (remains per 1 cm3) (light brown s.) or presence/absence data (dark red symbols). Zonation (Zone 1a, Zone 1b, Zone 2, and Zone 3) is defined by clustering of diatom and chironomid assemblages using CONISS (stratigraphically constrained cluster analysis) and Broken-Stick model.

Fig. 4: Summary stratigraphical diagram of main proxies for reconstruction of brownification in Prášilské jezero showing (from left to right): influx of siliceous algae (chrysophytes – golden silhouette, diatom periphyton – light green s., euplanktonic diatom *A*. *ralfsii* – dark green s.), C:D – ratio between chrysophyte stomatocysts and diatom valves (golden shaded values > 1, green shaded values < 1), Si/Ti ratios (orange line) with running average-window width 11 samples (dark brown bold line), DI-pH – diatom-inferred pH (black line; blue shaded values – mean value >5.9, red shaded values – mean value < 5.9) with standard errors (light grey bars), DI-TP – diatom-inferred total phosphorus (black line) with standard errors (light grey bars), P (mg g-1) – phosphorus sediment dry mass concentrations (green shaded area), concentration of chironomid head capsules (HC cm-3) (red silhouette), Ti concentration (µg g-1) (light blue line), Al/Rb and Al/Ti ratio running average-window width 11 samples (Al/Rb - dark blue line, Al/Ti - pink), Fe/Ti ratio (red line) and Mn/Ti ratio (light blue line). Zonation (Zone 1a, Zone 1b, Zone 2, and Zone 3) is defined by clustering of diatom and chironomid assemblages using CONISS (stratigraphically constrained cluster analysis) and Broken-Stick model.

# Discussion

## Ecosystem functioning thresholds at Prášilské jezero

Fig. 5: Conceptual model of main phases of Prášilské jezero water brownification. Short anomalous phases connected to the “8.2 ka event” and the last 500 years are excluded.

One hundred and fifty years of hydrobiological research of Bohemian Forest lakes have documented complex changes in their water chemistry, including changes in water colour and transparency (e.g., Veselý et. al., 1994, Vrba et al. 2000). However, that longer-term perspective on millennial-scale water changes in brownification had remained elusive before the application of paleolimnological methods (e.g., Vondrák et al. (2019b) and Moravcová et al. (2021)). Here, we focus on more detailed history and causes of brownification episodes at Prášilské jezero, where brownification was inferred using biotic and geochemical proxy records. Those data revealed (i) a long history of direct impacts of high humic acid concentrations– water acidification and light limitation, and (ii) equivalent duration of indirect impacts – enhanced thermal stratification, bottom water anoxia and shifts in nutrient availability in the lake. There have been three main alterations in the aquatic biota, and these occurred around ~10.7, ~5.5 and ~4.2 cal. ky BP (see Fig. 5) suggesting significant changes in the lacustrine ecosystem millennia before known anthropogenic influences, e.g., modern browning of surface waters (Kritzberg, 2017; Meyer-Jacob et al., 2019) and surface water acidification (Hruška et al., 2009; Monteith et al., 2007).

## Natural acidification and light limitation

The aquatic assemblages testify to brown and humic acid rich character of Prášilské jezero throughout the postglacial period, which aligns with previous research at the lake (Vondrák et al., 2019b; Moravcová et al., 2021).The diatom species composition presented here reveals a comprehensive postglacial evolution of Prášilské jezero with diatom species throughout taxa that prefer acidic and typically dystrophic waters (e. g. Houk, 2003; Lange-Bertalot et al., 2017; Lange-Bertalot and Metzeltin, 1996).

Humic compounds appear to have influenced the Prášilské jezero’s ecosystem since ~10.7 cal. ky BP when the productivity of periphytic diatoms started to decrease (influx of diatom periphyton; Fig. 4), suggesting shading of the water column possibly by browning (Karlsson et al., 2009; Vasconcelos et al., 2016). However, the drop in diatom productivity mainly reflects a bloom of *Aulacoseira pfaffiana* before ~10.7 cal. ky BP and its decline afterwards (Fig. 2). As heavily-silicified *Aulacoseira* taxa can cope with strong light limitation if they are intermittently floated by turbid mixing (Reynolds, 2006; Rühland et al., 2015), we suggest strong mixing of the lake waters rode over the shading effects of DOC ~10.7 cal. ky BP. The Holocene sequence at Prášilské jezero involves a first stage in the aquatic succession that was driven mainly by stratification of water column after an initial more turbid phase (Zone 1a) that potentially obscured inference of pH and TP from the diatom record before ~10.7 cal. ky BP. The subsequent gradual shift from diatoms of circumneutral to weakly acidic waters to those preferring moderate to strongly acidic waters (Moravcová et al. 2021) suggests little or no change in concentration of humic acids, and the presence of caddisfly *Limnephilus coenosus* points to peaty waters in Zone 1a (Vondrák et al.,2019b). Therefore, we expect broadly consistent relatively humic-rich conditions and no sharp step in brownification around 10.7 cal. ky BP (Fig. 5).

Distinct falls in pH at Prášilské jezero are suggested by decreases in DI-pH between ~5.5 and ~4.2 cal. ky BP (Zone 2, Fig. 4). At this time, all (sub)dominants in the diatom assemblage (Fig. 2, A.4; successively *Aulacoseira alpigena*, *Brachysira brebissonii*, *Asterionella ralfsii*) belong to taxa typical of waters acidified by humic acids (Houk, 2003; Lange-Bertalot et al., 2017; Pappas and Stoermer, 2001). This succession shows the transition from periphytic (*A*. *alpigena*, *B*. *brebissonii*) to pelagic (*A*. *ralfsii*) primary production. These findings confirm a major role for light attenuation in the collapse of aquatic macrophytes (*Isoëtes* spp.) at Prášilské jezero ~4.2 cal. ky BP (Moravcová et al., 2021). This decrease in primary production in deeper water benthic habitats represents an aquatic ecosystem response typical of light limitation (e.g., brownification) and is a feature found at other nutrient-poor boreal lakes (Brothers et al., 2014; Karlsson et al., 2009; Vasconcelos et al., 2016). At Prášilské jezero ~5.5–4.2 cal. ky BP, a temporary increase in the relative abundance of non-planktonic diatom periphyton (including *B*. *brebissonii*), resembles the periphytic dominance due to lower UV exposure caused by DOC shading seen at a Canadian Shield lake by Pienitz and Vincent (2000). In contrast, our diatom productivity decreased as the periphyton to euplankton proportion increase, which suggests light attenuation by DOC reached levels that limited both planktonic and periphytic primary production (Carpenter et al., 1998; Jones, 1992) as well as that of herbivorous planktonic cladocerans (Fig. 3). However, other factors such as less intensive water mixing and/or reduced nutrient availability also influence the dynamics of phytoplankton at Prášilské jezero.

Other factors complicate the pH-indicative value of the bloom of *A*. *ralfsii* ~4.2–0.5 cal. ky BP. *A*. *ralfsii* has often served as an indicator of acidification by humic acids given an association with very low pH dystrophic waters (Jüttner et al., 1997; Liehu et al., 1986; Stabell, 1993), but sensitivity to effective silica-uptake and/or Al concentrations complicates this interpretation of a competitive advantage in humic waters (Gensemer et al., 1993a; Gensemer et al., 1993b; Stokes, 1986). Unfortunately, the physiological experiments exploring this were focused only on the variety *A*. *ralfsii* var. *americana* (Robert W Gensemer et al., 1993; Robert W. Gensemer et al., 1993). Nonetheless, *A*. *ralfsii* at Prášilské jezero does define a period of enhanced concentrations of DOC. Moreover, our DI-pH record decreased simultaneously with the onset of *A*. *ralfsii* bloom ~4.2 cal. ky BP, and is independent of *A*. *ralfsii* though constrained by being based only on periphytic species. *Bosmina longispina*, a cladoceran adapted to fish predation, disappeared after ~3.7 cal. ky BP from Prášilské jezero, indicating a possible collapse of a potential fish population (see Johnsen and Raddum, 1987). Starving of fish after the loss of periphytic resources has been attributed to light limitation in humic lakes (Brothers et al., 2014; Kankaala et al., 2019; Karlsson et al., 2009). *A*. *ralfsii* suddenly decreases in abundance ~0.5 cal. ky BP probably reflecting changes in lake’s hydrology connected to intensifying human impact in last 500 years (Vrba et al., 2000) and the decrease in periphytic DI-pH in the top sample probably reflects anthropogenic acidification of Prášilské jezero (Fott et al., 1994; Vrba et al., 2006).

Overall, although we observed the first signs of browning after ~10.7 cal. ky BP, other processes such as a water-level change and/or wave mixing of the water column contributed to the “delayed onset” of pronounced thermal stratification influencing the lacustrine biota (Fig. 5). Significantly, we found strong evidence of a critical threshold in humic substances, acidification, and light limitation of the water column, and this was crossed between ~5.5 and ~4.2 cal. ky BP (Zone 2) producing conditions that persisted almost to the present.

## Lake water mixing and bottom water anoxia

Turbid waters most likely affected aquatic biota during the initial phase of postglacial lacustrine development (Zone 1a; Fig. 4) as indicated by the bloom of heavily-silicified *Aulacoseira pfaffiana* (Fig. 2), which was probably kept afloat by water mixing (Reynolds, 2006; Rühland et al., 2015). Besides the influx and relative abundance of facultatively planktonic (tychoplanktonic) diatoms (g. *Aulacoseira*), chironomid concentrations and proportion of chironomid taxa preferring well-oxygenated profundal correlated throughout the profile with mutual trends of Mn/Ti and Fe/Ti (Fig. A.9). These independent proxies point to prolonged thermal stratification with periods of bottom anoxia in Prášilské jezero since ~10.7 cal. ky BP. The abrupt decrease of chironomid concentrations (Fig. 4), including the fall in relative abundances of taxa indicating well-oxygenated profundal zone (Fig. 3), supports the near-bottom anoxia along with the inverse trends in Mn/Ti and Fe/Ti reflecting greater relative concentrations of Fe in the sediment (Fig. 4). Reducing Mn in sediment produces highly mobile Mn2+ ions while Fe3+ ions become immobile in complexes under anoxic conditions (Kylander et al., 2013).

Development of catchment soils through Zone 1a (decrease in Ti and Rb input; Fig. 4, A.7) contributed greater transport of DOC to the lake and probably restricted water seepage through the moraine dam. Potential consequent lake-level rise flooding fresh substrates could also increase the relative abundance, effective number of species (Fig. 2), and influx (Fig. A.5) of low-profile diatoms known to be effective colonizers (Leira et al., 2015; Pla-Rabés and Catalan, 2018). Additionally, the denser forest canopy around the lake after ~10.7 cal. ky BP (Carter, et al., 2018a) potentially mitigated wind-induced mixing and turnover of the waters (Klaus et al., 2021). Aided by supposed lake-level rise, the reduced water clarity by DOC input from soils and vegetation could encourage more pronounced thermal stratification ~10.7 cal. ky BP.

The chironomid taxa mentioned above as indicating availability of dissolved oxygen in the profundal waters are only abundant in Zone 1a (Fig. 3). Three of them, *Heterotrissocladius grimshawi*-type, *Micropsectra insignilobus*/*conctracta*-type, and *Tanytarsus lugens*-type, exceed 19 % (57 % cumulatively) of the total chironomid assemblage (Fig. A.6) but they do not appear again at these high relative abundances and the latter two taxa become very rare. Similar early-Holocene chironomid fauna with *H. grimshawi*-type and *M. insignilobus*/*conctracta*-type was recorded in sediments at Plešné jezero nearby in the Bohemian Forest (Tátosová et al., 2006), but T. *lugens*-type was not recorded and replaced by *Procladius*. *Procladius* is known to be common in lakes with near-bottom oxygen depletion (Brooks et al. 2007), and we interpret its presence as a sign of profundal oxygen limitation. This process occurred earlier in Plešné jezero likely due to its mesotrophic character (P-rich granite in bedrock) whereas *Procladius* became the dominant profundal taxa in Zone 1b at Prášilské jezero, i.e. after ~10.7 cal. ky BP. On the other hand, bottom water anoxia at Plešné jezero has never eliminated *Procladius* from Holocene chironomid assemblages unlike Prášilské jezero. These differences between nearby lakes likely reflect the respective bathymetries (Šobr and Janský 2016), with long periods of anoxia prevented in the elongated basin of Plešné jezero where the deepest part is close to the outflow contrasting the prolonged anoxia in the circular more symmetric basin of Prášilské jezero.

Two anomalies interrupted the otherwise continual record of dystrophic waters and likely thermal stratification in Prášilské jezero. The first ~8.1–7.6 cal. ky BP, besides harmonized Mn/Ti and Fe/Ti ratios reflecting lower relative concentrations of Fe in the sediment, occurred as distinct shifts across nearly all recorded geochemical proxies (Fig. A.7), which suggests a complete change of the lacustrine sedimentation. Disturbance of the water column was also visible in the high-resolution chironomid record, particularly in temporary recovery of oxygen-demanding deep-water chironomids (namely *Heterotrissocladius grimshawi*-type) (Fig. 3) and increased total chironomid concentrations (Fig. 4). Lower resolution of the algal record reveals at least some major trends indicating similarly the shift to more turbid conditions. Decrease in the proportion of chrysophyte stomatocysts (C:D ratio; Fig. 4) probably resulted from losing their competitive advantage of active movement in a well-mixed water column (Özkundakci et al., 2016; Sand-Jensen and Borum, 1991; Werner and Smol, 2005). Additionally, the dominance of heavily-silicified diatom *Aulacoseira lirata* (Fig. 2) suggests facilitating its floating by more intensive water mixing (Reynolds, 2006; Rühland et al., 2015).

Whereas we consider the 8.1–7.6 cal. ky BP period to represent a direct signal of a change in the mixing regime in Prášilské jezero and from increased flux of clastic material from the catchment, the second anomaly ~6.8–4.2 cal. ky BP requires more complex explanation. Although trends of Mn/Ti and Fe/Ti harmonized at this time, chironomid indicators of oxygenated bottom did not recover. Chironomids (and especially the typical lake taxa) remain at very low concentrations (Fig. 4) and show the highest proportion of semiterrestrial and rheophilic taxa. These represent inhabitants of the very shallow part of the littoral zones, inflows, and wet habitats in the catchment (Brooks et al., 2007) (Fig. 3, A.6). This event is also characterized by peaking *Aulacoseira* species (Fig. 2); however, *A*. *alpigena* could indicate declines in water conductivity rather than a physical disturbance of the water column (Houk, 2003; Leira et al., 2015). Altogether, the biotic proxies indicate persistent thermal stratification and in-lake anoxia ~6.8–4.2 cal. ky BP (Fig. 5), which points to another cause of the relative enrichment by Mn in the sedimentary record. Potential mechanisms employ processes connected with the brownification of lake water identified in Prášilské jezero for this period. First, as the dark colour of humic waters can trap radiation in the surface layers and reduce the mixing depth by heating the epilimnion in small lakes (Fee et al., 1996; Wetzel, 2001), more frequent meromixis (i.e., very limited mixing of the hypolimnion) is a likely outcome. Consequent pronounced or nearly permanent bottom anoxia could reverse otherwise higher Mn mobility and result in the diagenetic formation of Mn compounds (Makri et al., 2021). Potential diagenetic precipitation of Mn was probably muted with the release from the most intense thermal stratification after ~4.2 cal. ky BP. Another mechanism lies in the input of Mn2+ from soils in the catchment. If oxygen depletion occurred in soils, e.g., due to water saturation, highly mobile Mn2+ would in-wash from soils to the lake and further compensate for the in-lake deficiency of Mn. This preferential reduction and mobilization of Mn4+ against Fe3+ was observed under anoxic conditions in flooded and wetland soils (Du Laing et al., 2009; Kröpfelová et al., 2009; Patrick Jr. and Jugsujinda, 1992). Moreover, in acidic soils, lower pH can facilitate reduction of Mn4+ under lower levels of redox potential (EH), i.e., under less oxygen depleted conditions (Frohne et al., 2011). When the supply of Mn in the eluvial soil horizon was depleted in the Prášilské jezero catchment, a terrestrial flux of Mn2+ would become insufficient to replenish the in-lake stock, which probably resulted in the renewal of inverse trends in Mn/Ti and Fe/Ti ratios since ~4.2 cal. ky BP. The tendency of Mn to deplete in soil systems is illustrated by a dependence of Mn loads on supply from silt deposits in boreal streams while soils on glacial sediments in upper parts of catchments already failed to release Mn (Björkvald et al., 2008). Additionally, a sharp downward decrease of Mn was documented in podzolized soil profiles (Riise et al., 2000), which indicates that Mn is released from the soils instead of precipitated in the illuvial spodic horizon.

A return to more frequent mixing of the water column was detected ~0.5 cal. ky BP in Prášilské jezero (Fig. 4) and coincided with human activities in the highest part of the Bohemian Forest. Although the first invasive anthropogenic interventions with the lake level were evidenced only since 19th century (Holcová et al., 2020; Švambera, 1914), other artificial activities, such as logging, started ca. 500 years ago in the proximity of Bohemian Forest lakes (Vrba et al., 2000). Nevertheless, the regional human impact has been growing at least for the last 1000 years as supported by continuous record of cereal pollen and opening of forest canopy (Carter et al., 2018a; Kozáková et al., 2021). The changes in lake’s hydrology culminated at the end of the 19th century and were followed by the onset of anthropogenic acidification (Fott et al., 1994; Vrba et al., 2015).

## Nutrient availability

Prášilské jezero was probably nutrient-poor throughout its postglacial evolution (DI-TP<10 µg l-1, Fig. 4), hence the reconstructed changes in phosphorus concentration acted within a restricted range. We suggested the increase of phosphorus availability based on DI-TP after ~10.7 cal. ky BP (peaking ~9.1 cal. ky BP) and after ~4.2 cal. ky BP. Slight fertilization of the lake could have resulted from co-export of DOC and phosphorus (Kopáček et al., 2011), as heightened input of dissolved organic matter was interpreted at these times. However, a more complicated explanation requires a mechanism behind the DI-TP ~7.5–4.2 cal. ky BP decrease, since simultaneous strengthened effects of water brownification were recorded. Three possible driving processes are proposed:

(i) The concentration of available phosphorus could decrease by its sedimentation and limited recycling from sediments. However, anoxic bottom conditions, which release phosphorus from sediments (Petticrew and Arocena, 2001), were indicated by chironomid species composition (decrease in taxa inhabiting profundal and deep littoral habitats), very low total chironomid HC concentrations, and divergent trends in Mn/Ti vs. Fe/Ti ~6.8–4.2 cal. ky BP in Prášilské jezero. Nevertheless, precipitation with Al hydroxides prevents phosphorus recycling even under bottom anoxic conditions (Kopáček et al., 2005; Vrba et al., 2006). Increased Al/Rb and Al/Ti (Fig. 4) suggest the input of Al into Prášilské jezero ~6.8–3.9 cal. ky BP, likely associated with humic compounds (Norton et al., 2011; Paludan and Jensen, 1995; Possinger et al., 2020). Concentrations of P in the sediment were the highest in the period ~7.5–5.8 cal. ky BP subsiding until ~4.2 cal. ky BP (Fig. 4), which further supports the probably strengthened phosphorus retention in the sediments. Moreover, it is the only period when DI-TP and sedimentary P trends disharmonized indicating the change in phosphorus regime in the lake (see their otherwise good correlation in Fig. A.9).

(ii) Onset of strong light limitation could prevent diatoms from utilizing nutrients and bias their transfer function based signal for concentrations of available phosphorus (Rivera-Rondón and Catalan, 2020). Nevertheless, brownification more often acts ambiguously favouring planktonic primary production by nutrients and reducing benthic phototrophs by shading (Karlsson et al., 2009; Nürnberg and Shaw, 1999), although planktonic algae can be suppressed by light attenuation in lakes rich with humic compounds (Carpenter et al., 1998; Jones, 1992). Note a temporary collapse of non-flagellated planktonic algae ~5.5–4.2 cal. ky BP (Fig. 2 in this study; *Botryococcus*, Fig. 3 in Moravcová et al., 2021), whereas after ~4.2 cal. ky BP its pelagic primary production partly recovered (*A*. *ralfsii*, Fig. 2 in this study; *Botryococcus*, Fig. 3 in Moravcová et al. 2021). Conversely, flagellated chrysophytes thrived ~5.5–4.2 cal. ky BP (rise in chrysophyte influx and C:D ratio, Fig. 4), which corresponds well with their competitive advantage of active movement and/or mixotrophy securing light and nutrients in stratified nutrient-poor waters (Olrik, 1998; Özkundakci et al., 2016; Sand-Jensen and Borum, 1991; Werner and Smol, 2005). Mixotrophic strategy could drive a success of chrysophytes especially in humic waters combining strong light limitation and high bacterial production as a prey (Bock et al, 2020; Drakare et al, 2002; Nürnberg et al., 1999; Pålsson and Granéli, 2004). This pattern suggests nutrient limitation of pelagic production until ~4.2 cal. ky BP and subsequent slight increase in nutrient availability, however, the strong shading of pelagic habitats and later recovery potentially became involved.

(iii) Finally, a potential change in the stoichiometry between DOC and TP for in-washed terrestrial dissolved organic matter (DOM) should not be neglected. Stetler et al. (2021) suggested three mechanisms of decreasing the P:DOC ratio during brownification (acidification of soils, storage of phosphorus in terrestrial vegetation, and change in the quality of DOM), and all of them could occur at Prášilské jezero. The ability of soils to bind phosphates decreases with increasing soil pH (Kopáček et al., 2015, 2011). As the increase in pH is an essential condition for reductive dissolution of organic matter (Grybos et al., 2009), leaching of DOC is accompanied by phosphorus originating from organic matter and binding sites in soils (Kopáček et al., 2011). Frequent disruption of reducing conditions in soils, e.g., during dry episodes (Evans et al., 2006), could result in a lower P:DOC ratio, since the phosphorus mobilization can delay recovery from acidifying (oxidizing) disturbance (Kopáček et al., 2015; Stuchlík et al., 2017). Acidification of soils was supported by higher mobility of Al ~6.8–3.9 cal. ky BP (Fig. 4) to Prášilské jezero, and is a feature of soil podzolization processes (Ewing and Nater, 2002; Krettek and Rennert, 2021). The second mechanism, immobilization of phosphorus in more intensively growing terrestrial vegetation proposed in the context of recent climatic warming by Stetler et al. (2021), corresponds in part with the timing of the Mid-Holocene “thermal maximum” (~8–5.5 cal. ky BP). Lastly, change in DOM quality could operate along with the progress of soil saturation in the catchment, as nutrient proportion probably decreased in soil organic matter with the onset of anoxic conditions in poorly-drained soils (Tipping et al., 2016). Saturation of soils in the catchment of Prášilské jezero was suggested by the flux of mobilized Mn (Fig. 4).

The spectrum of potential mechanisms illustrates how complex the phosphorus dynamics are and it is beyond this study's compass to disentangle them fully. Regardless, the DI-TP corresponds well with the geochemical proxies for pedogenetic and hydrological development and together they fit the hypothesised biogeochemical mechanisms of phosphorus dynamics during brownification. Therefore, we consider our DI-TP data for Prášilské jezero as a realistic signal of decreased phosphorus availability ~7.5–4.2 cal. ky BP. An inferred value from the topmost sample (11 µg l-1) loosely corresponds to recent measurements at the lake (5.8 µg l-1; Tab. 1), though this is the largest standard error among all samples (Fig. 4, A.3). The surface peak in P sedimentary concentrations (Fig. 4) most likely reflects the widely reported enrichment of the uppermost sediment layers in lakes (Carignan and Flett, 1981; Engstrom and Wright, 1984; Moyle and Boyle, 2021), which often holds stationary relative to the sediment surface reflecting the diagenetic transport of P from deeper anoxic sediment to the oxygenated surface (Farmer et al., 1994).

After this sensitive response to reduced phosphorus, diatoms can also be limited by concentrations of available silica (SiO2) (Battarbee et al., 2001). Therefore it is worth considering silica's role in diatom succession, although limitation by other nutrients usually precedes silica-limitation in oligotrophic lakes (Kilham, 1971). Hence, in the oligotrophic/dystrophic conditions of Prášilské jezero, the simple gradient of Si or Si/P ratio available in the water should fail to explain diatom succession unlike at eutrophic lakes (Kilham, 1971; Tilman et al., 1982). Nevertheless, the diatom succession from genus *Aulacoseira* to g. *Asterionella* (and in subdominant level also to g. *Fragilaria* and g. *Tabellaria*) observed in Prášilské jezero (Fig. 2, A.4) is similar to that reflecting Si depletion in more productive lakes (Kilham, 1971; Tilman et al., 1982). The role of Si in Prášilské jezero’s diatom succession ~5.5–4.2 cal. ky BP was probably mediated by a combination of strengthened thermal stratification and light limitation. An absence of pronounced mixing prevented heavily-silicified *Aulacoseira* taxa from reaching the insolated epilimnion (Rühland et al., 2015) along with strong shading of the silica-rich upper hypolimnion, which silica-demanding diatoms such as *Aulacoseira* taxa used to occupy (Cantonati and Lowe, 2014; Pla-Rabés and Catalan, 2018). The resulting lack of suitable habitats likely led to the decrease in the relative abundance of *Aulacoseira* taxa starting ~5.5 cal. ky BP in Prášilské jezero. Moreover, epilimnion probably became depleted in silica soon without its recycling from deeper parts of the lake as this mechanism is the only effective supply of silica to the surface waters besides an allochthonous input (Lampert and Sommer, 2007). The episodic in-wash layers (Ti, Zone 2–3, Fig. 4) are low magnitude and less frequent than in the earlier Holocene and they are buried rapidly with organic gyttja suppressing the availability of detrital silica. Then, effective competitors for silica, such as *Asterionella ralfsii* (Stokes, 1986), dominated the epilimnetic diatom production. Overall, we can interpret the switch from *Aulacoseira* to *Asterionella* in Prášilské jezero as the suppression of diatom production in silica-rich habitats by strong light limitation.

The elevated Si/Ti ~6.3–3 cal. ky BP (peaking ~4.2 cal. ky BP) in Prášilské jezero, unsupported by a similar increase in production of siliceous algae (Fig. 4) or heightened sedimentation of sand fraction (low Zr/Rb ratio, Fig. A.7), opens the possible influence of humic acids bounded supply of Si. Although Si was traditionally considered to form complexes with humic substances (Wetzel, 2001), the substantial extent of Si-humic complexes in natural waters is still disputed (Kubicki and Heaney, 2003; Pokrovski and Schott, 1998; Viers et al., 1997). Thus, we downplay this scenario of in-lake precipitation of available Si via the allochthonous input of humic substances. The peak of Si/Ti could result from processes connected to brownification without direct complexation with humic substances. Increased in-wash of dissolved organic carbon as well as silica has been observed after snowmelt pulses to lakes (Dyson et al., 2011; Schaetzl et al., 2015). The potential climatic shift to higher winter precipitation could result in enhanced chemical weathering in soils and explain the increased input of Si without signs of more intense erosional activity in Prášilské jezero sediments. Higher input of Si coincided loosely with an increase in Al at Prášilské jezero ~6.8–3.9 cal. ky BP (Fig. 4), therefore, both elevated mobility of Al and Si can stem from an intensified podzolization process supported generally by humid climatic conditions (Krettek and Rennert, 2021; Lundström et al., 2000).

## Climatic ecosystem forcing and regional context

Brownification of surface waters likely contributed to all three main shifts in species composition of aquatic biota in Prášilské jezero at ~10.7, ~5.5 and ~4.2 cal. ky BP. Early input of humic acids into the Bohemian Forest lakes after the Pleistocene-Holocene transition (Moravcová et al., 2021; Pražáková et al., 2006; Steinberg et al., 1991; Vondrák et al., 2019b) was probably induced by regional afforestation ~10.5-10.3 cal. ky BP (Carter et al., 2018a; Vočadlová et al., 2015). Heightened input of humic compounds from dead vegetation and side-effects of the afforestation, i.e., soil stabilization and the beginning of podzolization increasing the soil carbon pool, contributed alongside a shift from a more energetic water body (Zone 1a, Fig. 4, Fig. 5) into a more stable water column with prolonged stratification and anoxia after ~10.7 cal. ky BP in Prášilské jezero. Probable lake-level rise after ~9.3 cal. ky BP potentially facilitated greater thermal stratification and successful colonization by the low-profile diatom guild (Fig. 2). This rise in the lake level after ~9.3 cal. ky BP has been identified as a plausible trigger of the decline in submerged macrophytes (*Isoëtes* spp.) at Prášilské jezero (Moravcová et al., 2021).

Interrupted briefly by the greater in-wash of detrital materials from the catchment ~8.1–7.6 cal. ky BP probably linked to the “8.2 ka climatic event” (Tinner and Lotter, 2001), the succession at Prášilské jezero demonstrates further thermal stratification. Signs of favourable conditions and potential longer vegetational season appeared as algal primary production generally increased ~7.6–5.5 cal. ky BP with both siliceous algae (Fig. 4) and *Botryococcus* (Fig. 3 in Moravcová et al. 2021). This period corresponds with the Mid-Holocene “thermal maximum“ indicated in the region of central Czech Republic (Bohemia) ~8–5.5 cal. ky BP by records of thermophilous plant species (Houfková et al., 2017; Pokorný et al., 2015) and strong growth of calcareous tufa deposits (Žák et al., 2002).

The onset of profound suppression of aquatic algal flora driven by surface water brownification occurred as two steps at ~5.5 cal. ky BP and ~4.2 cal. ky BP. The step-wise character of the succession stems probably from increased saturation of catchment soils with podzolization and paludification with wetter climate of the late Holocene. More humid climatic conditions were suggested by the macrophysical climate model (Carter et al., 2018b; Dreslerová, 2012) and encouraged lower forest fire activity (Carter et al., 2018b; Florescu et al., 2019) in Bohemia during a more widespread climatic transition ~6 cal. ky BP (Magny et al., 2006; Wanner et al., 2008). Inception of peat development in the catchment of Prášilské jezero occured ~8.2 cal. ky BP as evidenced by increased proportion of the *Sphagnum* spores from the total pollen sum (Moravcová et al., 2021). Then peatland gradually expanded and reached the littoral waters probably ~6.5 cal. ky BP as moss-inhabiting diatoms increased in abundance at these times (e.g., *Chamaepinnularia mediocris* and *Eunotia paludosa*; Fig. A.4, A.5). Although chrysophytes are considered to be mostly planktonic in temperate mountain lakes (Rivera-Rondón and Catalan, 2017), it is worth regarding the potential influence of moss habitats on the rising chrysophyte influx and C:D ratio (Fig. 4) as periphytic chrysophytes were abundant in semi-aquatic mosses in arctic ponds (Douglas and Smol, 1995). Recently, *Sphagnum*-covered wet forest floors with shallow peats occupy substantial parts of the Prášilské jezero catchment, especially on flat ground close to the main lake inlet (Fig. 1).

Although impermeable horizons in podzolic soil profiles are probably not the only prerequisite of paludification (Payette et al., 2012; Schaffhauser et al., 2017), intensified podzolization is suggested by the increase in Al mobility ~6.8–3.9 cal. ky BP (Fig. 4). Until paludification established stable anoxic conditions in soils after ~4.2 cal. ky BP, unstable shifts between oxidizing and reducing conditions with changing soil saturation had probably mobilized both redox-sensitive Mn (Fig. 4) and DOC within the catchment. For efficient mobilization of DOC, the regular alternation between oxic and anoxic conditions in catchment soils is the most favourable mechanism, and is a feature of the seasonal dynamics in wetlands (Olivie-Lauquet et al., 2001) and experiments saturating forest soils (Possinger et al., 2020). Inputs of DOC into lakes has been a feature of wetlands after drainage or other degradation (Brothers et al., 2014; Liehu et al., 1986), essentially reflecting perturbation of stable anoxic conditions. Decreases in Fe/Ti ~6.8–4.6 cal. ky BP and subsequent falls in both Al/Rb and Al/Ti after ~4.2 cal. ky BP in Prášilské jezero (Fig. 4) further characterise this transition from a fluctuating to more stable soil saturation regime, because pedogenic organic matter interactions can shift from Al to Fe3+ with decreasing frequency of saturation (Possinger et al., 2020).

Short-term episodes with saturated soils of the Prášilské jezero catchment were probably driven by oscillations between wet and dry climate after ~6.5 cal. ky BP (Žák et al., 2002). Initially, what were relatively unsaturated and more oxidized soils were probably overtaken by paludification from ~6.8 cal. ky BP, and then more permanently saturated soils established after ~4.2 cal. ky BP. In this, greater quantities of soil organic matter began to accumulate under persistent anoxic conditions (Kayranli et al., 2010; Sutfin et al., 2016), with decreases in the portion of DOC leached into the lake.

In summary, the observed transitional character of ecosystem succession ~6.8–4.2 cal. ky BP in Prášilské jezero likely reflected changes in mechanisms of brownification before and after ~4.2 cal. ky BP, and these coincide with timing of the Middle to Late Holocene transition. Synchronous onset of enhanced lake-water brownification and catchment paludification ~6.8 cal. ky BP corresponds with a moist climatic phase in central Europe suggested by increased lake water levels (Magny, 2004; Pleskot et al., 2018; Starkel et al., 2013; Theueurkauf et al., 2021). Paludification at higher elevations of central European mountain ranges was reported after ~6 cal. ky BP (Beug et al., 1999; Obidowicz, 1996) as well as natural acidification of regional montane forest lakes (Pražáková et al., 2006; Sienkiewicz, 2016). The peak of acidity was potentially accompanied by the highest input of colloidal Si ~4.2 cal. ky BP in Prášilské jezero, and this coincides with unprecedented in-wash of organic matter and/or Si at several central European lakes (Pleskot et al., 2020; Schütze et al., 2018; Steinberg, 1991). The regional character of these changes suggests climate drivers probably associated with the “4.2 ka climate oscillation”, specifically greater seasonality and increased higher winter precipitation (Pleskot et al.,2020) as greater snowmelt fluxes produce pulses of chemical weathering and acidity (Dyson et al., 2011; Schaetzl et al., 2015; Schmidt et al., 2002).

After ~4.2 cal. ky BP, more saturated soils and advanced paludification in the Prášilské jezero catchment caused probably slight decreases in the input of DOC to the lake and lake ecosystem remained relatively stable until the disturbances of the last 500 years. Such a conservation of lake conditions has been reported from northern Europe when peatlands took full control of the biogeochemical processes in those catchments (Myrstener et al., 2021; Solovieva and Jones, 2002). Time lags between peat inception (~8.2 cal. ky BP), intensified pedogenesis with lateral spread of peatlands (~6.8 cal. ky BP), and full paludification of catchment soils (~4.2 cal. ky BP) are the likely factors governing the step-wise evolution of brownification at Prášilské jezero. Similar timing to the pattern of paludification in boreal regions (Bauer et al., 2003; Le Stum-Boivin et al., 2019) supports the value of central European lakes on poorly-buffered bedrocks in tracking climatically-driven brownification. Moreover, particular research potential of Bohemian Forest is promised by successional changes in terrestrial vegetation and submerged macrophytes at lakes across the Bohemian Forest (Carter et al., 2018a; Moravcová et al., 2021) suggesting regional-scale brownification.

The strong role for soil saturation and peatland development in surface water brownification over millennial time scales confirms importance of extent and long-term trends for wetland areas in these catchments (Kortelainen, 1993; Laudon et al., 2011; Rantala et al., 2016), information that is not tractable from decadal-scale environmental monitoring (Stetler et al., 2021). Moreover, the association of climate and intensive browning leading to substantial impacts on aquatic ecosystem functioning has implications for discussion about brownification across a range of time scales (Clark et al., 2010). The absence of a widespread trend in the precipitation regime is the only reservation in proposing a hydrological driver of recent brownification (Evans et al., 2006). Using this millennial scale perspective, there is a correspondence of brownification and hemispheric climate moistening after ~6 cal. ky BP (Routson et al., 2019).

# Conclusions

Browning of surface waters at Prášilské jezero occurred as three successive steps and varied in scale of impacts and probable driving factors. The lake experienced elevated input of humic compounds from formation at the onset of the Holocene. The first step in browning appeared ~10.7 cal. ky BP and probably originated from soil stabilization with the catchment afforestation. We propose that browning supported thermal stratification and bottom anoxia of the lake, but shading effects were probably negligible until ~6.8 cal. ky BP. Since then, the mineralized organic matter washed in from developing peaty horizons in saturated forest soils resulted in stronger light limitation, and probably also reduced nutrient availability. After ~4.2 cal. ky BP, soils in the catchment of Prášilské jezero became fully paludified and muted the formerly effective leaching of DOC.

Climate probably contributed to this brownification in part through major events or oscillations known as the “8.2 ka” and “4.2 ka events”. At the time corresponding to “8.2 ka event”, the gradual browning was interrupted by substantial catchment erosion and water mixing, whereas the leaching of organic matter to the lake temporarily enhanced ~4.2 cal. ky BP. The onset of the distinct browning ~6.8 cal. ky BP at Prášilské jezero corresponds with the general moistening of climate across central Europe and northern hemisphere (Magny, 2004; Routson et al., 2019; Wanner et al., 2008). Mid-Holocene climate humidity sustained greater saturation of soils and paludification in the catchment establishing these processes as key factors in surface water brownification at Prášilské jezero.

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