ORIGINAL ARTICLE

WILEY | Freshwater Biology

Climate drivers of diatom distribution in shallow subarctic lakes

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Abstract

1. Global warming can induce profound changes to the functioning of northern freshwater ecosystems. Diatom (Bacillariophyceae) communities often provide early warning signs of associated ecological regime shifts, responding sensitively to alterations in underwater light climate, nutrient regimes, habitat availability and lake water acid–base balance. The underlying mechanisms are manifold and may be mediated via direct climate impact on the physical and chemical properties of lakes or via changes in the terrestrial environment and catchment-lake coupling.

2. To address catchment-mediated climate effects on diatom community composition, spatial diatom distribution in the surface sediments of 31 subarctic treeline lakes displaying a broad gradient in terrestrial dissolved organic matter (tDOM) was contrasted with limnological indices of light climate, nutrient availability and lake water pH. To evaluate direct and indirect climate impacts on the long-term development of benthic phototrophic communities at the subarctic treeline, fossil diatom assemblages in the sediments of a shallow oligotrophic lake were examined against established temperature variability and inferences of terrestrial influence over the past 600 years. The regional lake set was used to test local calibration models for reconstructing dissolved organic carbon as well as lake water pH that is a fundamental environmental determinant for diatom distribution and may echo temperature variability in dilute lakes.

3. Across the treeline, lake water pH imposed primary control over the benthic-dominated surface sediment diatom communities. The pH influence was connected to catchment geomorphology, soils and vegetation cover and, together with habitat controls, largely superseded tDOM impact on underwater light attenuation and nutrient levels. Similarly, temporal changes in diatom distribution in the sediment core appeared to be relatively little affected by tDOM variability. The species shifts were subtle yet occurred in distinct synchrony with centennial temperature fluctuations, attributed to changing length of the ice cover period and associated effects on lake water chemistry, nutrient regimes and physical habitats.

4. Our results suggest that diatom flora in shallow lakes at the subarctic Fennoscandian treeline may be comparatively resilient towards climate-driven

changes in terrestrial carbon and nutrient fluxes. Diatom communities in poorly buffered lakes may, however, be susceptible to catchment greening and changes in hydrology through effects on lake water acid–base balance. While diatom responses in the sediment sequence were subtle, the palaeolimnological record indicates that periphytic diatom communities in shallow oligotrophic subarctic lakes may be sensitive to the effects of global warming.

KEYWORDS
climate change, coloured dissolved organic carbon, diatoms, lake water pH, subarctic lakes

1 | INTRODUCTION

Remote lakes across northern regions are manifesting widespread changes in their ecological structure and functioning in response to anthropogenic climate change (Smol et al., 2005). Warming temperatures and altered hydrological conditions have induced changes to the length of the growing season, attenuation of solar radiation, mixing dynamics and nutrient regime in lake ecosystems, affecting resource and habitat availability for aquatic biota (Pienitz & Vincent, 2000; Prowse et al., 2006; Solomon et al., 2015). Other human-induced disturbances, such as atmospheric deposition of fertilising or acidifying compounds, may interact to transform even the most remote, seemingly undisturbed aquatic ecosystems (Battarbee, Charles, Bigler, Cumming, & Renberg, 2010; Holtgrieve et al., 2011). The biotic responses are often displayed most vividly at the base of the food web, yet the effects may cascade across all trophic levels (Karlsson et al., 2009; Smol et al., 2005).

Diatoms (Bacillariophyceae) constitute an important component in the phototrophic communities of high-latitude lakes and have proven an invaluable indicator of the ongoing global change for their wide distribution, taxonomic diversity and sensitivity to environmental change (Stevenson, Pan, & van Dam, 2010). In northern regions, lake ice regimes impose a particularly profound control over vital ecological constraints on diatom communities, and lengthening of the ice-free period under warming temperatures has had a marked impact on the structure and productivity of the algal communities (Prowse et al., 2006; Smol & Douglas, 2007). In particular, recent studies have focused on widespread biotic turnovers related to warming-induced changes in water column mixing and thermal structure, often displayed as a shift from small benthic and heavy tychoplanktonic diatom flora to small planktonic cyclotelloids (Boeff, Strock, & Saros, 2016; Rühland, Paterson, & Smol, 2015; Sorvari, Korhola, & Thompson, 2002). In shallow unproductive lakes, widely distributed across northern high latitudes (Rautio et al., 2011; Smol, 2016), planktonic growth is often inhibited and thus different responses may be expected. The autotrophic communities of shallow lakes are dominated by benthic life forms (Lim, Kwan, & Douglas, 2001; Rautio et al., 2011; Vadeboncoeur, Vander Zanden, & Lodge, 2002) that are particularly responsive to changes in underwater light climate (Karlsson et al., 2009; Vadeboncoeur, Peterson, Vander Zanden, & Kalff, 2008). While the periphyton are often considered

relatively insensitive to nutrients (e.g. Bonilla, Villeneuve, & Vincent, 2005; Daniels, Kling, & Giblin, 2015), a growing number of studies are suggesting that also nutrient forcing affects the productivity and composition of the benthic community (Hogan, McGowan, & Anderson, 2014; Lange, Liess, Piggott, Townsend, & Matthaei, 2011; Lepori & Robin, 2014). Habitat diversification under lengthening growing season is another potential key driver of change in periphytic diatom communities, as illustrated by studies from the High Arctic (Douglas, Smol, & Blake, 1994; Griffiths, Michelutti, Sugar, Douglas, & Smol, 2017). Another characteristic feature of small and shallow lakes is their tight connection with the terrestrial environment. The export of terrestrial dissolved organic matter (tDOM) from the catchment often governs both the availability of light and nutrients for autotrophic production in shallow oligotrophic lakes, restraining resource and habitat availability (Karlsson, Jonsson, & Jansson, 2005; Williamson et al., 2015). In addition to constraining light availability for photosynthesis, tDOM controls aquatic UV exposure (Nevalainen, Luoto, Rantala, Galkin, & Rautio, 2015; Pienitz & Vincent, 2000) that has been shown to induce species-specific responses in periphytic communities (Vinebrooke & Leavitt, 1996). Climate-induced changes in the terrestrial-aquatic coupling may therefore provide yet another control on the future development of benthic diatom flora in shallow northern lakes (Karlsson et al., 2009; Solomon et al., 2015).

In addition to resource and habitat controls, and coupled to them, lake water pH is a fundamental driver of diatom distribution in freshwaters (Battarbee et al., 2010; Hustedt, 1937–1939). Spatial variability in lake water pH is largely determined by local geology and hydrology (Kähkönen, 1996; Soininen & Weckström, 2009), yet pH values in a given water body may vary in reflection of lake ontogenetic processes, climate fluctuations or catchment disturbances. Where climate variability evokes a strong terrestrial response, changes in catchment alkalinity generation or the input organic acids from catchment vegetation and soils may induce changes to lake water pH and diatom communities. In dilute arctic and alpine lakes, pH variability may carry a climate signal as changes in the length of the ice-free season affect aquatic primary production as well as carbon speciation and efflux that regulate lake water acid–base balance (Finkelstein et al., 2014; Sommaruga-Wögrath et al., 1997; Wolfe, 2002). The relative importance of each of these environmental stressors on benthic diatom communities in shallow lakes in the subarctic

is poorly understood and necessitates consideration of multiple environmental parameters and their variability in space and time.

The aim of this study is to advance our understanding of the varied direct and indirect climate controls on benthic diatom community composition in shallow subarctic lakes. We first examine spatial diatom responses to key limnological gradients in 31 subarctic lakes spanning the Finnish treeline, with particular focus on catchment-lake coupling and terrestrial carbon and nutrients. The studied lakes display a broad gradient in tDOM (Rantala, Nevalainen, Rautio, Galkin, & Luoto, 2016), providing an analogue for catchment-mediated climate impact on the shallow lakes in the region. Our primary hypothesis is that the composition of the surface sediment diatom assemblages is affected by the strong gradients in light-absorbing terrestrial organic carbon and nutrients, inducing selective pressures on the periphytic community and favouring species with opportune ecological traits. We then explore temporal changes in benthic diatom assemblages in the sediments of a shallow oligotrophic lake, with a focus on the effects of late neoglacial temperature variability and associated changes in the physical and chemical characteristics of the lake as well as catchment-lake coupling. The surface sediment diatom assemblages are used to test local inference models for dissolved organic carbon (DOC) and for lake water pH that may be coupled with temperature variability in dilute lakes (Wolfe, 2002). We expect that the centennial climate fluctuations have affected the composition of the benthic diatom communities, linked to temperature-driven changes in tDOM flux or to direct temperature effects on the length of the ice cover period and related changes in lake water chemistry, nutrient cycling and habitat availability.

2 | METHODS

2.1 | Regional setting

The 31 study lakes are situated in northern Finland (68–70°N) extending from the northernmost limit of boreal coniferous forest to the treeless tundra (Figure 1). The lakes encompass a gradient from highly transparent oligotrophic tundra lakes to strongly coloured mesotrophic lakes receiving humic organic matter from surrounding wetlands. Most of the lakes are polymictic and shallow closed basins with clear, circumneutral to alkaline waters (Table 1) characteristic of lakes in northern Fennoscandia (Korhola & Weckström, 2004). Climate in the region is subarctic with both maritime and continental influence. Mean annual air temperature is approximately −2°C and mean July air temperature 13°C. Lakes in the region are typically at least partially covered in ice from 7 to 9 months a year (Korhola & Weckström, 2004). The lakes lie atop the Lapland granulite belt with granite gneisses in the northeastern corner of the study area. The lakes are subjected to very few or no direct human disturbances. The lake used for the temporal study, Lake Námmájávri, is situated in a sheltered valley in the tundra region near the northern edge of the study area (69°5′N, 26.6′E). The lake is small and shallow, characterised by clear, oligotrophic, alkaline water (Table 1). The

catchment area is large (900 ha) and topographically diverse, dominated by treeless shrub tundra and bedrock outcrops. The immediate surroundings of the open basin are characterised by relatively lush mountain birch groves and the input stream is surrounded by water-logged soils. Detailed description of catchment characteristics, limnological properties and sediment geochemistry of the regional lake set are provided in a previous study (Rantala, Nevalainen, et al., 2016) that examined landscape controls on the limnology and carbon biogeochemistry of the lakes, and the coupling between lake water characteristics and surface sediment geochemistry. More information on Lake Námmájávri is presented in Rantala, Luoto, and Nevalainen (2016).

2.2 | Analytical methods

Samples for diatom analysis were prepared from freeze-dried sediments following standard procedures (Battarbee et al., 2001). Organic matter was removed by oxidising sediment samples with 30% hydrogen peroxide solution in a hot water bath. Where required, coarse minerogenic matter was removed physically by swirling the sample solution in a beaker and decanting the diatom suspension. Samples were dried on coverslips and mounted with Naphrax® (Brunel Microscopes Ltd, Wiltshire, U.K.). Diatoms were enumerated under a light microscope at $1,000\times$ magnification, setting the minimum counting sum for the surface sediment samples at 400 diatom valves. From four lakes (#5, 10, 11, 25) with scarce diatom valves and low diversity, 200–300 valves were identified. For the temporal sediment profile, a minimum of 300 diatom valves were identified from each sample. Taxonomic determination was mainly based on the flora of Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), with nomenclature updated where relevant (Table 2). Methods for determining catchment characteristics, limnological properties and sediment geochemical parameters in the regional lake set are described in Rantala, Nevalainen, et al. (2016), and biogeochemical analyses, chronological methods and Chironomidae-based mean July air temperature reconstruction for Lake Námmájávri are presented in Rantala, Luoto, et al. (2016).

2.3 | Numerical methods

Ordination analyses were employed to examine spatial variation in diatom community composition across limnological gradients. Initial detrended correspondence analysis (DCA) was performed to assess diatom responses in the surface sediments. The obtained gradient length implied high species turnover between the surface sediment assemblages (3.1 SD units) and therefore unimodal canonical correspondence analysis (CCA) was deemed suitable for further analyses. Owing to high collinearity between various limnological characteristics (Rantala, Nevalainen, et al., 2016), CCAs were performed individually on each environmental parameter to first select variables that most strongly contribute to diatom distribution in the lakes. Of variables connected to nutrients, total nitrogen (explained variation 5.7%) was selected over total phosphorus (4.3%). A variety of
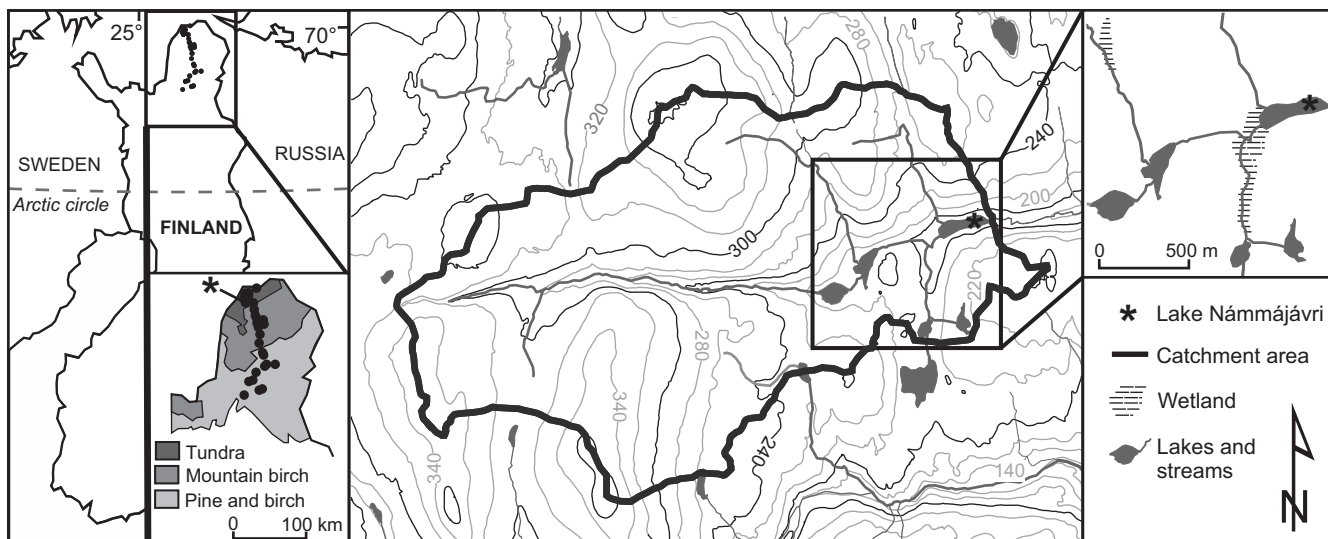
FIGURE 1 Location of the regional lake set (68–70°N) and Lake Námmájávri (69°5′N, 26.6′E) in northern Finland

TABLE 1 Summary of limnological characteristics of the regional lakes (N = 31) and Lake Námmájávri in northern Finland. Methods for obtaining the data are described in Rantala, Nevalainen, et al. (2016)

	Regional lake set				
	Mean	Median	Min	Max	Námmájávri
Lake water pH (units)	7.1	7.1	5.1	8.4	7.8
Dissolved organic carbon (mg L^{-1})	5.2	4.0	1.7	16.6	1.8
Absorbance at 320 nm (m^{-1})	8.9	6.1	1.1	34.9	4.0
Specific UV absorbance (mg C L^{-1} m^{-1})	1.9	2.0	0.7	3.2	2.4
Fluorescence index (ratio)	1.3	1.3	1.2	1.6	1.2
Total nitrogen, unfiltered (µg L^{-1})	416	338	138	806	138
Total phosphorus, unfiltered (µg L^{-1})	9.3	7.3	4.7	24.1	5.9
Chlorophyll-a (µg L^{-1})	1.8	1.4	0.2	6.1	0.6
Depth (m)	2.7	2.0	0.3	7.5	1.7

spectrophotometric and spectrofluorometric parameters were used to describe variability in tDOM influence (for details refer to Rantala, Nevalainen, et al., 2016), including specific UV absorbance (5.2%), absorption coefficient at 320 nm (3.4%), fluorescence index (4.7%) and the intensities of terrestrial humic fluorescence components differentiated using parallel factor analysis of excitation-emission matrices (3.1%). Of the spectral carbon indices, specific UV absorbance (SUVA) was subsequently selected. DOC (4.5%) was strongly correlated both with indices of tDOM and nutrients, yet was not deemed redundant based on variance inflation factors (cut-off value 20) and was thus included as an explanatory variable. In addition, lake water pH (11.6%) and water column depth (6.0%) were included in the

analyses. Taxa present in two or more lakes or having a relative abundance of ≥1% in at least one lake were included in the numerical analyses, and diatom relative abundance data were square root transformed to stabilise variance between lakes. The deepest lakes (>5 m, N = 4), displaying clearly anomalous diatom flora relative to the shallower sites, were omitted from the final CCA as other physical processes such as light attenuation with increasing depth may confound the effects of terrestrial carbon and nutrients. To display species distribution across environmental gradients, an additional CCA was performed including only the most common taxa (N ≥ 15, max ≥ 3%) or genera (where individual species abundances were low but all species under the genus showed uniform patterns in their distribution). Monte Carlo permutation tests with 999 permutations were used to assess significance of the primary ordination axis and overall models. Downweighting of rare species was applied in the unimodal ordination analyses apart from the initial DCA used to extract gradient lengths. Prior to the ordination analyses, Shapiro–Wilk normality (α = .05) and skewness (targeted below ±0.1) were tested for each environmental variable. Log_{10} transformations were performed where appropriate. The ordination analyses were carried out using CANOCO 5 (Šmilauer & Lepš, 2014).

The surface sediment assemblages were used to test local DOC and pH inference models for temporal reconstructions. Similar to the ordination analyses, taxa present in two or more lakes or having a relative abundance of ≥1% in at least one lake were included in the models. Simple weighted averaging (WA) based models were preferred over more complex mode types, and Lake Námmájávri was removed to avoid bias in the reconstructions. The reduced number of counts in four of the lakes should be sufficient for WA models (Bennett, Rühland, & Smol, 2016) and the lakes were also included in the model. PCA was used to compare the reconstructed values with the distribution of the diatom taxa along the primary ordination axis. The transfer functions and reconstructions were developed using the program C2 (Juggins, 2003).

TABLE 2 List of most common ($N \geq 15$, max $\geq 3\%$) taxa in the regional lake set, with abbreviations (Figure 3b), number of occurrences, mean and maximum relative abundances, Hill's N2 and weighted averaging (WA) optima for pH

Taxon	Basionym	Abbreviations	N	Mean	Max	Hill's N2	pH WA
Tabellaria cf. *flocculosa* (Roth) Kützing		TabFlo	26	1.4	9.0	10.1	6.8
Pinnularia cf. *viridis* (Nitzsch) Ehrenberg		PinVir	25	1.9	8.7	13.9	7.2
Pinnularia abaujensis (Pantocsek) Ross		PinAba	24	0.7	4.0	10.8	7.1
Pinnularia rupestris Hantzsch		PinRup	21	0.9	7.4	8.0	6.8
Encyonopsis cesatii (Rabenh.) Krammer	*Cymbella cesatii* (Rabenh.) Grun. ex A.S.	EncCes	17	1.5	5.8	12.5	7.5
Encyonopsis descripta (Hustedt) Krammer	*Cymbella descripta* (Hustedt) Krammer & Lange-Bertalot	EncDes	19	1.1	5.3	12.6	7.5
Encyonema lunatum (Smith) V. H.	*Cymbella lunata* W. Sm.	EncLun	26	1.3	6.4	15.0	7.3
Encyonopsis microcephala (Grunow) Krammer	*Cymbella microcephala* Grunow	EncMic	19	0.8	3.8	10.4	7.7
Eunotia faba Ehrenberg		EunFab	15	1.0	14.4	3.5	6.9
Eunotia praerupta Ehrenberg		EunPra	22	0.7	5.3	9.6	7.2
Eunotia exigua (Bréb. ex Kütz.) Rabenh.		EunExi	18	0.8	3.8	11.1	6.6
Brachysira brebissonii Ross		BraBre	29	5.7	20.2	17.9	7.2
Brachysira vitrea (Grunow) Ross		BraVit	29	6.5	23.9	14.9	7.3
Frustulia rhomboides var. *saxonica* f. *undulata* Hustedt		FrsRhmUn	26	5.4	20.1	15.5	7.0
Frustulia rhomboides var. *saxonica* (Rabenh.) De Toni		FrsRhmSx	27	7.7	27.2	16.2	6.9
Navicula radiosa Kützing		NavRad	21	0.9	3.8	13.3	7.5
Chamaepinnularia mediocris (Krasske) Lange-Bertalot	*Navicula mediocris* Krasske	ChaMed	21	0.8	4.1	10.7	7.1
Kobayasiella subtilissima (Cleve) Lange-Bertalot	*Navicula subtilissima* Cleve	KobSub	30	6.6	50.5	8.7	6.7
Achnanthidium minutissimum (Kützing) Czarnecki	*Achnanthes minutissima* Kützing	AchMin	23	3.0	8.1	16.6	7.4
Eucocconeis flexella (Kütz.) P.T. Cleve	*Achnanthes flexella* (Kützing) Brun	EucFle	18	0.5	3.9	6.8	7.6
Stauroforma exiguiformis Flower, Jones, Round	*Fragilaria exigua* Grunow	StaExi	18	6.2	34.6	10.2	7.2

3 | RESULTS

3.1 | Diatom distribution across the treeline

A total of 177 taxa, representing 25 genera, were identified from the surface sediments of the regional lake set. Benthic life forms dominated the communities, whereas centric species were sparse and primarily restricted to lakes with depths exceeding 3 m. Taxa encountered in more than half of the lakes with a mean relative abundance of >1% include *Kobayasiella subtilissima* (30 lakes), *Brachysira brebissonii* (29) *Brachysira vitrea* (29), *Frustulia rhomboides* var. *saxonica* (27), *F. rhomboides* var. *saxonica* f. *undulata* (26), *Encyonema lunatum* (26), *Encyonopsis descripta* (19), *Encyonopsis cesatii* (17), *Achnanthidium minutissimum* (23), *Pinnularia* cf. *viridis* (26) and *Tabellaria* cf. *flocculosa* (26). The most common taxa are shown in Figure 2 and Table 2.

Of the limnological variables examined, ordination analyses distinguished lake water pH as the most important driver of diatom community composition in the regional lake set (Figure 3a). The secondary environmental gradient describing diatom distribution was connected to the concentrations of total nitrogen and DOC (Figure 3a), although individual CCAs suggested relatively low explanatory power for both variables. The two variables were strongly correlated in the lake set ($r = .83$, $p < .001$), though only total

nitrogen was close to significant ($p = .05$) in explaining variation in the diatom community composition based on the individual CCAs. Total phosphorus had an effect similar to total nitrogen, whereas the indices of carbon quality showed generally very little relationship with diatom distribution based on the CCAs. Lake water pH was not significantly correlated with any of the carbon indices but showed a negative correlation with total nitrogen ($r = -.40$, $p < .05$). Overall, the selected environmental variables explained 29.5% of variation in the diatom assemblages, with eigenvalues of 0.29 and 0.11 for the primary and secondary axes respectively. The range of variability in pH and other limnological variables for the lake set are presented in Table 1.

A few distinct patterns were observed in the distribution of the lakes and diatom taxa along environmental gradients based on the CCAs and visual scrutiny of the data. A group of very shallow lakes situated in the treeless tundra ecotone (#25, 28 and 34), with circumneutral to acidic waters (pH from 5.6 to 7.1), were distinguished with high values for both axes. The lakes were dominated by few species of *Frustulia* (*F. rhomboides* var. *saxonica*, and *F. rhomboides* var. *saxonica* f. *undulata*), *Eunotia* (*E. faba*, *E. praerupta*, *E. diodon*, *E. monodon* as the most abundant) and *Pinnularia* (*P.* cf. *viridis*). The rest of the lakes across vegetation gradients, including strongly coloured wetland lakes with distinctly elevated concentrations of coloured dissolved organic matter (CDOM) and mesotrophic waters
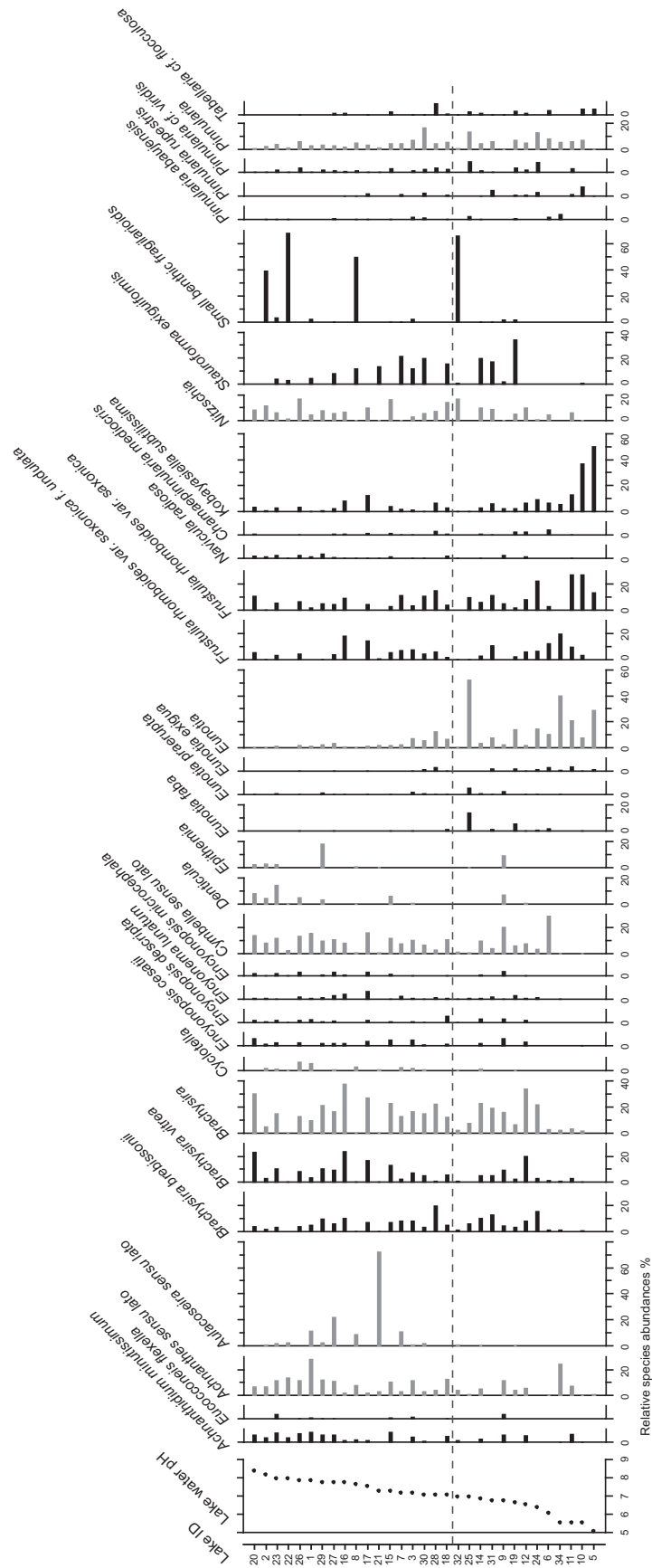
FIGURE 2 Lake water pH and the relative abundances of the most common (N ≥ 15, max ≥ 3%) taxa in the 31 lakes in northern Finland. Grey bars represent the combined abundance of all taxa under the genus. Lakes above and below pH 7 are divided by a dotted line

(#14, 15, 18, 19), displayed more consistent values along the axes. A few lakes in the forested zone (#5, 10 and 11), characterised by acidic waters (pH ≤ 5.6) and more or less elevated nutrient and DOC concentrations, were additionally distinguished in the ordination space with high and low values for axes 1 and 2 respectively. The species assemblages were dominated by few taxa of *Frustulia* (*F. rhomboides* var. *saxonica*), *Eunotia* (*E. triodon, E. bilunaris, E. bactriana* as the most abundant) and *K. subtilissima*. A few general patterns were further observed in the distribution of the species across the primary environmental gradient (Figures 2 and 3b). *Epithemia* (mostly *E. sorex* and *E. argus*) and *Denticula* (*D. tenuis, D. kuetzingii*) were primarily affiliated with alkaline waters in the studied lake set. In contrast, species of the genus *Eunotia* as well as *K. subtilissima* were associated with the acidic sites. Fragilarioids were found in high abundance in a few lakes, often forming characteristic long chains. To avoid false identification, all cells of small-sized fragilarioids (comprising mostly *Staurosirella pinnata* and *Staurosira construens*) present in girdle view in the samples were grouped together. All fragilarioids were absent from the most acidic lakes, and were primarily found in high abundance in deeper oligotrophic lakes and in shallow lakes with high CDOM concentrations. Overall, fragilarioids were restricted to lakes with either depth ≥3.5 m or CDOM (measured as a_{320}) ≥7.6 m^{-1}. Only the former relationship was displayed in the CCA (Figure 3b) as the concentrations of terrestrial carbon and depth were negatively correlated in the lake set (Rantala, Nevalainen, et al., 2016).

3.2 | Centennial variability in diatom assemblages and lake water pH

From Lake Námmájávri 129 diatom taxa from 23 genera were identified. The dominant taxa in the lake, present in all samples with a mean relative abundance of >3%, comprise *A. minutissimum, Rossithidium pusillum, B. brebissonii, B. vitrea, E. descripta, D. kuetzingii, F. rhomboides* var. *saxonica* and *Nitzschia fonticola* (Figure 4). Overall variability in the species assemblages was small in scale, yet a few patterns could be detected. A distinct increase was observed in *Epithemia* (*E. sorex, E. argus*) and *Denticula* (*D. tenuis, D. kuetzingii*) over the 20th century. Concurrently, a number of species of the genus *Cymbella* sensu lato (*E. cesatii, E. silesiacum, C. helvetica, C. cistula*) were found in higher frequency and abundance. In contrast, several species of *Achnanthes* sensu lato and *Fragilaria* sensu lato together with *B. brebissonii* var. *borealis* and *N. fonticola* showed lower relative abundances during the 20th century. *Pinnularia abujensis* var. *linearis, P. biceps* and *Fragilaria* sensu lato displayed elevated relative abundances between c. 1700 and 1900 C.E.

Lake water DOC yielded a very weak species-environment relationship (best inference model r^2_{jack} = 0.10) and changes in terrestrial influence were thus considered qualitatively based on biogeochemical data described in detail in Rantala, Luoto, et al. (2016). For lake water pH, the WA model using classical deshrinking had a cross-validated (jackknifing) r^2 of 0.70, maximum bias of 0.54 and root mean square error of prediction (RMSEP) of 0.47. The
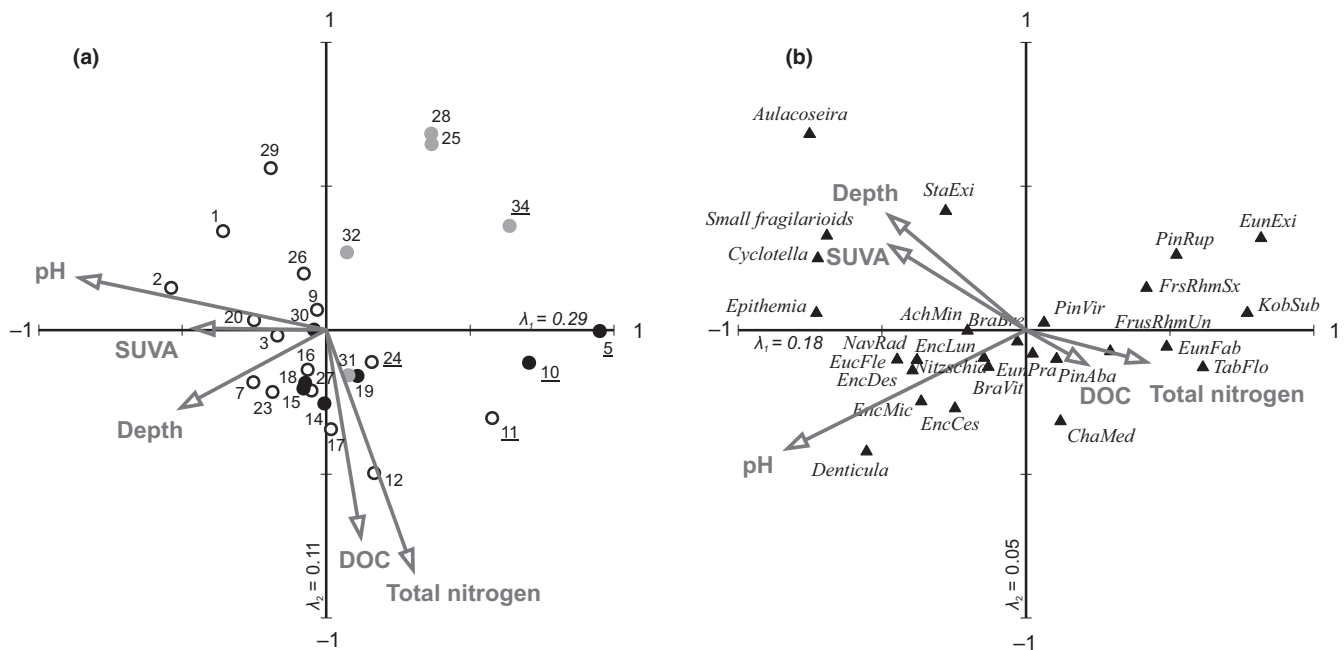

FIGURE 3 Canonical correspondence analysis biplots based on surface sediment diatom assemblages displaying (a) the distribution of lakes (circles) across environmental gradients (arrows) and (b) relationships between the most abundant taxa (triangles) and environmental variables (arrows) in northern Finland. Full taxon names are provided in Table 2. For (a) taxa present in at least two lakes with a relative abundance of 1% in at least one lake were included, for (b) only the most common taxa, present in at least half of the lakes (N ≥ 15) with a relative abundance of 3% in at least one lake, were included. Mesotrophic lakes (chlorophyll-*a* >2.6 μg/L) are indicated with black circles, lakes in the treeless tundra with grey circles and the rest of the oligotrophic lakes across vegetation gradients with white circles. Lakes with pH ≤6.5 are underlined

principal environmental gradient obtained from the PCA was strongly correlated with the inferred pH variability ($r^2 = 0.61$, $p < .001$), implying that diatoms were responding to the inferred variable. Measured and diatom-inferred pH values in the 29-lake calibration data set further showed good correspondence (Figure 5). Based on the residual plot, lake #9 was omitted from the final model as an outlier. The distinction of the lake may be related to elevated conductivity (based on crude field measurements) which could be related to salting of a nearby road. The reconstructed pH value for the topmost sample (pH 8.0) was slightly higher than the present measured value (pH 7.8) yet well within the model's RMSEP of 0.47. The most distinct features in the pH reconstruction for Lake Námmájávri were consistently low values between c. 1700 and 1900 C.E., and a subsequent distinct increase towards the surface (Figure 6).

4 | DISCUSSION

4.1 | Terrestrial influence on diatom distribution across the treeline

Climate impact on freshwater ecosystems is often mediated through altered coupling between the terrestrial and the aquatic environment (Leavitt et al., 2009; Solomon et al., 2015). Changes in catchment-lake interaction, linked to warming temperatures or altered hydrology, have the potential to induce marked changes to the physical and chemical properties of lakes, affecting vital ecological conditions for biota (Karlsson et al., 2005, 2009; Williamson

et al., 2015). In the shallow lakes of the studied region, terrestrial inputs exert primary control over solar radiation attenuation and nutrient regimes (Nevalainen et al., 2015; Rantala, Nevalainen, et al., 2016) that constitute fundamental constraints on diatom growth. The lack of clear-cut patterns in diatom assemblages along the gradient of terrestrial coloured organic carbon in part contradicts the established paradigm of the importance of light for periphytic growth in shallow oligotrophic lakes (Karlsson et al., 2005, 2009; Vadeboncoeur et al., 2008), yet is not entirely unexpected. The concentrations of DOC or total organic carbon, most commonly measured in spatial surveys, often arise as significant though more rarely as primary environmental determinants of diatom distribution (Antoniades, Douglas, Michelutti, & Smol, 2014; Gregory-Eaves, Smol, Finney, Lean, & Edwards, 2000; Rühland, Smol, & Pienitz, 2003; Weckström & Korhola, 2001). As yet, few studies have attempted to relate diatom community composition with indices of carbon quality that provide a more direct correlate of DOC functionality in lakes, particularly with regard to light attenuation. A conspicuous feature in the species assemblages potentially linked to increased shading by CDOM was the elevated relative abundance of fragilarioids in shallow strongly coloured lakes, as in deeper oligotrophic lakes, which could be partly related to their ability to withstand low light conditions (Anderson, 2000; Lotter, Pienitz, & Schmidt, 2010). Predominantly, however, the shallow waters appear to allow sufficient light penetration for benthic diatom flora in the lakes. Furthermore, the effect of terrestrial organic carbon in lakes is coupled to, and may
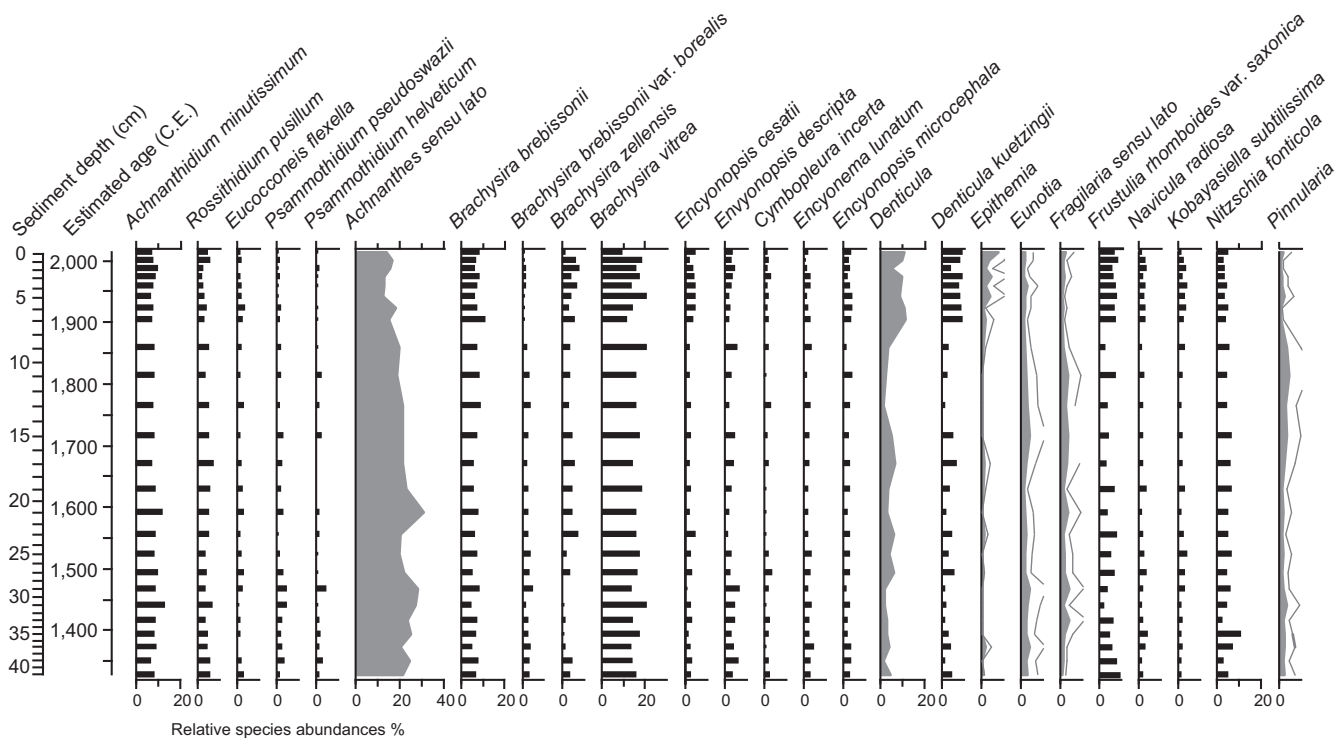

FIGURE 4 Relative abundances (%) of the most common ($N \geq 20$, max $\geq 3\%$) diatom taxa in Lake Námmájávri. Grey silhouettes represent the combined abundance of all taxa under the genus
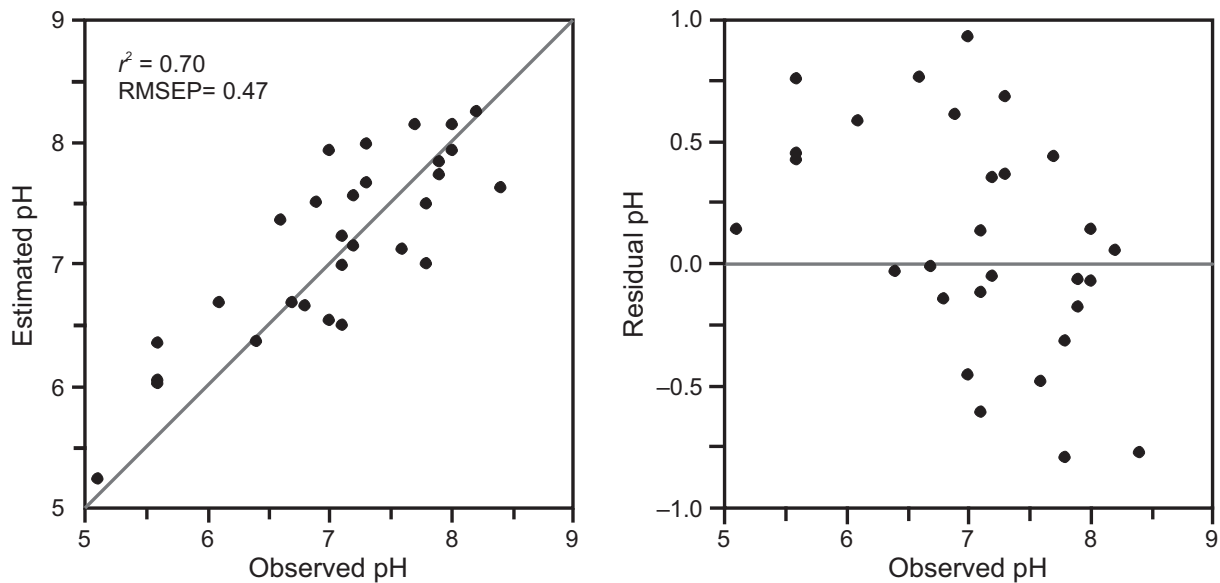
FIGURE 5 Diatom-inferred pH against measured values of lake water pH in the 29-lake calibration set in northern Finland and the distribution of residuals based on weighted averaging regression using classical deshrinking and jackknife cross-validation
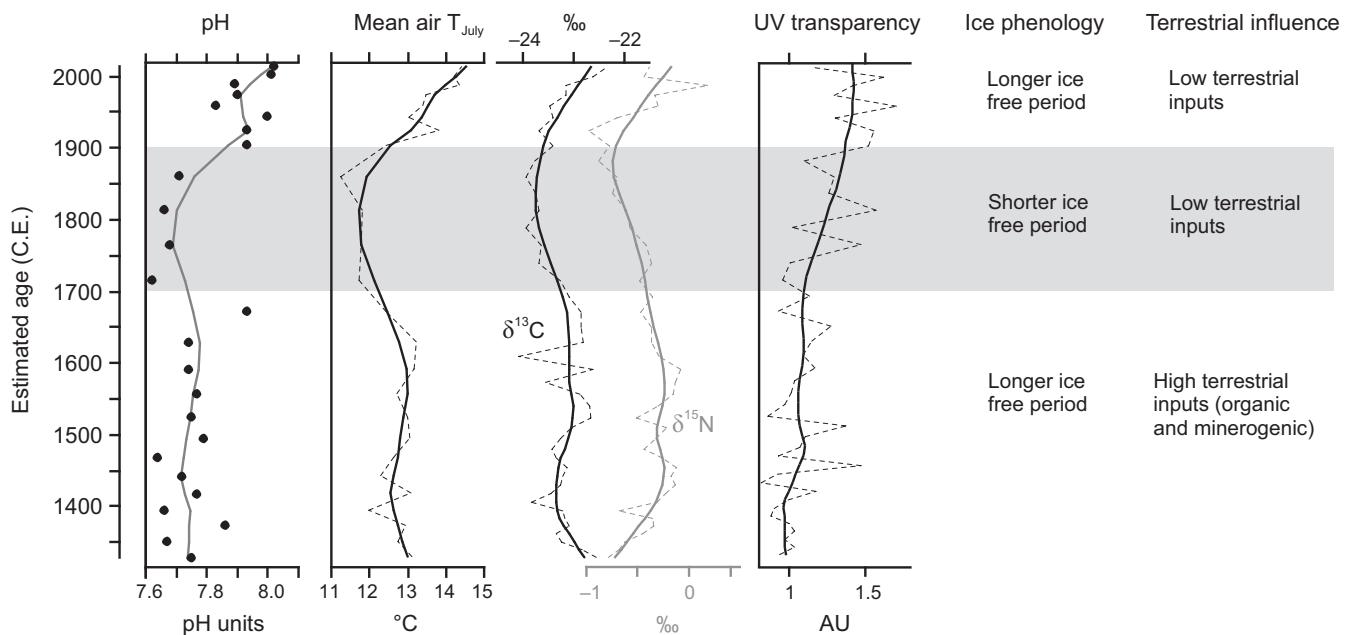

FIGURE 6 Diatom-inferred lake water pH in Lake Námmájávri sediment core, displayed with chironomid-inferred mean July air temperature, carbon and nitrogen stable isotope signature in sediment, and UV transparency (as absorbance units, AU) based on UV absorbances in benthic Cladocera published originally in Rantala, Luoto, et al. (2016). Inferences of temporal patterns in the length of the ice cover period and terrestrial influence are presented. Thick lines represent locally weighted scatter plot smooths (span 0.3) and the grey-shaded area marks the coolest period of the Little Ice Age

be overridden by, other vital environmental preconditions, such as nutrient and habitat availability or lake water pH.

In concert with our data analyses (Figure 3a), limnological surveys on subarctic lakes at the Canadian treeline (Gregory-Eaves et al., 2000; Rühland et al., 2003) and in the High Arctic (Bouchard, Gajewski, & Hamilton, 2004; Lim, Douglas, & Smol, 2001) have

identified nutrients, and particularly total nitrogen, as important determinants of diatom distribution. In the more northerly sites, the connection has been associated particularly to moss habitats (Lim, Kwan, et al., 2001) and more lush arctic regions (Keatley, Douglas, & Smol, 2008) likely attributable to overriding influence of physical constraints in more extreme polar environments. The result also

agrees with previous works on northern Fennoscandian lakes (Karlsson et al., 2005; Seekell et al., 2015) indicating that in shallow waters the benefit of increased nutrients overweighs the effect of increased light limitation by coloured organic carbon on primary production. Accordingly, pelagic algal production (indicated by chlorophyll-*a*), was shown to increase with tDOM in the present lake set (Rantala, Nevalainen, et al., 2016) across the gradients of DOC and CDOM (Table 1). In the benthic diatom communities, however, no specific taxa were distinctly affiliated with high nutrient status, which may indicate confounding or overriding influence of yet other environmental parameters. In effect, we suspect that the nutrient gradient distinguished by the data analyses may in part be an artefact driven by lake water pH. Species assemblages in the few lakes in the forested region and in the treeless tundra, distinguished at the opposite ends of the secondary CCA gradient linked to nutrients (Figure 3a) and dominated by few taxa of *Frustulia*, *Eunotia* and *Pinnularia* (Figures 2 and 3b), resemble those commonly associated with low pH (Beaudoin, Pienitz, Francus, Zdanowicz, & St-Onge, 2016; Korhola, Weckström, & Nyman, 1999; Weckström, Korhola, & Blom, 1997). The lakes were acidic (pH < 5.6) aside from two of the tundra lakes (#25, #28) that displayed neutral pH values upon measurement. However, pH may undergo large diurnal and seasonal variations and the one time measurement (summer daytime) likely represents the higher extreme. Although pH appears as the most likely driver of diatom community composition in these distinct lakes, mesotrophic lakes were nevertheless generally distinguished from clear and oligotrophic lakes in the ordination space (Figure 3a), which lends some support to the importance of nutrients in controlling diatom distribution in these shallow subarctic lakes.

Overall, our results underscore the paramount importance of lake water pH for freshwater diatoms (Figure 3a). Earlier surveys from northern Finland have similarly highlighted the importance of pH and related water chemistry variables, such as alkalinity and conductivity, for diatom community composition (Albert, Sorvari, & Korhola, 2009; Soininen & Weckström, 2009; Weckström et al., 1997). Majority of the studied lakes had circumneutral to alkaline waters (11 lakes exceeding pH 7.5) likely attributable to bedrock composition in the region. The acidic sites displayed consistent landscape features commonly linked to poor buffering ability. The lakes were primarily characterised by small catchment areas where the small reserve of exchangeable base cations often results in lowered acid-neutralising capacity (Houle, Ouimet, Couture, & Gagnon, 2011; Kähkönen, 1996). A couple of the lakes were further situated within or in the proximity of eolian or glaciofluvial deposits (Rantala, Nevalainen, et al., 2016) in which the sandy soils, with characteristic low cation exchange capacity, may partly account for the lowered buffering ability. The rest of the low pH lakes lay in catchments with very little vegetation and soils to retain rainwater acidity. Aside from the prevalence of neutral to acidic waters in the treeless tundra, we discerned no consistent patterns in lake water pH along the latitudinal vegetation transition from coniferous forest to tundra, nor along the wetland gradient, emphasising the role of local catchment characteristics. Wetland cover had a pronounced influence on carbon

geochemistry and nutrient concentrations in the lakes (Rantala, Nevalainen, et al., 2016), however, wetlands in the region comprise mostly minerotrophic fens that are generally characterised by neutral to alkaline waters, which likely explains their low influence on lake water acidity.

The acidic lakes were mostly characterised by low values of SUVA (Figure 3a) indicating low contribution of terrestrial aromatic organic compounds in the lake water (Weishaar et al., 2003). While the data thus do not allow the assessment of potential effects of the CDOM gradient on diatom distribution in the poorly buffered sites, the results may provide some insights into the interrelationship between lake water pH and coloured organic carbon in lake water. The low availability of high molecular weight organic carbon in the lakes with low pH may partially be attributable to the scarcity of organic substrate in the catchments, yet also other mechanisms related to biogeochemical processing of DOM in lake water as well as catchment hydrology may explain the connection. For one, increasing acidity tends to reduce the aromaticity of organic molecules, lowering their light absorption capacity while making them less labile to photochemical mineralisation (Pace et al., 2012). In addition, coagulation and flocculation of aromatic DOM in low pH could contribute to increased transparency. Both processes may in part explain elevated sediment organic content in majority of the acidic lakes, demonstrated also as a strong negative correlation between lake water pH and weight percent of sediment carbon, nitrogen and bulk organic matter in the studied lakes (all pairwise correlations $r > -.60$, $p < .001$). In addition, the elevated nutrients and productivity in many of the acidic lakes situated in sandy soils may also partly explain the high organic content of the sediments. The combination of high nutrients and low CDOM in these lakes was partly presumed to reflect higher contribution of groundwater discharge carrying waters rich in nutrients relative to terrestrial coloured organic carbon (Rantala, Nevalainen, et al., 2016). The connections between lake water pH and aquatic organic carbon pools have also implications for the mineralisation and burial of tDOM in lakes, and therefore on aquatic carbon balance (Pace et al., 2012).

A hierarchy of environmental controls govern the distribution of diatoms in freshwaters. Often the availability of physical habitats may superimpose the effects of resource availability and lake water chemistry, and may be considered of particular importance for periphytic taxa that dwell on diverse bottom substrate. Some species may be restricted to specific microhabitats, whereas many display a more diverse distribution with an affinity for particular substrate type, such as aquatic plants, rock surfaces or sediment grains (Lim, Kwan, et al., 2001; Michelutti, Holtham, Douglas, & Smol, 2003). Majority of the shallow lakes were characterised by rich benthic growth (e.g. benthic mats, aquatic mosses and macrophytes) providing diverse microhabitats for periphytic diatoms. The most numerous and frequent taxa of *Brachysira* and *Frustulia* (Figure 2) are common in lakes across boreal and subarctic regions, being often associated with circumneutral to slightly acidic waters, low conductivity and dystrophic environments (Beaudoin et al., 2016; Weckström & Korhola, 2001). Their high relative abundance in the studied lakes that

were characterised mostly by relatively alkaline and clear waters denotes their cosmopolitan nature, but could also partly reflect abundance of moss habitats (Beaudoin et al., 2016) in the littoral and riverine marshes around the lakes (Rantala, Nevalainen, et al., 2016). Species under the genus *Cymbella* sensu lato are common epiphytes, yet the dominant taxa in the lakes (Figure 2) have been shown to occupy diverse habitats (Lim, Kwan, et al., 2001; Michelutti et al., 2003) and were similarly widespread in the studied lakes showing few directional changes along the examined environmental gradients. The near absence of cymbelloids in the most acidic (pH ≤ 5.6) lakes and their low presence in the most barren lakes in the treeless tundra (Figures 2 and 3b) may in part be explained by narrowed habitat availability (Bouchard et al., 2004) as many of the lakes were characterised by sandy or rocky bottoms. However, it could also indicate low tolerance for strongly acidic waters, or nutrient deprivation in the tundra lakes. The abundant *E. cesatii*, and *E. microcephala*, for instance have been previously associated with high nutrients and pH in arctic and subarctic lakes (Keatley et al., 2008; Lim, Kwan, et al., 2001; Rühland et al., 2003).

4.2 | Implications on diatom resilience to increasing terrestrial influence

Temperatures particularly during wintertime have been and are projected to continue increasing in Finland and across northern Fennoscandia under the ongoing climate change (ACIA, 2004; Ruosteenoja, Jylhä, & Kämäräinen, 2016). While associated effects on terrestrial vegetation development and catchment-lake coupling remain uncertain, warming climate has the potential to increase terrestrial influence on subarctic freshwater ecosystems through the poleward advance of vegetation zones (Finstad et al., 2016; Larsen, Andersen, & Hessen, 2011) or through increasing wetland influence (Freeman et al., 2004), the latter identified as a primary control over the limnology of the studied lakes (Rantala, Nevalainen, et al., 2016). The present results suggest that, under such scenario, diatom flora in shallow lakes in the region may be relatively resilient to associated increase in light attenuation by coloured DOC, as suggested by the apparent stability of the *Brachysira-Frustulia-Cymbella* dominated periphytic community across the gradient of terrestrial carbon encompassed by the lakes (Table 1). The results do not contradict earlier studies displaying distinct transitions in limnology and diatom communities across the subarctic treeline (e.g. Gregory-Eaves et al., 2000; Rühland et al., 2003), or indicate insignificance of organic carbon for diatom distribution, but rather imply that in certain settings, or at certain spatial scales, other environmental attributes may superimpose their influence. In this study, the shallow waters inherently counteract the shading effect of CDOM, and the effects of increased light attenuation may further be overridden by the parallel nutrient impact, although associated effects on diatom distribution were difficult to pinpoint. Finally, the high availability and diversity of physical habitats in these shallow subarctic lakes could potentially stabilise diatom responses to resource (light, nutrients) variability.

Although we could not evaluate the effects of terrestrial influence on the poorly buffered sites owing to their short tDOM gradient, the results carry some implications on catchment-mediated climate impact on the diatom flora. Poor buffering capacity was partly attributed to time-invariant catchment properties such as catchment area, but also to catchment vegetation and soils/hydrology that are prone to change under warming climate. Diatom communities particularly in lakes in the barren tundra may respond sensitively to climate-induced greening of the catchment that may enhance buffering capacity as well as improve nutrient availability. The acidic lakes in the forested region, characterised by catchments rich in sandy soils, may respond to changes in catchment flow pathways that controls acid–base balance, carbon biogeochemistry and nutrient concentrations in the lake water. Generally, increased diversity of organic substrate may allow the establishment of a more diverse benthic flora in the lakes.

4.3 | Diatom responses to centennial temperature variability

Growing number of studies across northern regions are evidencing widespread regime shifts in diatom communities in response to the ongoing warming, connected to the lengthening of the growing season and often initiated at around the mid-19th century (Smol et al., 2005). The proposed mechanisms are diverse, including changes in thermal regimes particularly pertinent to deeper lakes (Boeff et al., 2016; Rühland et al., 2015; Sorvari et al., 2002), diversification of benthic habitats identified as a key mediator of change in the High Arctic (Douglas et al., 1994; Griffiths et al., 2017), and alterations to lake water acid–base balance observed from dilute lakes in alpine and arctic environments (Sommaruga-Wögrath et al., 1997; Wolfe, 2002). Potential synergistic or antagonistic effects of increasing tDOM export with the ongoing warming (Finstad et al., 2016) are less well documented, although analogies from past Holocene warm periods have evidenced that this may be a highly important mechanism at the treeline ecotone (Jones et al., 2011; Pienitz, Smol, & MacDonald, 1999; Seppä & Weckström, 1999). In the late neoglacial record from Lake Námmájávri (Figure 1), the most distinct changes in the diatom community took place concurrent with the 20th century warming, manifested as a distinct increase in common alkaliphilous and alkalibiontic taxa primarily from the genera *Epithemia* and *Denticula* (Figure 4), mirrored also as an increase in the diatom-inferred pH (Figure 6). Overall, the pH reconstruction showed a strong correlation with the independent, chironomid-based mean July air temperature reconstruction (*r* = .69, *p* < .001). The lowered pH values between *c.* 1700 and 1900 C.E. correspond with the timing of the coolest period of the "Little Ice Age" (LIA) in the region, and the following increase with the recent warming (Figure 6, Rantala, Luoto, et al., 2016). On the basis of this apparent coupling, and the ecological preferences of the key taxa, we suggest that temperature-driven changes in lake water chemistry are a key determinant of diatom community development in the lake through time. However, a number of related environmental variables may contribute to the observed species patterns, as discussed below.

Air temperature imposes strong control over ice cover dynamics that in turn regulate lake water acid–base balance (Livingstone, Adrian, Blenckner, George, & Weyhenmeyer, 2010; Weckström, Hanhijärvi, Forsström, Kuusisto, & Korhola, 2014). Several records from poorly buffered high-altitude and high-latitude lakes have illustrated coupled variation between temperature and lake water pH (Finkelstein et al., 2014; Koinig, Schmidt, Sommaruga-Wögrath, Tessadri, & Psenner, 1998; Sommaruga-Wögrath et al., 1997), attributed to climate regulation of the timing and extent of snow and ice cover. The mechanisms are manifold, with many studies highlighting alterations to aquatic primary production and carbon uptake, dissolved inorganic carbon (DIC) speciation and carbon dioxide (CO_2) supersaturation under the ice (Wolfe, 2002). Some studies have also suggested importance of enhanced terrestrial weathering and eolian dust fluxes in contributing to increased catchment export of base cations into lakes (Sommaruga-Wögrath et al., 1997). Based on biogeochemical evidence, the elevated pH values in Lake Námmájávri during warmer periods were paralleled with increased aquatic production, whereas terrestrial influence appeared relatively low particularly during the recent warming. Specifically, warmer temperatures were associated with elevated $\delta^{13}C$ and $\delta^{15}N$ values presumed to reflect ^{13}C and ^{15}N enrichment of lake water carbon and nitrogen pools under increased primary production (Figure 6, Rantala, Luoto, et al., 2016). Increasing UV transparency, inferred from melanin pigmentation in benthic macrofauna, and coincident decline in sediment mineral component in turn suggested lower terrestrial influence over the 20th century (Figure 6, Rantala, Luoto, et al., 2016). We therefore suspect that enhanced production and biological carbon uptake together with improved CO_2 equilibration with the atmosphere under lengthened growing season are primary drivers of pH variation in the lake over the warm intervals. Conversely, lower production and saturation of CO_2 under extended ice cover period would explain the lowered pH values during the LIA. Temperature-driven fluctuations in lake water pH are generally observed in lakes with acidic waters as the DIC pool in alkaline lakes is dominated by bicarbonate that counteracts increasing acidity. However, the high measured pH (7.8) in the lake represents only one point in time and is likely lower throughout the ice cover season.

The observed species shifts may also be related to a number of other climate-driven processes that may be coupled to, coincide with, or potentially confound the apparent changes in lake water pH. For one, lake water pH is tightly connected to other chemical parameters such as alkalinity, DIC concentrations and conductivity that were not assessed in this work. Many of the species displaying changes over the LIA and the 20th century (Figure 4) could be responding also to improved nutrient cycling and changes in physical habitats that are often associated with the lengthening of the ice-free period. For instance D. kuetzingii, D. tenuis and E. cesatii have been associated with high conductivity and nutrient preference in arctic lakes in addition to being affiliated with alkaline waters (Antoniades & Douglas, 2005; Keatley et al., 2008; Lim, Kwan, et al., 2001; Michelutti, Smol, & Douglas, 2006). Similarly, Epithemia are often shown to prefer alkaline waters but are also common

euryhaline taxa (Patrick, 1977), and E. sorex has also been associated with high nutrients status (Shala et al., 2013). Lengthening of the growing season generally promotes diversification of aquatic habitats (Smol & Douglas, 2007), often increasing the availability of mosses and other epiphytic habitats relative to rock and sediment substrate. In more lush environments, the effect may be more related to compositional shifts in the epiphytes (Griffiths et al., 2017). Epithemia are commonly described as epiphyton, and D. kuetzingii and D. tenuis have shown a preference for moss substrate in arctic lakes (Michelutti et al., 2006). The increase in several species of Cymbella sensu lato over the 20th century may also illustrate changes in the type of habitable substrate. Similarly, the decline in small-sized benthic fragilarioids over the 20th century may demonstrate overall improved resource and habitat availability in the lake, providing increasing opportunities for more complex and less competitive diatom life forms (Bouchard et al., 2004; Douglas et al., 1994; Griffiths et al., 2017). The taxa have been frequently associated with colder temperatures and extensive ice cover (e.g. Lotter et al., 2010; Schmidt, Kamenik, Lange-Bertalot, & Klee, 2004; Weckström et al., 2016). Most probably, the species shifts were driven by the combined influence of changing lake water chemistry and nutrient and habitat availability, all driven by temperature control over lake ice regimes.

Where the terminal phase of the medieval warm period was associated with lower UV transparency as well as high sedimentation rates and elevated mineral content in the sediments, suggesting higher catchment inputs, an apparent decoupling between temperature and terrestrial influence was observed in the record in association with the recent warming (Figure 6, Rantala, Luoto, et al., 2016). This was presumed to reflect a delayed response by catchment vegetation and soils to increasing temperatures after the LIA, implying that terrestrial influence on the lake might increase with prolonged warming (Rantala, Luoto, et al., 2016). Although the species assemblages at the termination of the medieval warm period and over the recent warming displayed similarities, the species shifts over the past c. 100 years were clearly distinct in the record (Figure 4). It is possible that this distinction is related to the combined effect of lengthened growing season and increased transparency on light supply that could, for instance carry a more pronounced impact on the composition of epiphytic habitats or induce higher UV stress on the benthic flora. Since the geochemical record yielded little evidence of marked changes in the input of terrestrial organic matter over the late neoglacial, and as the spatial examinations suggested that diatom communities in shallow lakes in the region may be relatively insensitive to tDOM variability, we consider temperature-driven changes in lake ice regimes as the primary driver. The connection between ice cover and diatom community change has been illustrated from diverse aquatic environments (e.g. Boeff et al., 2016; Griffiths et al., 2017; Rühland et al., 2015; Sorvari et al., 2002), however, instrumental or observational ice cover data from comparable remote small and shallow lakes in the study region are few (Weckström et al., 2014). While this prevents attempts to quantitatively assess the link between temperature, ice cover dynamics and diatom community change in the lake, it does not undermine the

assumption of the importance of ice regimes. Temperature imposes fundamental control over ice phenology and the chironomid-based temperature model and reconstruction are considered robust based on statistical validation, earlier palaeoclimate inferences and instrumental data (Luoto, Kivilä, Rantala, & Nevalainen, 2017; Rantala, Luoto, et al., 2016). The inferred range of change is comparatively large, which may be related to the development of a strong microclimate in the sheltered valley (Figure 1, Luoto et al., 2017). The relationship between temperature and ice cover also varies as a function of local factors such as basin shape, snow cover and wind regimes (Livingstone et al., 2010). In the context of Lake Námmájávri, the sheltered location and shallow characteristics of the basin could further enforce the impact of warming on lake ice dynamics.

4.4 | Implications on diatom responses to warming climate

Ice cover imposes profound control over aquatic ecosystem functioning and diatom distribution in northern lakes (Smol et al., 2005; Weckström et al., 2014). Instrumental records have demonstrated increasingly late freeze-ups and earlier ice break-ups across northern regions since the mid-19th century (Magnuson et al., 2000), a trend that has also been displayed in Finnish monitoring records since the late 19th century (Korhonen, 2006). Diatom community change in the studied shallow oligotrophic lake at the subarctic treeline was relatively small in scale, primarily conspicuous for its close correspondence with the geochemical record and the chironomid-based temperature reconstruction. Temperature-driven changes in ice regimes appear a probable cause for the observed species shifts and may be linked to a number of environmental forcings including alterations in water chemistry, improved nutrient availability and changes in physical habitats. Lowered terrestrial influence over the recent warming may have further contributed to the distinctiveness of the topmost sequence relative to the previous warm interval. On the basis of the close correspondence between the diatom-based pH and inferred temperature patterns, as well as the affinity of the key taxa to alkaline waters, we deduce that changes in lake water chemistry are a key driver of diatom distribution in Lake Námmájávri. However, a myriad of synchronous physical, chemical and biological interactions likely shape the benthic diatom community and extracting their respective roles would necessitate improved knowledge on the sensitivity of the diatom taxa to the differential drivers. In comparison with records from arctic or more barren subarctic environments, the responses of the periphytic diatom community to the effects of warming in Lake Námmájávri appear muted. Regardless, the record contributes to the growing evidence of ecological change in aquatic communities under the ongoing warming.

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