Neoglacial lake-ecosystem changes above and below the subarctic Fennoscandian treeline inferred from changes in diatom functional groups

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Neoglacial lake-ecosystem changes above and below the subarctic Fennoscandian treeline inferred from changes in diatom functional groups

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Abstract Algal communities act as sensitive indicators of past and present climate effects on northern lakes, but their responses can vary considerably between ecosystems. Functional trait-based approaches may help us better understand the nature of the diverse biotic responses and their underlying ecosystem changes. We explored patterns in diatom (Bacillariophyceae) growth forms and species composition during the Neoglacial in two shallow lakes typical of subarctic regions, including a dark-colored woodland lake and a clear tundra lake. Sediment carbon and nitrogen elemental and isotope biogeochemistry and spectral indices were used to track broadscale changes in lake productivity, the inflow of organic carbon from land, and benthic substratum over the past three millennia. The biogeochemical indices tracked declines in land-lake connectivity as well as lake-water and sediment organic enrichment above and below the subarctic treeline driven by Neoglacial cooling. This broadscale environmental transition was intercepted by periods of elevated primary production associated with transient Neoglacial warm anomalies and, in particular, the twentieth century warming. Although the Neoglacial development of the lakes showed conspicuous similarities, diatom functional and taxonomic responses were not uniform between the lakes pointing to intrinsic differences in the development of benthic habitats and underwater-light regimes. Many of the observed biotic shifts aligned with expectations based on earlier research

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linking diatom functional traits to changing light and organic levels but the results also point to further research needs, particularly to better differentiate the individual and interactive effects of substratum and light. Despite distinct anthropogenic imprints in the biogeochemical record, the scale of human impact on the lakes' biota has not, as yet, been profound, but the changes are nonetheless clear when compared to the previous three millennia of natural lake development.

Keywords Climate change · Growth form · Lake sediment · Neoglacial cooling · Substrate · Underwater light

Introduction

Northern lakes are highly vulnerable to climate change (Walsh et al. 2011) and their microscopic algal communities often act as sensitive indicators of the myriad climate effects on fundamental lake-ecosystem functions (Smol et al. 2005; Smol and Douglas 2007). Diatoms are an important group of algae contributing to the flow of matter and energy in northern lakes. Due to their ubiquity, high sensitivity to environmental change, and preservation potential, diatoms are a widely used bioindicator in lake research (Battarbee et al. 2001). Their siliceous and species-specific cell walls are well preserved in lake sediments forming important records of changes occurring at the level of whole ecosystems at time scales meaningful for understanding the multifaceted interactions between climate and lakes (Smol and Stoermer 2010; Smol 2019). Such records are especially valuable in remote northern lake environments where observational records are few and far between and, where available, short in duration. Yet, climate effects on lake ecosystems are multifarious and so are the responses of their biota; diatom communities in nearby lakes may display striking species turnover next to no change despite uniform climate forcing (Keatley et al. 2008; Griffiths et al. 2017). Our incomplete understanding of the ecological and ecosystem implications of the diverse biotic responses hampers our interpretation of the responses of northern lakes to human activities.

In spite of the prevailing challenges, predictable patterns are emerging from the growing body of paleolimnological research carried out across the circumpolar North. Of particular note are the widely observed increases in small centric diatom species in deeper stratifying lakes linked to decreasing ice covers and/or increased periods of thermal stratification (Rühland et al. 2015; Saros et al. 2016). Distinct diatom-community turnovers have also been recorded in the sediments of shallow high Arctic lakes where reductions in ice cover and development of aquatic plants have led to the diversification of diatom communities previously dominated by few stress-tolerant species (Smol et al. 2005; Keatley et al. 2008). The circumpolar Arctic region is characterized by myriad shallow lakes that do not develop permanent stratification and have supported diverse benthic diatom communities before any human impact. In these types of systems, recent diatom community shifts are often more subtle implying that critical ecological thresholds are not as easily crossed (Griffiths et al. 2017; Rantala et al. 2017). Importantly, the lack of abrupt species shifts does not necessarily mean lack of change and studying systems that resist change can carry powerful information of compensatory processes (Connell and Ghedini 2015) and add to our understanding of resilience in ecosystem functioning.

To extract patterns from the subtle and varied responses in diatom assemblage changes across landscapes, it is important to identify and understand the prevalent underlying environmental factors affecting lake-ecosystem change, such as the depth gradient dictating whether climate variability is likely to induce changes to lake thermal structure. Lake-bottom substratum (Michelutti et al. 2003; Yang and Flower 2012) and underwater light (Karlsson et al. 2009; Lange et al. 2011), including both the availability of photosynthetically active radiation (PAR) and exposure to ultraviolet (UV) radiation (Scholz et al. 2014; Tanabe et al. 2019), are considered critical for benthic algae, but little is understood how these factors structure benthic diatom-community development under natural and anthropogenic climate changes. The difficulty of interpreting biotic changes is further complicated by the large diversity of benthic diatom species. However, the identification of shared responses among and between species occupying a similar ecological niche can simplify the picture and eventually help unravel emergent biotic patterns. A growing number of studies are applying functional approaches alongside traditional taxonomic assessments prompted by the notion that functional traits

may express stronger connections to environmental factors than those species alone would, and help avoid redundancy related to the niche overlap among species (Passy 2007; Tapolczai et al. 2016). A compelling advantage of trait-based applications is that they provide a means to synthesize biotic response patterns among systems hosting specific diatom floras. Among the array of approaches, the use of algal growth forms or 'life forms' (Passy 2007; Rimet and Bouchez 2012) provides an ecologically meaningful classification to study benthic diatom dynamics as growth morphology is tightly connected to substratum type, as well as species' position in benthic biofilms with their sharp light, nutrient and disturbance gradients (Round et al. 1990; Johnson et al. 1997; Lange et al. 2011; Marcel et al. 2017). Presently, few studies have employed functional classifications in paleolimnological investigations of northern lakes, while decades of research endeavors have generated a wealth of knowledge on diatom habitat associations and ecological preferences at the species and genus level. Functional classification adapted to northern lake environments may help distil scalable patterns from this information.

Here, we investigated the Neoglacial development of two subarctic lakes in northern Fennoscandia (Kilpisjärvi region, Finnish Lapland) focusing on changes in diatom assemblages over the past three millennia to provide a background against which to assess recent biotic and ecosystem changes. Earlier records from deeper stratifying lakes in the region indicated distinct diatom assemblage turnovers initiated around the turn of the twentieth century manifested as an increase in small planktonic species (Sorvari et al. 2002) echoing the widespread circumarctic trend (Rühland et al. 2015; Kahlert et al. 2022). We conducted our study on two shallow lakes that have characteristic benthic-dominated algal communities overlain by unproductive waters but that differ in terms of their optical conditions and benthic substratum due to their situation above and below the mountain birch (*Betula pubescens* spp. *czerepanovii*) treeline. The lakes are too shallow to experience sustained thermal stratification and both have comparatively well-developed benthic habitats. We therefore expected the lakes' biota to display discernible but less dramatic responses to natural and anthropogenic climate variability, and aimed to investigate whether a functional diatom approach could help us better understand the nature of the algal community and ecosystem changes (or lack thereof). We classified the diatom species based on their growth form and integrated the functional assessment with taxonomic analysis and a detailed biogeochemical multiproxy investigation combining spectral indices (lake-water total organic carbon [TOC] and sediment chlorophyll *a* [CHLa]) and carbon (C) and nitrogen (N) isotopes ($\delta^{13}C$, $\delta^{15}N$) and elemental (C/N) ratio. The biogeochemical data were used to outline temporal patterns and interconnections between lake primary production, the inflow of organic matter from surrounding land areas, and sediment organic content that tightly relate to resource (especially light) availability and the character of benthic substratum. We used the broad body of earlier paleoclimate research from northern Finland and the Northern Hemisphere as a reference of Neoglacial climate changes. The growth forms considered have been earlier found to reflect changes in key elements directing benthic diatom community succession, including substratum type and underwater light, yet we acknowledge prevailing uncertainties regarding species-specific growth form. For example, some species may represent different growth forms at different stages of their life cycle and in different lake environments. We therefore draw heavily on the multiproxy biogeochemical analysis to first outline a comprehensive picture of broadscale ecosystem changes over the Neoglacial and consider our findings in light of current ecological knowledge at the taxonomic level. Ecosystem changes that often concur with warming in northern lakes are presented in Supplementary Figure 1 together with common functional diatom responses observed in earlier studies. Overall, our aim was to explore trait-environment associations that can help us shed further light into the development of shallow northern lakes across common lake types. At the same time, the results contribute to a better understanding of the heterogeneity of northern lake ecosystem responses to growing global human pressure.

Materials and methods

Study area

The landscape in the Kilpisjärvi region in northwestern Finnish Lapland is dotted with small lakes and
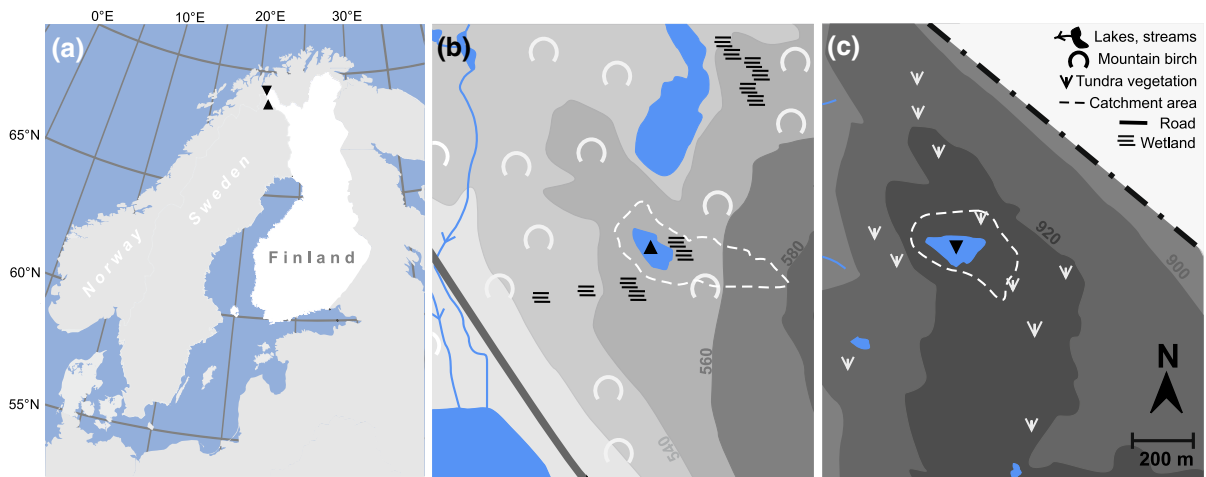
Fig. 1 **a** Map of the study region and catchment characteristics of the studied, lakes in northern Finnish Lapland. **b** woodland lake (68.91°N, 21.00°E) and **c** tundra lake (69.07°N, 20.88°E)

wetlands, typical of northern Fennoscandia and the circumpolar North more broadly. Cold climate prevails and the growing season spans around one hundred days between June and early September. Instrumental records indicate a warming trend comparable to the northern hemispheric mean over the past century in northern Finland (Sorvari et al. 2002; Finnish Meteorological Institute). We conducted our study on two small and shallow lakes with characteristic unproductive, dilute (low electrolyte content) and circumneutral waters (Fig. 1). There is no direct human activity in the vicinity of the lakes. Both lake basins are hydrologically isolated with no permanent inlets or outlets. Apart from the shared characteristics, the two lakes have markedly different underwater optical environments and levels of organic enrichment related to their position above and below the subarctic mountain birch treeline. The lake in the mountain birch woodlands (unofficial name Mukkavaara, hereafter referred to as the 'woodland lake') is situated at an elevation of 545 m a.s.l.. The altitudinal mountain birch treeline is presently situated at around 600 m a.s.l. and the limit for coniferous forests some 50 km southward. Aside from mountain birch stands, the vegetation in the watershed consists of dwarf birch and willow growing alongside a diversity of shrubs, herbs and mosses. The soils are organic rich and waterlogged near the eastern margin of the lake. The lake margins are covered with semiaquatic mosses and sedges, and the lake bottom is carpeted by thick

loose benthic mats barely visible through the water column in the deepest (maximum depth ~ 1.2 m) parts of the lake basin. The dark brown color and spectral characteristic of the lake water together with the biogeochemical composition of the surface sediments indicate that the lake receives high inputs of allochthonous organic matter from the watershed. The means of water quality measurements carried out in July and August 2018 indicate dissolved organic carbon (DOC) concentrations of 8 mg L^{-1} and chromophoric organic matter (CDOM) concentrations of 21 m^{-1} estimated by absorption at 320 nm. Source components of lake-water DOM identified by parallel factor analysis (PARAFAC) modeling indicate a high share of microbial organic matter (~ 55%) followed by autochthonous (~ 29%) and allochthonous (~ 17%) sources. Lake-water total phosphorus (7 μg L^{-1}) and total nitrogen (405 μg L^{-1}) concentrations are characteristic of oligotrophic waters. The other lake (unofficial name Iso-Jehkas, hereafter referred to as the 'tundra lake') is situated on top of a fell in the treeless tundra at an altitude of 925 m a.s.l. some 20 km northwest of the woodland lake. The thin mineral soils support a mosaic of small shrubs, herbs, lichens and mosses amidst bedrock outcrops. Patches of submerged vegetation, clearly visible even in the deepest areas of the basin (maximum depth ~ 4 m), dot the lake bottom. The concentrations of DOC (~ 1.6 mg L^{-1}), CDOM (~ 2 m^{-1}), total phosphorus (2 μg L^{-1}) and total nitrogen (115 μg L^{-1}) in

the lake water are low and the relative contribution of allochthonous and autochthonous organic matter equal (~43%) with low contribution of organic matter from microbial sources (~14%). Detailed description of the limnological measurements are provided in Nevalainen et al. (2020a).

Sediment sampling and dating

Sediment cores were recovered from the deep basin in each lake in summer 2018 using a Uwitec gravity corer (Uwitec Ltd., Austria). The cores were sectioned at the laboratory at 1-cm intervals and the samples were kept in sealed containers in a cool and dark environment. Sediment chronologies were constructed based on radiometric dating combining radio-lead (^{210}Pb) and radiocesium (^{137}Cs) analyses for the recent (~past century) and radiocarbon (^{14}C) analysis for the older sediments. Details on the sediment dating for the tundra lake were presented in a previous study investigating the development of underwater UV regimes in the lake during the Holocene (Nevalainen et al. 2020b). Following similar procedures, ^{210}Pb and ^{137}Cs dates for the woodland lake sediment core were analyzed at the Paleoecological Environmental Assessment and Research Lab (Queens University, Kingston, Ontario, Canada) using the constant rate of supply (CRS) model. Radiocarbon analysis was carried out at Beta Analytic (Miami, Florida, USA) on six plant macrofossil remains (Supplementary Table 1). Age-depth estimates were obtained with Bacon 2.3. (Blaauw and Christen 2011) in R 3.6.1 (R Core Team 2019) using Bayesian modeling in 2-cm increments and employing the IntCal13 calibration curve (Reimer et al. 2013) and Markov Chain Monte Carlo (MCMC) iterations (Supplementary Figure 2).

Diatom analysis

Sediment samples for diatom analysis were treated with hydrogen peroxide and hydrochloric acid following standard procedures (Renberg 1990), and permanent microscope slides were prepared using Naphrax (Brunel Microscopes Ltd.) as the mounting medium. Identification was performed using a light microscope (under oil immersion lens at 1000×magnification) based on standard floras (Krammer and Lange-Bertalot, 1986, 1988, 1991a, b) supported by online identification tools (Spaulding et al. 2021). A minimum of 300 valves were identified from each sample to the lowest taxonomic level possible, updating nomenclature where relevant. The diatom cell counts were converted into relative abundances for subsequent data analyses. Diatom species were classified based on their growth form applying the classification by Rimet and Bouchez (2012) with some modifications. As originally proposed by Passy (2007), diatom-growth forms sharing a similar niche can be further classified into broader functional groups or 'ecological guilds' and we loosely applied the guild classification by Rimet and Bouchez (2012) as a reference while focusing on the more detailed morphological classification. Where no data were available for a given species, the classification was done at the genus level if all species of that genera shared the same growth form. For a few rare taxa growth form could not be assigned and these species were omitted from the functional assessment. The growth form classes used characterize differences in the association between cells (solitary, colonial), the attachment of solitary species (unattached, attached), and the aggregation type of colonial species (species found to form mucous tube, ribbon, filament or zigzag colonies). In addition, we divided unattached species included in the fast-moving 'motile' group by Rimet and Bouchez (2012) into three categories (highly motile, moderately motile, slightly motile) based on size and raphe placement; highly motile included species with raphe raised on a keel promoting rapid movement, the moderately motile group included larger naviculoid species, and the slightly motile included small naviculoid species that due to their small size were considered slower. Unattached species not included in the motile guild were included in the 'low profile' group together with attached species. Colonial species were classified either in the 'high profile' or 'tychoplanktonic' functional group.

Biogeochemical analyses

An array of biogeochemical techniques was used in combination to track changes in lake-water and sediment organic matter origin and content. The biogeochemical analyses were carried out following standard procedures as detailed in Nevalainen et al. (2020b). Before analysis, the sediments were freeze dried and homogenized and further sieved (125 μm mesh) for the spectroscopic analyses. Carbon (C)

and nitrogen (N) content and isotope composition ($\delta^{13}C$, $\delta^{15}N$) in bulk sediment organic matter were analyzed at the NIWA Environmental and Ecological Stable Isotope Facility (Wellington, New Zealand). The bedrock in the watersheds of the lakes contains no carbonates and therefore the samples were not treated to remove carbonates to avoid potential bias associated with the pretreatment. The isotope data are expressed in delta (δ) notation as parts per thousand (‰) relative to international standards (Vienna Pee Dee Belemnite and atmospheric nitrogen). Spectroscopic inferences of lake-water total organic carbon (TOC) and sediment chlorophyll a (CHLa) concentrations were carried out at the Paleoecological Environmental Assessment and Research Lab (Queens University, Kingston, Ontario, Canada). The visible near-infrared (VNIR) spectra for each sediment sample represents a mean of 32 scans performed at 2-mm resolution over the wavelength range from 400 to 2500 nm (Michelutti et al. 2010). Past trends in lake-water TOC were estimated by a partial least squares regressions (PLSR) model based on VNIR spectra of surface sediments and corresponding lake-water TOC concentrations as detailed in Meyer-Jacob et al. (2017). The calibration model is based on 138 lakes in northern Fennoscandia situated within 300 km of the studied lakes and covering a TOC range from 0.5 to 14.9 mg L^{-1} with a crossvalidated R^2 of 0.62 and prediction error of 1.6 mg TOC L^{-1}. Sediment CHLa concentrations were inferred using log transformed data from Michelutti et al. (2010) with the equation: chlorophyll a + derivatives = EXP(0.83784 * LN(peak area 650–700 nm) + (− 2.48861)). The estimates capture primary chlorophyll a together with its main degradation products reducing the influence of potential diagenetic effects (Michelutti and Smol 2016; Rydberg et al. 2020).

Numerical analyses

We used constrained ordination to outline main patterns of temporal variation in the functional diatom community composition in the studied lakes and to determine how the selected biogeochemical indices contribute to this variation. Among the biogeochemical variables, sediment C was selected over N to represent sediment organic enrichment, and $\delta^{13}C$ was chosen over C/N as the main indicator of allochthony following initial data scrutiny. Initial

detrended correspondence analysis (DCA) indicated short gradient lengths (0.4 SD) for both lakes and we selected linear redundancy analysis (RDA) for subsequent analyses. Diatom relative abundances were square-root transformed prior to the analyses. Before analysis, biogeochemical variables departing from normality, assessed by skewness, were transformed as appropriate and the data were standardized. The uppermost samples representing the past two decades were omitted from the biogeochemical data for all data analyses to avoid possible influence of post-depositional processes. The ordination analyses were carried out using vegan 2.5–7 (Oksanen et al. 2020) in R 4.0.5 (R Core Team 2021). In addition, we applied constrained incremental sum of squares (CONISS) cluster analysis using Bray–Curtis distance to identify distinct zones of functional diatom-assemblage change. Broken stick model was used to determine the number of significant zones in the cluster analysis. Both analyses were carried out using rioja 0.9–26 (Juggins 2020).

Results

Biogeochemical patterns

The biogeochemical indices displayed similar trends in the studied woodland lake and tundra lake (Fig. 2), but their ranges varied. Sediment CHLa showed greater values and variability in the woodland lake (ranging from 0.1 to 0.2 mg g^{-1}) compared to the tundra lake (0.04 to 0.07 mg g^{-1}) as did lake-water TOC (4.8 to 7.8 mg L^{-1} and 1.4 to 3.2 mg L^{-1}, respectively). Similarly, sediment C content was higher in the woodland lake (26.6 to 31.3%) relative to the tundra lake (7.6 to 13.6%). Sediment C/N values were more uniform between the woodland and tundra lake (12.9 to 15.5 and 13.3 to 16.0, respectively), whereas $\delta^{13}C$ values (−25.4 to −23.8‰ and −23.0 to −21.7‰, respectively) and $\delta^{15}N$ values (−1.3 to −0.3‰, 0.4 to 1.6‰, respectively) were lower in the woodland lake relative to the tundra lake.

In the woodland lake, elevated lake-water TOC and sediment C content prevailed from 700 BCE until the turn of the last millennium (Fig. 2a). From around 1000 CE onward, lake-water TOC declined first gradually and then more sharply (overall by −2.6 mg L^{-1}), reaching minimum values around the early twentieth
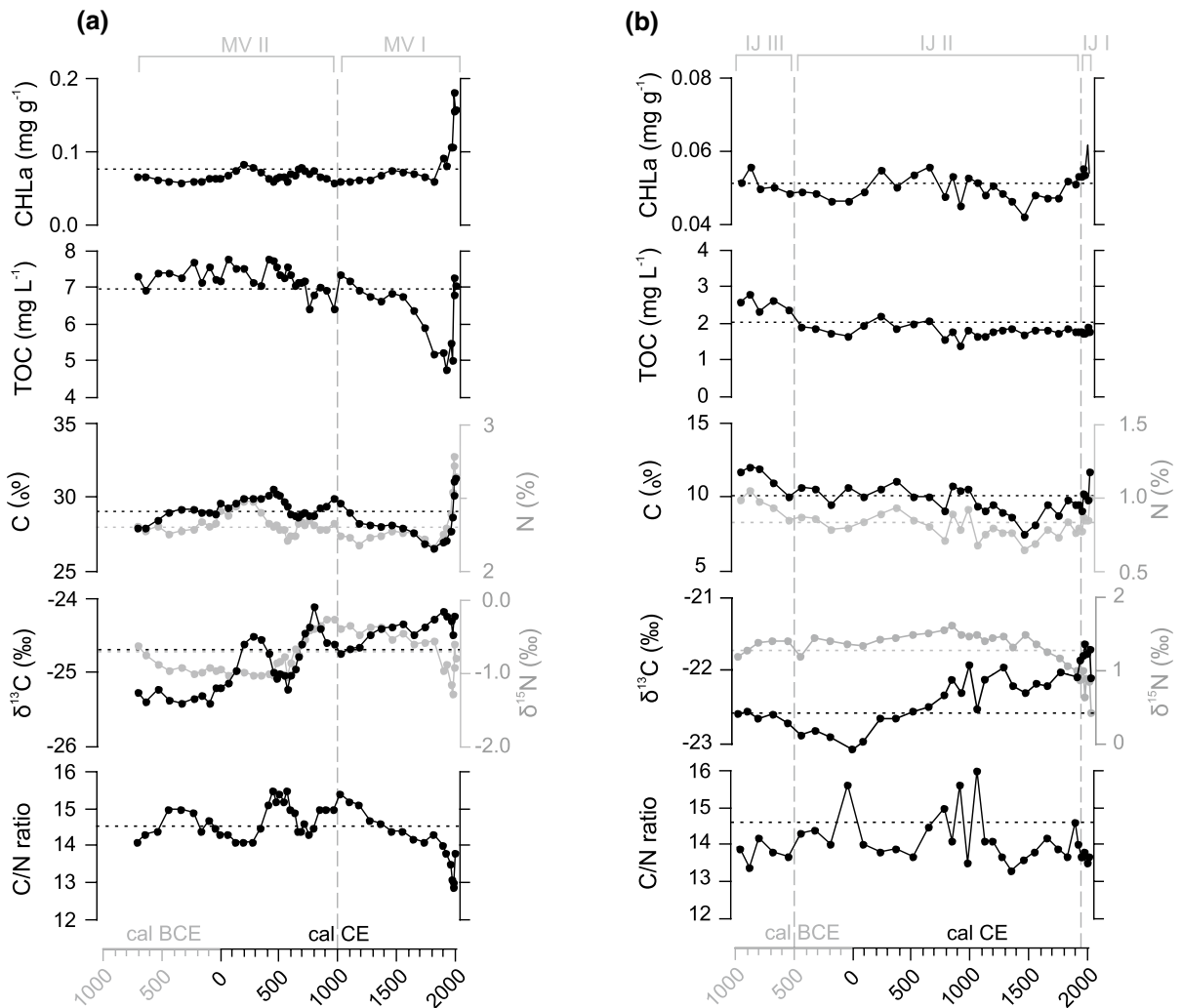
Fig. 2 Biogeochemical indices in the sediments of the woodland lake (**a**) and tundra lake (**b**), including sediment chlorophyll *a* (CHLa), inferred lake-water total organic carbon (TOC) concentrations, sediment carbon (C) and nitrogen (N) content and atomic ratio (C/N), and organic matter carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope composition. Horizontal dotted lines depict the mean value of each biogeochemical variable in the sediment core. Vertical dashed lines delimit distinct time periods identified with cluster analysis

century. Subsequently, lake-water TOC increased (+2.3 mg L^{-1}) rapidly toward the sediment surface. Sediment C content followed a similar pattern, dropping by 2.5% and then increasing by 4.2% toward the surface, and was overall positively correlated with lake-water TOC (R=0.67, $p < 0.001$). During the early time period with elevated lake-water TOC and sediment C content, CHLa was comparatively low but displayed two transient peaks around 100–400 CE and 600–900 CE, increasing by up to 0.02 mg g^{-1}. Near the sediment surface, CHLa showed a distinct

increase by 0.14 mg g^{-1} alongside the increasing lake-water TOC and sediment C content. Sediment δ^{13}C values displayed an overall increasing trend toward the sediment surface, with two distinct transient peaks (up to +0.9‰) coincident with the CHLa peaks around ~100–400 CE and ~600–900 CE. In contrast to δ^{13}C, sediment C/N values were generally elevated during the earlier phase with high lake-water TOC and sediment C content, and dropped by 2.5 coincident with TOC and C decline initiated around 1000 CE. Coincident with the CHLa

peaks around 100–400 CE and 600–900 CE, C/N dropped (up to −1.2) to lower values. The δ¹³C values were negatively correlated with lake-water TOC (R = −0.72, p < 0.001) and positively correlated with sediment CHLa (R = 0.57, p < 0.001), whereas sediment C/N was positively correlated with lake-water TOC (R = 0.44, p = 0.002) and negatively correlated with CHLa (R = −0.67, p < 0.001). Sediment δ¹⁵N showed low values during the early phase of elevated TOC and sediment C, then increased (+0.8‰) by the turn of the past millennium followed by a matching decline around the nineteenth century.

In the tundra lake, the lowermost samples between 1000 BCE and 0 CE were characterized by elevated but gradually declining lake-water TOC (−1.5 mg L⁻¹) and sediment C content (−4.2%) (Fig. 2b). After around 0 CE, lake-water TOC showed a slight increase (+0.4 mg L⁻¹) and stabilized coincident with sediment C content. Following the turn of the past millennium, lake-water TOC stabilized at low levels but sediment C content (−3.0%) declined, reaching minimum values around 1500 CE, followed by an increase (4.1.%) toward the sediment surface. Sediment C content showed a strong positive correlation with lake-water TOC (R = 0.57, p < 0.001) as well as with sediment CHLa (R = 0.42, p < 0.001). Similar to lake-water TOC and sediment C content, sediment CHLa was elevated but gradually declining (−0.01 mg g⁻¹) between 1000 BCE and 0 CE. Around 100 CE, CHLa increased by 0.01 mg g⁻¹ and remained generally elevated until around 1000 CE. Subsequently, sediment CHLa declined reaching minimum values around 1500 CE coincident with sediment C. From this minimum, sediment CHLa increased by 0.02 mg g⁻¹ toward the surface. Sediment δ¹³C values declined between 1000 BCE and 0 CE (−0.6‰) and thereafter increased toward the surface by 1.4‰. Sediment C/N values showed few directional changes in the tundra-lake sediments. Sediment δ¹⁵N values showed a slight gradual increase (+0.2‰) until around 1000 CE followed by a decline (−1.1‰) toward the sediment surface.

Diatom taxonomic and functional patterns

The sediments of the two study lakes were dominated by benthic diatoms totaling 63 species in the woodland lake (Fig. 3, Supplementary Table 2) and 59 species in the tundra lake (Fig. 4, Supplementary

Table 3). The assemblages in both lakes were dominated by *Brachysira* (mean relative abundance 22 and 18%, respectively), *Frustulia* (19 and 20%, respectively), and *Pinnularia* (15 and 18%, respectively) species representing unattached, tube-forming and moderately motile growth forms, respectively (Figs. 3, 4). The growth form and functional group associations of the diatom species are listed in Table 1. The biogeochemical variables explained 46.7% of the variation in the functional diatom data in the woodland lake and 56.3% of the variation in the tundra lake.

In the woodland lake, the period between 700 BCE and 1000 CE, characterized by elevated lake-water TOC and sediment C content, was associated with high abundances of motile species including, in particular, moderately motile *Pinnularia* (*P.* sp.1 and *P. subanglica*) and slightly motile *Cavinula* (*C. cocconeiformis*) and *Chamaepinnularia* (*C. mediocris* and *C. vyvermanii*) species (Figs. 3, 5). In the ordination diagram, the samples representing this time period were spread across the right-hand side of the biplot with high axis 1 values (Fig. 5). These samples were identified as a distinct cluster (MV II) also by the CONISS cluster analysis. After around 1000 CE, the motile species declined and gave way to unattached *Brachysira* species (*B. brebissonii*) that remained elevated in abundance up to the sediment surface. Other notable features in the sediment profile coincided with the transient CHLa peaks around 100–400 CE and 600–900 CE. Most notably, the moderately motile *Pinnularia* together with ribbon-forming *Eunotia* species (*E. faba*) and tube-forming *Frustulia* species (*F. saxonica*) declined, whereas the slightly motile *Chamaepinnularia* and especially *Cavinula* (*C. cocconeiformis*) species increased. Similar patterns were associated with the CHLa peak during the twentieth century, whereon the moderately motile *Pinnularia* (*P.* sp.1, *P. subanglica, P. rhombarea, P. biceps*) and tube-forming *Eunotia* (*E. faba, E. rhomboidea, E. mucophila*) species declined and the slightly motile *Cavinula* (*C. cocconeiformis*) species increased. Increases were also associated with the highly motile *Nitzschia* (*Nitzschia perminuta* complex) and the attached *Kobayasiella* (*K. subtilissima, K. micropunctata*) species.

In the tundra lake, distinct taxonomic and functional changes took place during the early period between 1000 BCE and 0 CE characterized by
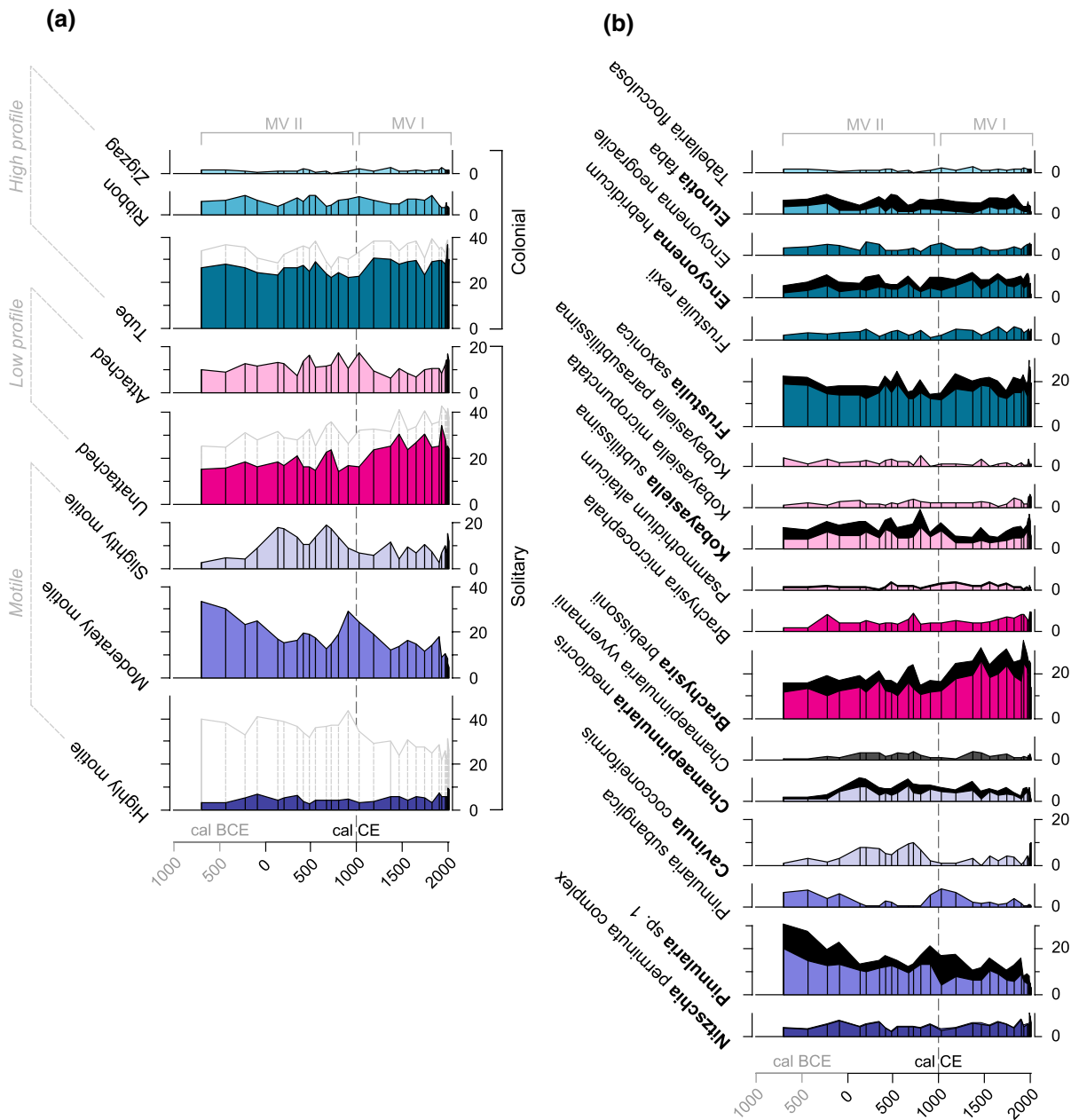
Fig. 3 Diatom **a** functional and **b** taxonomic community composition in the woodland-lake sediments indicated as relative (%) abundances. The growth forms considered in the study are divided into functional groups (motile, low profile, high profile) with total abundances indicated in grey line. In the species diagram, species present in at least half of the samples with at least 1% mean or 3% maximum abundance are shown and total abundances of the genera are indicated in black. Vertical dashed lines delimit distinct time periods identified with cluster analysis

declining CHLa, lake-water TOC and sediment C content (Figs. 4, 6). Tube-forming *Frustulia* (*F. saxonica*) and ribbon-forming *Eunotia* (*E. faba, E. incisa, E. mucophila*) species declined whereas

moderately motile *Pinnularia* species (*P. microstauron* var. *nonfasciata, P. subanglica*) and attached *Kobayasiella* (*K. subtilissima*) and *Psammothidium* (*P. scoticum, P. acidoclinatum*) and *Encyonopsis* (*E.
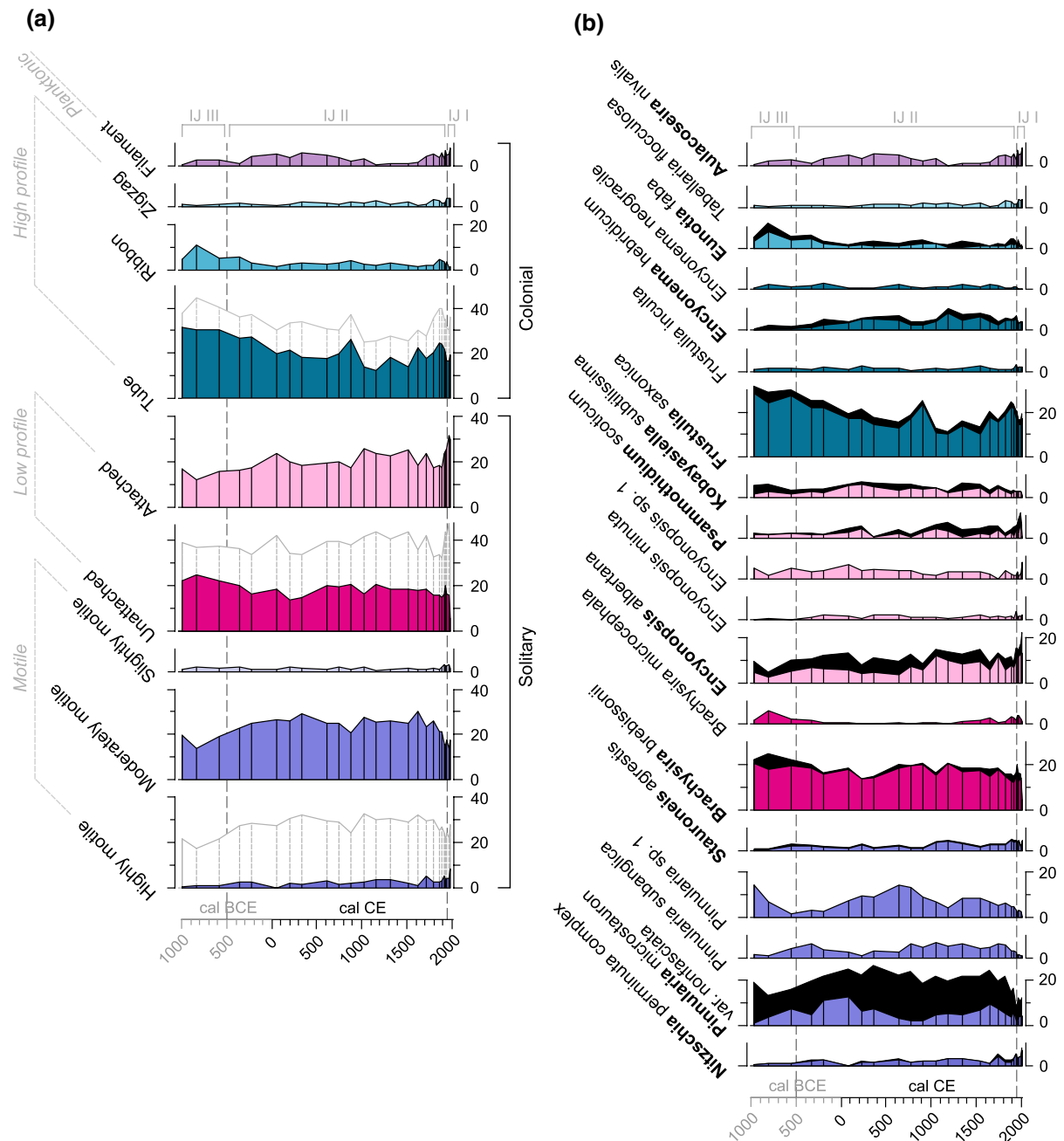
Fig. 4 Diatom **a** functional and **b** taxonomic community composition in the tundra-lake sediments indicated as relative (%) abundances. The growth forms considered in the study are divided into functional groups (motile, low profile, high profile, planktonic) with total abundances indicated in grey line.

In the species diagram, species with at least 1% mean or 3% maximum abundance are shown and the total abundances of the genera are indicated in black. Vertical dashed lines delimit distinct time periods identified with cluster analysis

albertana, E. minuta, E. sp. 1) species increased. The samples representing the period 1000–500 BCE, in particular, were clearly distinguished in the ordination

diagram with low values along axis 1 (Fig. 6), and were identified as a distinct sample cluster (IJ III) by the CONISS analysis. Between around 0 and 1500

Table 1 Diatom genera in the woodland and tundra lakes assigned by their growth form and functional group with slight modification of the classification by Rimet and Bouchez (2012)

Functional group	Growth form	Genera
Motile	Highly motile	*Nitzschia, Stenopterobia, Surirella*
	Moderately motile	*Pinnularia, Navicula, Stauroneis, Neidium*
	Slightly motile	*Cavinula, Chamaepinnularia, Nupela*
Low profile	Unattached	*Brachysira*
	Attached	*Kobayasiella, Encyonopsis, Psammothidium, Achnanthidium, Gomphonema, Stauroforma, Staurosirella, Kurtkrammeria*
High profile	Filament	*Aulacoseira*
	Tube	*Frustulia, Encyonema*
	Ribbon	*Eunotia, Stauroforma, Staurosirella*
	Zigzag	*Tabellaria*

While not always the case, all species belonging to the same genus shared their functional traits in the study lakes

Fig. 5 Redundancy analysis (RDA) biplot of functional diatom community composition and biogeochemical variables, including sediment chlorophyll *a* (CHLa), inferred lake-water total organic carbon (TOC) concentrations, sediment carbon (C) content, and organic matter carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope composition, in the woodland-lake sediments. Time periods associated with elevated CHLa are indicated with dashed lines. Groups of samples forming statistically significant clusters, determined with cluster analysis and broken stick model, are indicated with shading
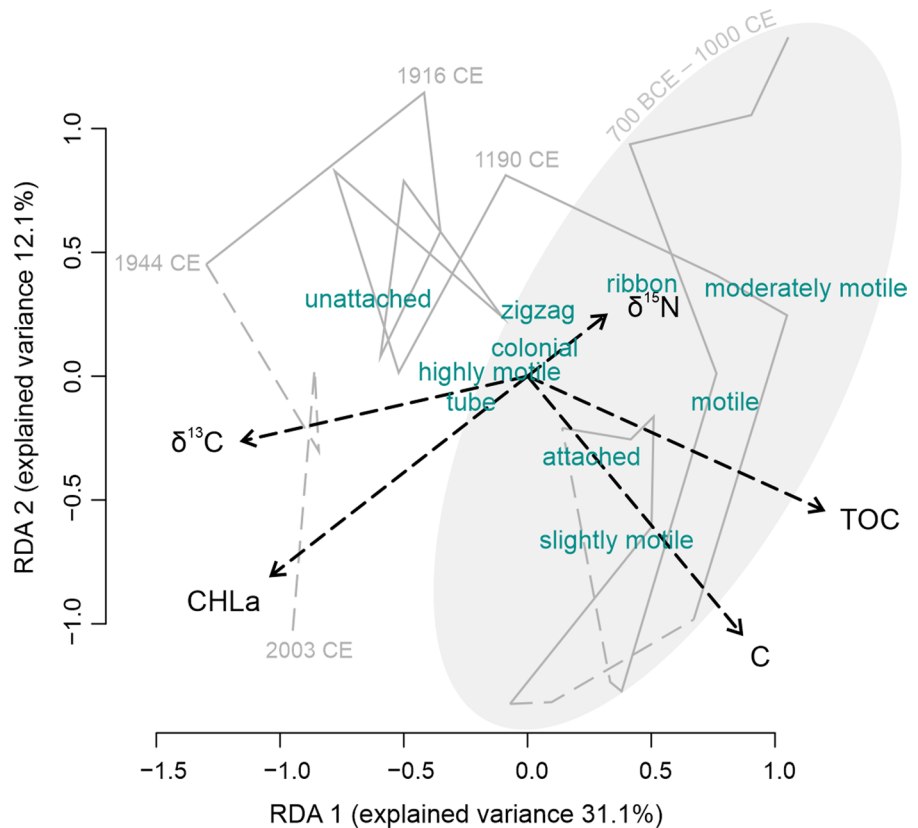
CE, few notable changes took place in the diatom assemblages aside from an increase in the abundance of filamentous *Aulacoseira* species (*A. nivalis*). Most conspicuous shifts near the sediment surface took place over the twentieth century characterized by a decline in the moderately motile *Pinnularia* species (*P. microstauron* var. *nonfasciata*, *P. subanglica*, *P* sp. 1,. *P. viridis*) and increases in the filamentous *Aulacoseira* species (*A. nivalis*), highly motile *Nitzschia* (*N. perminuta* complex) and *Surirella* species, slightly

Fig. 6 Redundancy analysis (RDA) biplot of functional diatom community composition and biogeochemical variables, including sediment chlorophyll *a* (CHLa), inferred lake-water total organic carbon (TOC) concentrations, sediment carbon (C) content, and organic matter carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope composition, in the tundra-lake sediments. Time periods associated with elevated CHLa are indicated with dashed lines. Groups of samples forming statistically significant clusters, determined with cluster analysis and broken stick model, are indicated with shading
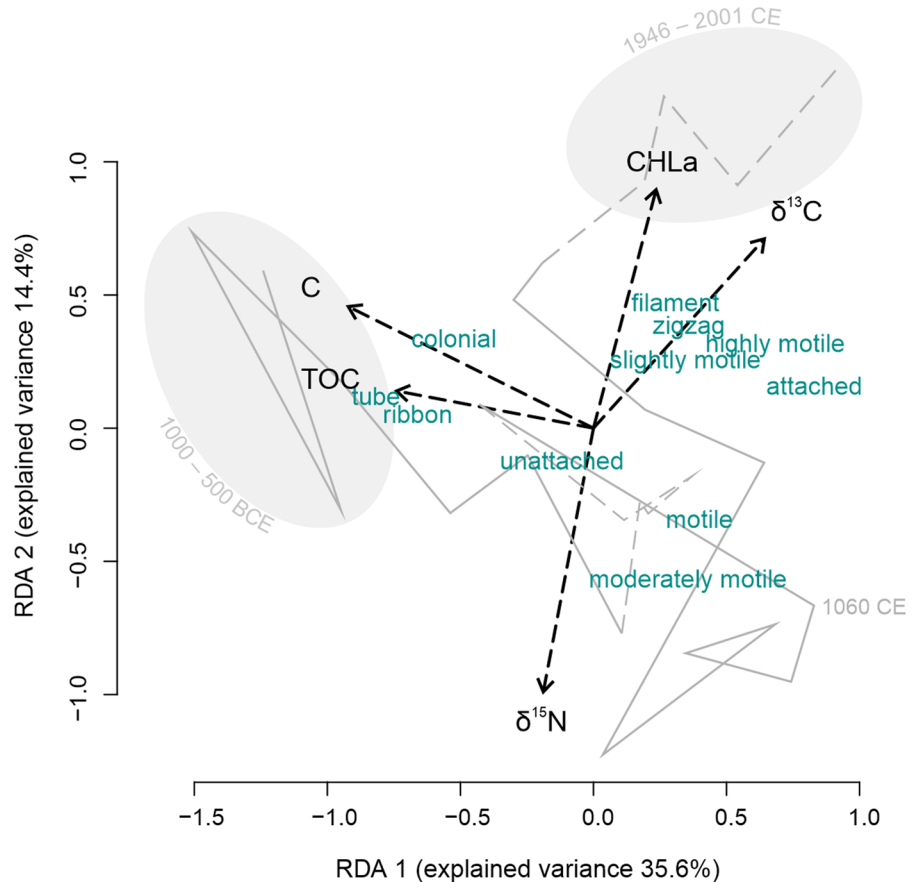
motile *Chamaepinnularia* (*C. mediocris*) and *Nupela* (*N. gracillima*) species, and attached *Encyonopsis* (*E. albertana*, *E.* sp. 1) and *Psammothidium* (*P. scoticum, P. microscopicum*) species. Samples representing the period from the mid-twentieth century onward also formed a distinct cluster (IJ I) based on the CONISS analysis and were oriented in the upper right quadrant with high values along axes 1 and 2 (Fig. 6).

Discussion

The biogeochemical patterns in the sediment cores of the studied tundra and woodland lakes indicate that, in spite of their differences, the limnological trajectories of the two lakes over the past three millennia have followed broadly similar patterns (Figs. 2, 7). On the whole, the diatom assemblages also displayed conspicuous similarity despite the stark differences in underwater light regimes and benthic substrate. The high abundance of motile and colonial species in both

lakes (Figs. 3a, 4a) indicates well-developed benthic biofilms and possibly also comparatively low disturbance and herbivory (Passy 2007). At the taxonomic level, the dominant species from the genera *Frustulia*, *Pinnularia* and *Brachysira* in both lakes are characteristic of oligotrophic, dilute and circumneutral to acidic waters (Wehr et al. 2015; Rantala et al. 2017) (Figs. 3b, 4b). Common pioneering species in northern lakes belonging to *Achnanthidium* and *Staurosirella* were present in very low abundances, indicating limnological conditions that were less severe than those encountered in polar lakes (Keatley et al. 2008; Griffiths et al. 2017). Despite the similarities in the baseline diatom flora and the millennial-scale development of the lakes, the diatom communities in the woodland and tundra lake responded to environmental changes over the past three millennia in different, and at times contradictory ways. The following paragraphs elucidate the overall patterns of environmental change and diatom functional and taxonomic responses to Neoglacial environmental transitions
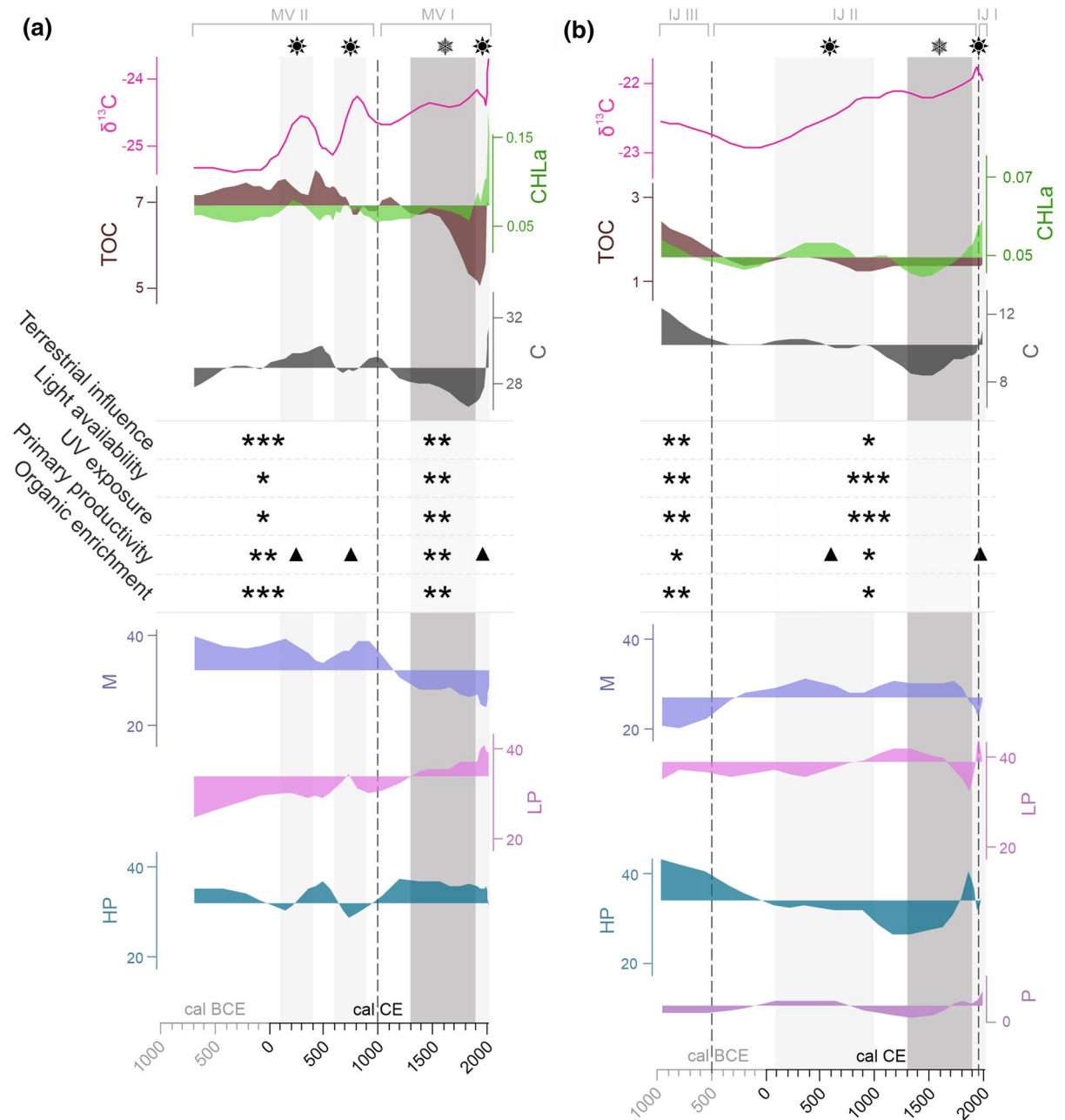
Fig. 7 Schematic summary of ecosystem changes and functional diatom responses in the **a** woodland and **b** tundra lake. The upper panels present locally weighted scatter plot smooth curves of key biogeochemical indices (lowess span 0.1), including sediment chlorophyll *a* (CHLa), inferred lake-water total organic carbon (TOC) concentrations, sediment carbon (C) content and isotope composition (δ13C), and the lower panels present diatom functional groups (lowess span 0.2), including motile (M), low profile (LP), high profile (HP) and planktonic (P) species. The midline of the smooth curves indi-cates the mean. Inferred ecosystem changes are indicated in the middle on a relative scale from high (***) to moderate (**) and low (*), comparing changes within and between the lakes. The arrowheads mark transient periods of elevated primary productivity associated with Neoglacial warm periods that are indicated with light grey shading. Dark grey shading indicates the approximate timing of the Little Ice Age (LIA). Vertical dashed lines delimit distinct time periods identified with cluster analysis

below and above the treeline, focusing first on the broadscale Neoglacial cooling trend and subsequently on the recent warming and past warm analogues.

Ecosystem changes and biotic responses under Neoglacial cooling

Woodland lake: biogeochemical evidence of ecosystem changes under Neoglacial cooling (MV II–MV I)

In the lake situated in the subarctic mountain-birch woodlands, the low $\delta^{13}C$ values, approaching typical terrestrial values of around $-27‰$ (Kivilä et al. 2019; Rantala et al. 2021), and the slightly elevated C/N values during the early phase of the Neoglacial indicate high inflow of allochthonous carbon from the watershed, contributing to the elevated lake-water TOC and sediment C content (Fig. 2a). In part, the elemental and isotope ratios likely reflect the comparatively low contribution of autochthonous organic carbon from algal production, particularly until the turn of the Common Era (~ 0 CE), as indicated by sediment CHLa. Notably, where $\delta^{13}C$ and C/N appeared to mirror changes in both the inferred lake-water TOC and sediment CHLa in this lake, the latter two showed no apparent connection contrary to earlier observations from the region (Rantala et al. 2016). This is likely partially related to the interplay between land-derived nutrients fueling primary production and increased shading by allochthonous carbon counteracting the fertilizing effect (Reuss et al. 2010; Seekell et al. 2015). Moreover, benthic phototrophic communities in northern lakes supporting thick benthic mats, such as those observed in the woodland lake, may be less sensitive to external nutrient stimuli due to effective nutrient recycling within the mats (Vadeboncoeur et al. 2006; Rautio et al. 2011). Either way, the biogeochemical indices depicted a shaded environment with abundant benthic organic substrate for over two millennia between ~ 700 BCE and ~ 1000 CE (Fig. 7).

The sharp decline in lake-water and sediment organic carbon matched by increasing $\delta^{13}C$ and declining C/N values after the turn of the past millennium indicate lowering supply of land-derived organic matter (Figs. 2a, 7). Considering the commonly chromophoric quality of allochthonous carbon, the decline is likely to have improved underwater light penetration (Pienitz et al. 1999) and increased

UV photodegradation rates (Nevalainen et al. 2020a). This may have further reinforced the TOC decline and could partially contribute to the patterns in sediment $\delta^{13}C$ and C/N (Rantala et al. 2021). The distinct biogeochemical transition likely relates to the broadscale Neoglacial cooling trend culminating during the cold climate period known as the Little Ice Age (LIA) (McKay et al. 2018). Previous paleoclimate records from the study region (Matskovsky and Helama 2014; Luoto et al. 2017) and the Northern Hemisphere more broadly (Moberg et al. 2005) indicate that cool temperatures prevailed over the past millennium and especially over the past five centuries persisting until the early twentieth century in northern Finland, consistent with the timing of the sharpest decline in lake-water TOC (Fig. 7). A similar pattern of declining lake-water TOC has been inferred from several lake sediment records in northern Sweden (Rosén 2005, Rosén et al. 2011), Russia (Jones et al. 2011) and Canada (Pienitz et al. 1999; Fallu et al. 2005) attributed to changes in catchment vegetation and soils driven by the prolonged cooling. An earlier palynological study from the region indicated that, during the warm climate interval preceding the Neoglacial cooling, the altitudinal limit of pine (*Pinus sylvestris*) may have extended to as high as 700 m a.s.l. (Seppä et al. 2002) supported by evidence from lakes in northern Sweden (Barnekow 2000). Pine decline was initiated already around 2000–1000 BCE in the region, yet some remnant influence of the retreating vegetation may have contributed to sustaining allochthonous carbon inputs to the lake. Moreover, the early Neoglacial period was characterized by intensive wetland expansion in the region driven by the declining temperatures and increased humidity associated with the new climate regime (Weckström et al. 2010). As suggested by previous studies from northern Sweden (Rosén 2005), this process likely promoted high input of allochthonous carbon to the woodland lake until the LIA.

Woodland lake: diatom responses to Neoglacial cooling (MV II–MV I)

Diatom functional and taxonomic shifts in the woodland lake were strongly connected to the changing allochthony and lake-water and sediment organic carbon levels. The period characterized by high lake-water TOC and sediment C content appeared

especially favorable to motile species (Figs. 3a, 5, 7) that have been previously affiliated with high organic levels, complex biofilms and epipelic substrate (Passy 2007; McGowan et al. 2018). The ability to move is an important trait in unstable fine sediment substrate where diatoms may be frequently buried and further allows the species to migrate to resource-rich areas in the organic matrix (Johnson et al. 1997; Passy 2007). Although rapid movement also allows the species to move up and down thick biofilms for light harvesting and motile diatoms have been shown to tolerate shaded conditions (Moss 1977; Stenger-Kovács et al. 2013), a number of previous studies have linked motile diatoms with high rather than low light (Lange et al. 2011; Marcel et al. 2017). However, in these and other studies high light availability is often coupled to (and indistinguishable from) high nutrients or complex organic biofilms both of which are thought to favor motile species (Passy 2007; Berthon et al. 2011; B-Béres et al. 2017). Here too, separating the role of substratum and light is difficult as the motile species were generally more abundant in the dark but also organic-rich woodland lake, and especially so during the period of elevated allochthonous (i.e., shading) lake-water TOC and sediment organic content. Whether related to the sediment substrate, (light) resources, or both, motile diatoms showed a clear step decrease coincident with the rapid decline in allochthonous inputs and lake-water and sediment organic carbon around the turn of the past millennium (Fig. 7).

An examination of changes at the genus and species level revealed that the patterns were not uniform among the motile species (Fig. 3b). The decline in the moderately motile *Pinnularia* species appears well aligned with the biogeochemical changes as the species are often associated with soft sediments, mosses and epiphyton in northern lakes (Lim et al. 2001; Michelutti et al. 2003). The abundance of the slightly motile *Chamaepinnularia* and *Cavinula* species during the initial period of high TOC and sediment C content, in turn, could be related to extensive growth of mosses in the littoral zone at the time as these small naviculoid species have been associated with moist subaerial habitats (Wehr et al. 2015; Spaulding and Edlund 2009; Spaulding et al. 2009). In common, the more rare highly motile *Navicula* species (comprising mainly *N. notha*) were primarily present during the period of high TOC and sediment

C content. In contrast, highly motile *Nitzschia* species appeared indifferent to the changing organic levels, although both *Navicula* and *Nitzschia* have been previously found to increase with organic enrichment in Arctic lakes (Keatley et al. 2006; Michelutti et al. 2007; McGowan et al. 2018). A broadscale spatial survey from Canadian Arctic lakes and ponds found the *Nitzschia perminuta* complex to be abundant across sediment, moss and rock habitats (Michelutti et al. 2003), which could indicate that this taxonomic grouping might be less sensitive to changing substrate, though it is also possible that the species in the complex have different substrate preferences. Remarkably, the patterns in *Nitzschia* and nearly all of the motile diatom species were also strongly influenced by the transient periods of increased lake productivity intersecting the Neoglacial cooling trend indicating that their responses were shaped or co-shaped also by other environmental factors.

Another notable feature in the sediment record was the lower abundance of *Brachysira* species (mainly *B. brebissonii*) during the period of elevated TOC and sediment C content and the following increase over the past millennium in a pattern largely opposite to that seen with the moderately motile *Pinnularia* species (Figs. 3b, 5). *Brachysira* were here considered separate from the other small unattached species due to their ability to form stalks and association with the low profile rather than the motile guild, although we cannot ascertain their specific growth form in the studied lakes. Both stalked (Berthon et al. 2011) and low profile (Passy 2007; Marcel et al. 2017) species have been associated with low levels of organic matter in earlier literature, although the attached species of similar low stature (dominated by *Kobayasiella* and *Psammothidium* species) displayed no consistent trends in relation to TOC and sediment C content in the woodland lake. *Brachysira* and *Pinnularia* are both cosmopolitan species frequently encountered in similar northern lake environments with dilute, oligotrophic and circumneutral to slightly acidic waters (Gottschalk and Kahlert 2012; Beaudoin et al. 2016) including in dark and organic-rich wetland lakes in northern Finland (Rantala et al. 2017). *Brachysira* species, however, have been more commonly associated with the epilithon (Sorvari 2001; Pla-Rabés and Catalan 2018) as opposed to the epipelon and epiphyton and their increase alongside the decline in sediment C content thus further supports the

interpretation that the broadscale biotic transition around the turn of the past millennium carries a signal of changing benthic substratum driven by the prolonged cooling.

Tundra lake: biogeochemical evidence of ecosystem changes under Neoglacial cooling (IJ III–IJ II)

In the tundra lake, the gradually decreasing sediment CHLa indicated declining lake primary productivity between ~ 1000 BCE and ~ 0 CE (Figs. 2b, 7). This was corroborated by the concurrent decline in sediment δ^{13}C and increase in C/N pointing to a relative increase in the contribution of allochthonous organic matter to the sediment-carbon pool. The synchronous decline in lake-water TOC implies that the lake-water organic carbon pool had a comparatively large autochthonous component, which is supported by the modern water chemistry and the surrounding landscape providing relatively few sources of allochthonous organic matter. Notwithstanding, some part of the lake-water TOC shift is likely related to a decline in land carbon input as the sharpest TOC decline around ~ 1000–500 BCE was followed by a stepwise ncrease in benthic macroinvertebrates (Cladocera) with intense pigmentation and affinity to clear waters suggesting increased underwater UV transparency (Nevalainen et al. 2020b). In the tundra lake overall, sediment δ^{13}C and especially C/N values, indicative of relative changes in organic matter source, did not show as clear cut a connection to the CHLa and lake-water TOC trends as recorded in the woodland lake. This could be due to a tighter coupling between allochthonous inputs and autochthonous production, whereby terrestrial nutrient inputs support lake primary productivity with less interference from shading and internal nutrient recycling compared to the woodland lake. In support, a study on Swedish and Alaskan lakes indicated that nutrient addition stimulated primary production mainly in transparent unproductive northern lakes because, where baseline organic carbon concentrations are low, nutrient availability increases proportionally faster than light attenuation in the water column (Seekell et al. 2015).

Additionally, field studies have shown that at low (below ~ 4 mg L^{-1}) levels of DOC in the lake water, even a small decline in land-derived chromophoric organic matter can markedly alter the spectral balance between UV and PAR (Schindler et al. 1996; Laurion et al. 1997). The resulting increase in underwater UV exposure may further impede algal production as suggested by a mesocosm experiment carried out in the tundra lake (Nevalainen et al. 2020a) and corroborated by earlier experimental and paleolimnological research from Canadian lakes (Vinebrooke and Leavitt 1996; Leavitt et al. 2003). Either way, parallel changes in the supply of allochthonous and autochthonous organic matter could partially cloud the signal retained in the sediment isotopic and elemental ratios. Whether of allochthonous or autochthonous origin, the decline in lake-water TOC in the tundra lake was also reflected as a decline in the sediment C content indicating a reduction in organic bottom substrate (Fig. 7).

As in the woodland lake, the above biogeochemical changes occurred most likely in response to the progressing Neoglacial climate regime, and marked a clear transition in the status of the tundra lake following one and a half millenium of comparatively stable and elevated CHLa and lake-water TOC (Nevalainen et al. 2020b). The timing and magnitude of the transition differs from that observed in the woodland lake where the decline in lake-water and sediment organic content was sharper and initiated much later. This may be attributed to the differences in watershed vegetation and soils between the two lakes ultimately related to the altitude gradient they represent. A pine forest likely never reached the tundra lake nor would we expect major wetland development to have occurred around the lake. Consistently, previous research from subarctic lakes in northern Sweden indicated more conspicuous declines in lake-water TOC near and below the treeline compared to lakes situated at higher altitudes (Rosén 2005). Notwithstanding, the treeline advance during the warm and dry climate period preceding the Neoglacial may still have promoted plant growth and increased soil organic carbon stocks subsequently mobilized during the early Neoglacial (Nevalainen et al. 2020b). Similar transient increases in the inwash of organic matter at the onset of climate deterioration have been observed from other northern tundra lakes (Liversidge 2012).

Tundra lake: diatom responses to Neoglacial cooling (IJ III–IJ II)

The environmental changes brought on by the Neoglacial cooling were clearly reflected in the functional diatom-assemblage composition in the tundra lake (Fig. 6). The most notable pattern was the decline in colonial life forms, especially tube-forming *Frustulia* species and *Eunotia* species forming ribbon colonies (Fig. 4a, b) alongside the decline in lake-water and sediment organic enrichment (Fig. 6). Around these times, the decline in sediment C content (Fig. 2b), together with changes in sediment lithology and a stepwise increase in the Cladocera *Alonopsis elongata* (Nevalainen et al. 2020b), suggested a clear decline in aquatic macrophytes and an increase in hard bottom (rock and sand) habitats that may underlie the decline in colonial life forms. A comparable trend of recessing aquatic macrophytes has been found from other tundra lakes in northern Finland and Russia associated with the Neoglacial climate deterioration and shortening of the growing season (Jones et al. 2011; Väliranta 2006). Colonial life forms are often associated with epiphyton and both *Frustulia* and *Eunotia* species are common to wetlands and dystrophic lake environments (Beaudoin et al. 2016; Rantala et al. 2017) and may have been growing epiphytic on macrophytes in the tundra lake before their decline set off by the Neoglacial climate transition. The parallel increase in low profile attached growth forms corroborates the picture of expanding hard bottom substrate as such species are generally associated with low organic environments and the epilithon and epipsammon (Passy 2007; Berthon et al. 2011; B-Béres et al. 2017; Griffiths et al. 2017). Some experimental studies have suggested that certain stalked diatoms (Bothwell et al. 1993) and epipsammon (Barnett et al. 2014) may also be well adapted to high UV environments. Changes in underwater UV regimes could thus also play a part, although we consider this explanation tentative as UV effects on diatom functional community composition are presently not well understood.

Even though these broadscale shifts in the diatom assemblage align with our current knowledge of the ecological indications of diatom life forms, not all changes were uniform among species and genera sharing a similar growth form. Most notably, the other tube-forming genus *Encyonema*, and mainly the

dominant species *E. hebridicum*, showed an opposing pattern with the *Frustulia* species (Fig. 4b). The two genera, and the dominant species *F. saxonica* and *E. hebridicum*, inhabit very similar environments across nutrient and organic gradients in the study region (Rantala et al. 2017) and in northern lakes generally (Van Dam et al. 1994; Rühland et al. 2003), and it is therefore difficult to pinpoint the cause for their contrasting responses. Deviating responses may be expected among growth forms occupying a similar niche, however, this could also be related to limitations in our knowledge of species-specific growth form and habitat preference in different lake types particularly as many colonial species, including *Eunotia*, *Frustulia* and *Encyonema* species, may grow also singly. As demonstrated by recent research on lotic ecosystems (B-Béres et al. 2017), abundant species with the potential to change their growth form can markedly alter the apparent relationship between an environmental variable and the functional class they are expected to represent.

The increase in moderately motile *Pinnularia*, *Stauroneis* and *Neidium* species and also the highly motile *Nitzschia* species after the early decline in lake-water TOC and sediment C content in the tundra lake (Figs. 4a, 6) contradicts the pattern found in the woodland lake. This may relate to differential development of the benthic substratum and light climate in the two lakes under Neoglacial cooling despite the shared broadscale trend of declining organic levels and terrestrial influence. In northern lakes, climate deterioration and reduction in the length of the growing season often results in the replacement of mosses and associated epiphyton with rock and sediment substrate supporting epilithic and epipelic diatoms (Douglas and Smol 2010; Smol and Douglas 2007; Sorvari 2001), which may best describe the changes seen in the tundra lake. In the transparent waters, increasing UV exposure could also have favored motile species as vertical migration is a key photoprotective mechanism (Perkins et al. 2010). In the woodland lake, high allochthonous supply of chromophoric organic matter during the earlier Neoglacial phase may have limited the growth of submerged macrophytes (Toivonen and Huttunen 1995) but likely promoted the formation of thick microbial mats comparable to those observed in the present lake, and also likely indicates abundant plant growth around the lake margins. This kind of environment would have

been especially well suited to the motile as well as subaerial species that, with the sharp decline in terrestrial influence during the LIA, may have eventually lost their competitive advantage.

Ecosystem changes and biotic responses under Neoglacial warm anomalies

Woodland lake: biogeochemical evidence of ecosystem changes under warming

The sediment CHLa patterns in the woodland lake indicate transient increases in primary productivity especially around ~ 100–400 CE, ~ 600–900 CE and, most conspicuously, from the late nineteenth century onward (Fig. 2a), which is supported by the synchronous increases in $\delta^{13}C$ and declines in C/N values pointing to increased autochthonous production in the lake. Post-depositional processes likely contribute to the biogeochemical patterns near the sediment surface; however, previous research suggests that diagenetic effects on sediment CHLa (using the approaches we employed) should be most apparent during the first 10–15 years after deposition (Rydberg et al. 2020) and should therefore not account for the observed recent increasing CHLa trend spanning over a century. Similarly, the recent changes in sediment $\delta^{13}C$ and C/N are sensitive to diagenetic effects primarily during the first decade, though for $\delta^{15}N$ possibly longer (Gälman et al. 2008, 2009). Lake-water TOC inferences have been shown to be relatively insensitive to diagenetic changes (Meyer-Jacob et al. 2017) but here too we regard the patterns especially in the uppermost one or two samples with some caution.

Considering the pivotal role of climate in driving algal productivity patterns in northern lakes, whether by direct or indirect influence (Vincent et al. 2008; Dranga et al. 2018), the two earlier productivity peaks are likely related to Neoglacial warm anomalies as identified by numerous paleoenvironmental records across the Northern Hemisphere. The timing of these events varies noticeably between studies and age-depth models always contain an element of uncertainty; however, evidence of warmer temperatures has been previously recognized during the first millennium CE in northern Finland (Korhola et al. 2000; Luoto and Nevalainen 2018) and the circumpolar Arctic more broadly (Kaufman et al. 2009). The most recent increase in CHLa corroborates the growing evidence of increasingly productive northern lakes (Michelutti et al. 2005; Ayala-Borda et al. 2021) and is most likely related to anthropogenic warming. For the lake flora, these productive periods were likely characterized by generally improved resource availability, especially as the record provides no evidence of increases in allochthonous (shading) lake-water TOC, and increased organic substrata but possibly also changes in water chemistry, habitats and predation (Smol and Stoermer 2010).

Woodland lake: diatom responses to Neoglacial warm periods

The periods of elevated lake productivity were clearly reflected in the diatom community composition in the woodland lake. Most notably, species forming ribbon colonies together with the moderately motile *Pinnularia* species showed a clear decrease during periods of increased productivity (Figs. 3, 5) and an overall strong negative relationship with CHLa. A similar but weaker relationship was displayed by *Psammothidium* species among the attached growth forms (Fig. 3b). Colonial species have the ability to extend to the surface of the biofilm allowing them to benefit from resources unavailable to the bottom canopy; however, whether this indicates an affinity to high resources (Passy 2007) or tolerance of low resources (Rimet et al. 2015) remains unclear (Tapolczai et al. 2016). In addition, no such consistent connection was observed with the other colonial growth forms and CHLa although tube-forming *Frustulia* had lower abundance around the earlier productivity peaks. Motile species, in turn, have often been found to thrive under high resource levels (Passy 2007; Lange et al. 2011; B-Béres et al. 2017) in agreement with the elevated abundance of the slightly motile *Cavinula* and *Chamaepinnularia* species and, less conspicuously, the highly motile *Nitzschia* during more productive periods contrasting the response by *Pinnularia* species.

Warmer temperatures and increased primary productivity tend to covary with an array of variables that could influence diatoms and, examining responses at the species and genus level, we suspect that several conditions may have interacted to shape the diatom community during the more productive periods. As in the tundra lake, the species forming ribbon colonies

belonged primarily to the genus *Eunotia* comprising mainly acidophilic and acidobiontic species that are usually associated with unproductive waters (Van Dam et al. 1994; Rantala et al. 2017). In common, the declining *Pinnularia* and *Psammothidium* are often found in slightly acidic and low nutrient water (Antoniades et al. 2004; Gottschalk and Kahlert 2012; Rantala et al. 2017), whereas *Nitzschia* species have been affiliated with elevated pH and nutrients in northern lakes (Keatley et al. 2009; Griffiths et al. 2017). Previous research from a large set of Swedish lakes suggested that functional diatom responses to resource availability may be tightly intertwined with, and at times confounded by, changes in lake-water pH in northern lakes (Gottschalk and Kahlert 2012; Gottschalk 2014), which is unsurprising considering the pivotal role of pH in controlling diatom distribution in lakes (Battarbee et al. 2001; Michelutti et al. 2007) including in lakes in northern Finland (Rantala et al. 2017). Although we might expect pH to exert a stronger influence on the benthic diatom flora relative to nutrients (Schneider et al. 2013), it is difficult to affirm its relative importance as elevated pH tends to be associated with improved nutrient availability and the other way around.

Notably, the common acid-indicator taxa such as *Eunotia* species provide no evidence of gradually increasing acidity in the woodland lake during the Neoglacial although natural acidification related to weathering processes and climate regulation of dissolved inorganic carbon dynamics has often been evoked as an important driver of Neoglacial diatom-community change in northern lakes (Wolfe 2002; Bigler and Hall 2003; Liversidge 2012). The overall high number of acidophilous species in the lake (as in the tundra lake) leads us to believe that common acidification processes associated with lake ontogeny have taken place during the earlier Holocene history of the lake (Engstrom et al. 2000; Reuss et al. 2010). The increases in slightly motile *Cavinula* and *Chamaepinnularia* species, especially during the earlier CHLa peaks, is likely related to other processes, such as the expansion of littoral moss beds during warmer periods, as previous studies provide no clear evidence of particularly high pH or nutrient preference for either species (Van Dam et al. 1994; Cvetkoska et al. 2014). Grazing pressure can also be expected to increase under more productive (and alkaline) conditions and this could have also contributed to the decline in colonial and larger motile species that are considered more sensitive to predation compared to low profile species (Passy 2007; Marcel et al. 2017; McGowan et al. 2018).

Tundra lake: biogeochemical evidence of ecosystem changes under warming (IJ II–IJ I)

In the tundra lake, the pattern of declining sediment CHLa early on in the sediment sequence was interrupted and reversed around 100 CE (Fig. 2b), broadly coincident with the first productivity peak in the woodland lake (Fig. 2a). The overall consistent timing of the transient increases in primary productivity in both of the studied lakes, accounting for some uncertainty in the age-depth models and different sensitivities to warming, suggests a common driving mechanism likely relating to the Neoglacial warm anomalies. The CHLa increase during the first millennium CE was still closely mirrored by lake-water TOC but less clearly reflected in the sediment C content. Remarkably, $\delta^{13}C$ values increased steadily until $\sim$ 1200 CE even after the increasing CHLa trend gradually came to a halt; thereon $\delta^{13}C$ values showed a strong positive relationship with CHLa. By further considering the stabilization of lake-water TOC around this time, we infer that terrestrial influence continued to decline throughout the first millennium CE in the tundra lake and that the watershed reached its current status around the turn of the past millennium. The evidence for a recent increase in productivity in the tundra lake was not as conspicuous as in the woodland lake, however, the tightly coupled trends in sediment CHLa, $\delta^{13}C$ as well as sediment C content point to a sustained increase in primary productivity toward the present following a period of low primary productivity likely associated with the LIA.

Tundra lake: diatom responses to Neoglacial warm periods (IJ II–IJ I)

The diatom community in the tundra lake showed few consistent responses to changing sediment CHLa aside from the increases in filamentous *Aulacoseira* species (mainly *A. nivalis*) alongside sediment CHLa especially after the early period with elevated TOC (Fig. 4). These commonly tychoplanktonic species were found only in the slightly deeper tundra lake consistent with their preference

for deeper waters and an open landscape promoting turbulence that the heavily silicified species require to remain in the photic zone (Rühland et al. 2003). The prolonged ice cover in lakes at high altitudes and latitudes impedes the development of planktonic diatom populations especially relative to the periphyton that benefits from the earlier ice melt near the shoreline (Smol 1983, 1988). Accordingly, the increased relative abundance of the *Aulacoseira* species during the productive periods is likely related to the lengthening of the open water period improving pelagic habitat and resource availability.

Apart from *Aulacoseira*, the diatom responses appeared to align most strongly with the pattern in sediment $\delta^{13}C$ values that carry signals of autochthonous production but also the millennial decline in terrestrial influence and coincident decline in benthic organic substrate. Most distinct responses were associated with the recent CHLa increase, especially during the latter half of the twentieth century (Fig. 6), whereas the more productive period during the first millennium CE and the subsequent decline in productivity associated with the LIA were only partly reflected in the diatom assemblages. Noticeably, the recent increases in highly motile species, including primarily *Nitzschia* but also the rare *Surirella* species, and the slightly motile *Chamaepinnularia* and *Nupela* species, coupled with a decline in moderately motile *Pinnularia* species are patterns shared by both study lakes (Figs. 3, 4), possibly related to improved resource availability but also to the development of new habitats, increased lake-water pH and predation. The distinct increases in attached low profile species over the twentieth century, despite their common association with unproductive conditions and firm bottom substrata (Hudon and Legendre 1987; Berthon et al. 2011; Lange et al. 2011), is also a pattern shared by the two lakes. Although periphyton are generally considered more sensitive to light than to nutrients (Cantonati and Lowe 2014), Vadeboncoeur et al. (2006) found that diatom species on firm substrate reacted to nutrient stimulus more readily than species inhabiting soft substrate (epipelon) as the latter have better access to nutrients in the interstitial waters of the biofilm. It is possible that the prolonged Neoglacial cooling opened new habitats for the low profile species that were then able to

take advantage of the improved resource availability associated with the recent warming.

Summary of Neoglacial ecosystem changes and biotic responses above and below the subarctic treeline

The shared pattern of declining organic levels and allochthony in the two shallow subarctic lakes agrees generally well with earlier Neoglacial sediment records from remote circumpolar Arctic lakes. In common, the differing characteristics of this change in the tundra lake and woodland lake, in terms of timing and magnitude, could be expected considering the differences in landscape context. In both lakes, the decline in benthic organic substrate had a marked, if not uniform, influence on the diatom flora underscoring the importance of substratum in directing benthic diatom-community development in shallow northern lakes. Both lakes showed an increase in low profile species indicating expansion of hard bottom habitats, but the species that declined underlined the differences in lake-ecosystem development above and below the treeline. We propose that the differences in prevailing underwater light regimes and allochthony between the two lakes may have contributed to their disparate responses on multiple levels. First, light levels and overall organic matter supply constrain the type of benthic organic substrate that was likely to have developed in the lakes before the decline in organic levels, promoting abundant aquatic plant growth in the tundra lake where the woodland lake likely hosted thick benthic microbial mats. Second, a decline in light-absorbing carbon constituents in the lake water is likely to have improved light availability in the dark woodland lake while increasing UV exposure in the tundra lake, though we could not differentiate the effect of light from that of the changing substrate here. Underwater light and benthic substratum are tightly interwoven and we propose that differentiating their role in controlling benthic (functional) diatom community composition will be an important step to enable more in-depth understanding of algal responses in shallow northern lakes. This could be accomplished by multifactor experiments combined with spatial and temporal investigations of diatom-trait distribution on different substrate along light (PAR and UV) gradients in natural systems.

Notably, the biotic and biogeochemical patterns associated with the known Neoglacial warm anomalies, intercepting the millennial cooling trend, did not characterize a system that was reverting back to its previous state, neither above nor below the treeline. Rather, the changes appeared superimposed on those initiated by Neoglacial cooling. Accordingly, the diatom responses during the past century were in many ways unique, especially in the tundra lake where the diatom assemblages did not show as conspicuous responses to the period of elevated primary production during the first millennium CE. In both lakes, sediment organic content rose sharply with the recent CHLa increase but the species that were associated with high organic levels earlier in the Neoglacial did not increase, aside from the slightly motile species that may have benefited from littoral plant growth. Remarkably, although the long-term cooling trend appeared to result in lowered allochthony in both lakes, our results provide no clear evidence of recent increases in terrestrial influence. This is in contrast to the hypothesis that the current warming will reinforce connectivity between land and lakes, as evidenced by the widespread browning trend in northern lakes (Kuhn and Butman 2021), albeit small increases in allochthonous inputs could be obscured by the sharp increase in primary productivity. Whether the changes in underwater-light regimes may have contributed to the unique recent diatom-community shifts cannot be affirmed without further investigation. All in all, we suspect that a number of environmental factors that often go hand-in-hand with changing lake productivity contributed to shaping the diatom communities during the warmer periods. Among them, increased lake-water pH and improved nutrient cycling may have been important but other drivers such as increased predation may have also played a part.

Our study suggests that a functional perspective, such as used here, can provide a useful complement to the traditional taxonomic approach, but also underlines the need for further study on live diatoms in natural environments to manage uncertainties related to the growth form and habitat associations of individual species in different lake types. Further testing and refinement of functional classes that effectively capture the most relevant niches in northern lake environments should also prove useful. The results indicate that diatom-growth forms are affected by multiple selective pressures that often interact and

can therefore result in apparently conflicting relationships between growth forms and environmental factors. For example, motile species declined in the woodland lake with lowering organic levels corroborating their role as an indicator of organic enrichment (Supplementary Figure 1); however, their responses in the tundra lake contradict this notion to some extent probably due to fundamental differences in the available benthic substrate (and light) in the lakes. Moreover, the motile species responded strongly and divergently to the productive periods particularly in the woodland lake and, whether related to lake-water pH or some other driver, this appeared to deviate from the responses within the motile functional group. Similarly, low profile species increased along with the decline in organic substrate over the Neoglacial in both lakes, as might be expected, yet their most distinct increase was associated with the past century despite the notable increase in benthic organic substrate. Despite the apparent complexity of diatom functional responses, we conclude that diatom growth forms can provide important information relevant for understanding the development of northern lake ecosystems under natural and human-induced climate variability, especially when employed within a multiproxy paleolimnological context. Combined with modern limnological approaches, which are needed to ascertain species' growth form and environmental associations, paleolimnological approaches can further provide an important means to assess whether trait-environment relationships extracted from spatial data sets and short-term observation persist over long time scales. Remarkably, whether evaluated from a functional or taxonomic perspective, the diatom-assemblage changes associated with the twentieth century in the two lakes were not pronounced compared to the overall variability during the Neoglacial, but they were still clearly distinct and may act as an early indicator of changes to come.

Author contributions MR, LN, HK and TL designed the study and aquired the research material. All authors contributed to sample and data analyses relating to diatoms (MR, SA), sediment chronologies (HK, CM-J, JPS), elemental and isotope

biogeochemistry (MR, LN, TP, HK) and spectral biogeochemistry (CM-J, JPS). MR wrote the manuscript which was reviewed by all authors.

Declarations

Conflict of interest The authors declare no conflict of interest.

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