



# Biodiversity patterns of Arctic diatom assemblages in lakes and streams: Current reference conditions and historical context for biomonitoring

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## Abstract

1. Comprehensive assessments of contemporary diatom distributions across the Arctic remain scarce. Furthermore, studies tracking species compositional differences across space and time, as well as diatom responses to climate warming, are mainly limited to paleolimnological studies due to a lack of routine monitoring in lakes and streams across vast areas of the Arctic.
2. The study aims to provide a spatial assessment of contemporary species distributions across the circum-Arctic, establish contemporary biodiversity patterns of diatom assemblages to use as reference conditions for future biomonitoring assessments, and determine pre-industrial baseline conditions to provide historical context for modern diatom distributions.
3. Diatom assemblages were assessed using information from ongoing regulatory monitoring programmes, individual research projects, and from surface sediment layers obtained from lake cores. Pre-industrial baseline conditions as well as the nature, direction and magnitude of changes in diatom assemblages over the past c. 200 years were determined by comparing surface sediment samples (i.e. containing modern assemblages) with a sediment interval deposited prior to the onset of significant anthropogenic activities (i.e. containing pre-1850 assemblages), together with an examination of diatoms preserved in contiguous samples from dated sediment cores.
4. We identified several biotypes with distinct diatom assemblages using contemporary diatom data from both lakes and streams, including a biotype typical for High Arctic regions. Differences in diatom assemblage composition across circum-Arctic regions were gradual rather than abrupt. Species richness was lowest in High Arctic regions compared to Low Arctic and sub-Arctic regions, and higher in lakes than in streams. Dominant diatom taxa were not endemic to the Arctic. Species

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richness in both lakes and streams reached maximum values between 60°N and 75°N but was highly variable, probably reflecting differences in local and regional environmental factors and possibly sampling effort.

5. We found clear taxon-specific differences between contemporary and pre-industrial samples that were often specific to both ecozone and lake depth. Regional patterns of species turnover ( $\beta$ -diversity) in the past c. 200 years revealed that regions of the Canadian High Arctic and the Hudson Bay Lowlands to the south showed most compositional change, whereas the easternmost regions of the Canadian Arctic changed least. As shown in previous Arctic diatom studies, global warming has already affected these remote high latitude ecosystems.
6. Our results provide reference conditions for future environmental monitoring programmes in the Arctic. Furthermore, diatom taxa identification and harmonisation require improvement, starting with circum-Arctic intercalibrations. Despite the challenges posed by the remoteness of the Arctic, our study shows the need for routine monitoring programmes that have a wide geographical coverage for both streams and lakes.

**KEYWORDS**

circumpolar, diatom biotypes, environmental monitoring, global warming, paleolimnology

## 1 | INTRODUCTION

The Arctic is warming at an unprecedented rate relative to the rest of the planet, largely due to a variety of climate feedback mechanisms (Walsh, Overland, Groisman, & Rudolf, 2011). Many freshwater ecosystems across the Arctic have already been affected by climate change, with notable modifications to the physico-chemical characteristics of remote aquatic ecosystems (Vincent et al., 2011). However, warming across the circum-Arctic region is not uniform, with some regions experiencing stronger and more rapid changes than others, which can be linked to differences in snow cover, and sea ice extent and phenology (Hochheim & Barber, 2010; Lind, Ingvaldsen, & Furevik, 2018). Because Arctic lakes and streams are closely linked with their surrounding catchments, shifts in abiotic and biotic ecosystem components of these systems are indicators of ecological change (Lento et al. 2019), and could be used to reflect climate- and human-induced changes to the landscape. For example, changes to temperature and light can directly and indirectly affect the assemblage composition of primary producers, such as diatoms. With a projected increase in air temperature of 2.8–7.8°C by 2050 (CAFF, 2013), it is anticipated that changes to Arctic aquatic ecosystems will be exacerbated in the future, making diatoms a valuable indicator of current and future changes in Arctic aquatic ecosystems.

Diatom assemblages are widely used in biomonitoring programmes as indicators of environmental conditions (Stevenson, Pan, & van Dam, 2010) and often dominate algal communities in freshwater systems (Smol, 2008). Diatoms are particularly good indicators of diverse environmental disturbances, including climate change, acidification and nutrient enrichment (Smol & Stoermer,

2010). In Arctic lakes and ponds, a strong linkage exists between diatom composition and climate-related variables, such as air temperature, wind patterns, and lake ice dynamics that can have strong moderating controls on fundamental limnological processes (Bigler, Larocque, Peglar, Birks, & Hall, 2002; Rühland, Paterson, & Smol, 2015; Smol et al., 2005; Sorvari, Korhola, & Thompson, 2002; Weckström, Hanhijärvi, Forsström, Kuusisto, & Korhola, 2014). For example, warmer temperatures and longer ice-free periods can develop new diatom habitats through establishment of aquatic vegetation, particularly in shallower systems (Douglas & Smol, 2010; Pienitz, Douglas, Smol, & Hamilton, 2004; Smol & Douglas, 2007a). In addition, increases in thermal stability and associated changes in resource availability, such as light and nutrients, may shift diatom life history strategies in deeper Arctic lakes experiencing warming and reduced periods of ice cover (Rantala, Luoto, Weckström, Rautio, & Nevalainen, 2017; Rühland, Paterson, & Smol, 2008; Rühland et al., 2015; Smol et al., 2005; Sorvari et al., 2002; Weckström et al., 2014).

Biogeographical variation in diatom diversity, including taxonomic richness and assemblage structure, is often related to local and catchment-scale influences, climatic variables, and dispersal limitation, all of which depend upon the geographic scale of the study (Jyrkänkallio-Mikkola et al., 2017; Keck, Franc, & Kahlert, 2018; Soininen, Jamoneau, Rosebery, & Passy, 2016; Soininen & Weckström, 2009; Vyverman et al., 2007). Differences in the physical settings (geology, hydrology, physiography) affect water chemistry across the vast circum-Arctic (Pienitz, Smol, & Lean, 1997a; Prowse et al., 2006a) and these limnological differences can play an important role in determining diatom assemblage composition at various spatial scales (Lotter, Pienitz, & Schmidt, 2010). In addition,

diatom species diversity has often been found to be inversely related to latitude across Arctic ecozones (e.g. Saulnier-Talbot, Antoniades & Pienitz, 2020) and this relationship has been associated with differences in the length of the ice-free season in lakes and ponds (Douglas & Smol, 2010; Michelutti, Douglas, & Smol, 2003a). In spite of the heterogeneous nature of the Arctic landscape, similar climate-related latitudinal trends in diatom assemblage composition exist across the Arctic treeline ecotone, with these patterns related to the degree of permafrost and soil development, vegetation cover, and the length of the ice-free period (Gregory-Eaves, Smol, Finney, & Edwards, 1999; Laing & Smol, 2000; Pienitz, Smol, & Birks, 1995; Rühland, Smol, & Pienitz, 2003; Weckström, Korhola, & Blom, 1997; Wrona et al., 2013). However, much less is known about latitudinal trends in diatom assemblage composition and richness of stream habitats (Passy et al., 2018). Given that one of the predicted consequences of climate warming in the Arctic is the northward displacement of ecotones (Callaghan et al., 2002), there is a need to better understand the current diatom species distributions and establish contemporary baseline conditions within the circum-Arctic region.

This paper is part of the first circumpolar assessment of Arctic freshwater biodiversity, led by the Freshwater Group of the Circumpolar Biodiversity Monitoring Program (CBMP; part of the Conservation of Arctic Flora and Fauna (CAFF) working group of the Arctic Council). Our study objectives were to: (1) establish a contemporary baseline of diatom diversity (a characterisation of the current state, rather than a historical baseline) in Arctic streams and lakes to act as a reference point for future monitoring programmes and assessments; (2) explore trends in diatom assemblage changes within the past c. 200 years to provide context to both contemporary and future diatom distributions; and (3) assess the potential of using lentic and lotic diatoms as bioindicators of environmental change across Arctic ecozones. We furthermore provide guidelines for establishing a globally coordinated, circumpolar bioassessment programme for diatoms.

## 2 | METHODS

### 2.1 | Study area and data collection

For the purpose of this assessment, the Arctic was considered to include the areas covered by the Arctic Biodiversity Assessment (ABA) and CAFF boundaries, whichever was more inclusive for a particular area (Culp, Goedkoop, et al., 2012a). We used existing lotic and lentic Arctic diatom data compiled for the CBMP Freshwater Database, which is stored in the Arctic Biodiversity Data Service (Table S1; www.abds.is). Data were available for all Arctic countries, although there was greater spatial coverage of sample sites in North America (Table S1).

Contemporary data included lake surface sediment samples and periphytic data from stream substrate scrapes. River samples were generally collected from 2003 to 2015 (one sampling event per river station), with the exception of samples from Norway,

which were primarily collected between 1981 and 1989. Although the Norwegian data were collected in an earlier decade than the remaining samples, they represented only approximately 5% of the river samples and were retained to improve spatial coverage of the data. Lake samples were collected between 1991 and 2013 (one sampling event per lake), with the exception of samples from northern Labrador, Canada, which were collected in 1979. However, northern Labrador has historically experienced very little warming (Prowse et al., 2006b), and these samples were therefore expected to characterise contemporary diversity patterns in this area of the Arctic.

Paleolimnological data were comprised of diatom assemblages preserved in: (1) contiguous intervals of dated sediment cores covering at least the past c. 200 years; and (2) surface (modern) and subsurface (pre-industrial) sedimentary intervals of a series of lake cores. The latter paleolimnological approach (commonly referred to as *top-bottom* or *before and after* analysis) provides a *snapshot* of diatom assemblages from these two discrete points in time to determine the direction and magnitude of change relative to pre-industrial baseline conditions (Smol, 2008). In this paper, we refer to these paleolimnological samples as *before* and *after* snapshot data. Paleolimnological samples were collected between 1993 and 2016.

### 2.2 | Protocols for diatom sampling and taxonomic analysis

Contemporary diatom samples from streams and lakes were collected during research programmes or for monitoring programmes following regional standards where available (USEPA, 2011, 2013 for the U.S.A.; EN, 2014a, EN, 2014b for Europe). Data used for the analyses were collected following comparable methods, although minor variations in sampling technique occurred depending on the origin of the data. In summary, stream biofilms were scraped from hard substrates or in a few cases (c. 5% of samples) from plants or surface sediments. Contemporary lake diatom samples, often collected for establishing training sets for paleolimnological studies, were taken by retrieving a short sediment core from the deepest part of a lake and retaining the top-most sedimentary interval (i.e. modern sample) for analysis. Methods used for collecting sediment samples for paleolimnological analyses were generally similar across study lakes. For the majority of the lakes, sedimentary records were retrieved from the deepest part of the lake using gravity corers and subsampled on site at 0.25–0.5-cm contiguous intervals using vertical extruders (e.g. Glew, Smol, & Last, 2001).

Preparation and analysis of contemporary and paleo diatom samples generally followed similar procedures. In brief, samples (sediment and scrapes) were treated with acid and/or peroxide using standard techniques to digest the cellular content of diatom frustules and to remove organic material (Battarbee, Jones, et al., 2001a). Diatom samples were mounted on microscope slides using high refractive index mounting media and, in most cases,

≥400 diatom valves were enumerated with a light microscope at 1,000× magnification. Diatom assemblages were expressed as percent relative abundance for analyses. Planktonic diatom taxa were not considered for stream data analyses as these were not considered in certain studies. In contrast, lake sediment samples incorporate both planktonic and benthic diatoms as these data consist of an integrated, spatial, and temporal sample from across each lake.

### 2.3 | Diatom taxonomic harmonisation

Harmonising large datasets from multiple sources is challenging because of differences in: (1) taxonomic precision (e.g. some researchers group varieties of diatom taxa, such as small *Fragilaria* sensu lato taxa, into species, others split these further into varieties); (2) nomenclature used among working groups; (3) identification of certain groups of similar taxa that can be difficult to distinguish (e.g. some small *Achnanthes* sensu lato taxa); and (4) accepted nomenclature at the time the data were analysed. To address these differences and minimise issues with possible identification errors, we harmonised diatom data with updated nomenclature to the lowest taxonomic level possible (usually species level). We then settled on a taxonomic nomenclature that combined diatom taxa into groups and complexes for those diatoms that are easily misidentified (e.g. a variety of small *Achnanthes* sensu lato taxa) or whose taxonomy was ambiguous. We also grouped taxa frequently identified at different levels of taxonomic precision (e.g. benthic fragilarioid taxa). Table S2 lists our database of diatom harmonisation including taxon names and taxa that were combined. Although data harmonisation can limit taxonomic resolution, it can also improve the detection of spatio-temporal patterns by reducing noise associated with errors resulting from taxonomic inconsistencies in large datasets (Lee, Bishop, Spaulding, Mitchell, & Yuan, 2019).

### 2.4 | Supporting variables

We extracted geospatial data for all stations using a geographic information system (ArcMap, Version 10.3, ESRI, St. Paul, MN, U.S.A.). Because of the large number of stations in the analysis, catchments could not be delineated for each site. Instead, sampling sites were grouped by hydrobasins, which are standardly-derived hydrologically based catchments with global coverage, delineated at different spatial scales ranging from level 01 (continental-scale) to level 12 at the smallest scale (Lehner & Grill, 2013). Sampling sites were grouped at a moderate spatial scale by level 07 hydrobasins and geospatial data were summarised for each hydrobasin. Geospatial data used in our analyses included latitude and longitude (site-specific), Arctic zone classification (ABA classification zones; <http://geo.abds.is/geonetwork>) and climate metrics. The Arctic zones (High Arctic, Low Arctic, and sub-Arctic) were defined by a set of biogeographical features, based on the Circumpolar Arctic Vegetation Map (Walker

et al., 2018) such as vegetation types (including the northern limit of trees), the duration of the biologically productive season, and mean annual air temperature (CAFF, 2001). Climate metrics were calculated from long-term (1970–2000) average temperature and precipitation layers (WorldClim version 2; <http://worldclim.org/version2>), and included mean annual air temperature within the hydrobasin (reflects the average climate), July mean temperature (reflects the Arctic region's growing season), and annual mean precipitation.

Water chemistry and field measurement data for lakes and streams were not available for every site due to field sampling differences, but we summarised data that did exist. The available environmental variables used for analyses included total nitrogen (TN), total phosphorus (TP), calcium (Ca), dissolved organic carbon (DOC), and pH. In addition to these variables, we also included lake maximum depth, lake catchment area, and stream substrate (percentage of sand), where these data were available.

### 2.5 | Data analyses

Many diatom valve counts or relative abundance data for statistical comparisons were available for most regions. However, some of the data collected for this study were recorded as presence/absence data (generally data recovered from published literature), and were therefore not included in our analyses. Furthermore, we only used data where diatom identification was performed to the lowest possible taxonomic level (i.e. below genus level). For the data retained in this assessment, we performed separate analyses for stream scrapes, lake surface sediment samples, before and after snapshot paleolimnological samples, and dated lake sediment cores (Table 1).

#### 2.5.1 | Contemporary data

Biodiversity patterns of contemporary diatom assemblages were evaluated by plotting local diatom richness per site ( $\alpha$ -diversity; Whittaker, 1960) against latitude and longitude to assess spatial trends. Taxa accumulation curves compared richness (standardised by sampling effort) among ABA Arctic zones, and among the geographical regions of Arctic North America, Europe, and the non-European region of Russia (Table 1).

A classification using self-organising maps (SOMs, R package diatSOM; Bottin, Giraudel, Lek, & Tison-Rosebery, 2014) was performed for biotypology, defined as the determination of diatom assemblages that are typical for certain habitats and environments. These typical diatom assemblages are then referred to as *biotypes*. The SOM classification relies only on diatom relative abundance data and thus is independent of environmental data. We removed diatom taxa with <2% relative abundance from the SOM analysis. Indicator species analysis (ISA) was used to identify diatom taxa with strong associations to a biotype (Dufrêne & Legendre, 1997). Indicator species analysis returns a species-specific index, the so-called Indicator value (IndVal, ranging from 0 to 1), based

**TABLE 1** Overview of selected sites for analyses. Selection based on samples collected with similar methods and diatom counts expressed as relative abundances

| Habitats sampled              | No. of sites | Geographical area           |   |
|-------------------------------|--------------|-----------------------------|---|
|                               |              | North American Arctic       | European/<br>Russian Arctic   |
| Lake surface sediment samples | 727          | 490 (Canada)<br>44 (U.S.A.) | 81 (Russia)<br>25 (Greenland)<br>49 (Iceland)<br>36 (Sweden)<br>2 (Finland) |
| Stream scrapes                | 426          | 249 (Canada)<br>26 (U.S.A.) | 23 (Sweden)<br>96 (Finland)<br>32 (Norway)                                  |
| Paleo before/after snapshots  | 116          | 106 (Canada)<br>5 (U.S.A.)  | 2 (Russia)<br>3 (Finland)   |
| Paleo full cores              | 52           | 50 (Canada)                 | 2 (Finland)   |

on a species' relative abundance within a site and its relative frequency of occurrence in the various groups of sites. Indicator species analysis also calculates the statistical significance (at a chosen  $\alpha$ -level of 0.05) of the IndVal to identify significant indicator taxa. We calculated IndVal for each diatom taxon in each biotype and considered taxa with an IndVal of 0.5 and higher strong indicators of the respective biotype. Because ISA does not reflect the structure of a diatom assemblage, we also chose to describe the composition of the biotypes by presenting the relative abundance of the present taxa.

We grouped existing environmental data based on site groupings in the SOMs to characterise habitat conditions for each biotype. The median and 10th–90th percentiles were calculated for environmental variables to test whether there were significant differences (at  $\alpha = 0.05$ ) among biotypes, and a non-parametric Kruskal–Wallis rank sum test with Mann–Whitney pairwise *post hoc* comparisons was performed with a Bonferroni correction for multiple testing. The advantage with this approach was that we were able to use all sites for which diatom data were available, even if some of the environmental variables were not measured for all sites.

## 2.5.2 | Paleolimnological data

Lakes in the paleolimnological portion of the study were categorised into ecoclimatic zones based largely on their geographical location and on vegetation distribution schemes. Similar to classifications used for the contemporary data, sites for the paleolimnological analysis were categorised into High Arctic, Low Arctic, and sub-Arctic. However, the sub-Arctic zone was further divided into high sub-Arctic (forest-tundra transitional region between tundra to the north and forest to the south) and low sub-Arctic (open crown boreal forest) zones, following as closely as possible the categories used in the original publications from which these data were derived. Therefore, the categories used for the paleolimnological data included High Arctic (HA), Low Arctic (LA), transition zone (T), and boreal forest (BF) with the latter two categories being equivalent to the sub-Arctic

zone of the ABA system for the contemporary data. Consult the original literature for site descriptions (see Table S1; [www.abds.is](http://www.abds.is)).

The Arctic landscape is dominated by relatively shallow lentic waterbodies, whereas deep lakes are less common compared to more southern latitudes (Grosse, Jones, & Arp, 2013; Rautio et al., 2011). As water depth in lentic systems affects diatom assemblage composition (Rautio et al., 2011; Vincent, Laurion, Pienitz, & Anthony, 2013), we separated paleolimnological lentic sites into depth categories: ponds ( $\leq 2$  m), shallow lakes ( $>2$  and  $\leq 6$  m) and deep lakes ( $>6$  m). In general, we consider ponds to be water bodies that freeze completely to the bottom each winter and with a maximum depth no greater than 2 m (and often  $<1$  m; Grunblatt & Atwood, 2014). Since there is no standardised system that classifies an Arctic lake as shallow or deep, we based our depth categories on diatom assemblage changes across maximum lake depth gradients from numerous Arctic lakes in the published literature, where compositional shifts towards greater abundances of planktonic taxa are particularly notable in lakes deeper than c. 5–6 m (Moser et al., 2000; Rühland et al., 2003).

The range of sampling dates (from 1993 to 2016) was taken into consideration when comparing and interpreting differences in the magnitude of diatom assemblage change over time. For example, *modern* data represent the past few years of sediment accumulation from the time that the samples were collected. In particular, there are regions where samples may have been collected prior to the onset of regional 20th century climate change such as parts of the eastern Canadian Arctic (Smol et al., 2005), where anthropogenic warming has only been observed within the past c. 15 years (e.g. Hochheim & Barber, 2010, 2014). *Pre-industrial* data used in the paleolimnological aspects of this study represent environments prior to the onset of significant global-scale anthropogenic disturbances from industrialisation (c. 1,800). The before and after snapshot dataset provided an efficient means to determine whether pre-industrial diatom assemblages differ from modern assemblages and what the nature of these changes is across relatively large regions (Smol, 2008). Chronologies for the detailed sediment cores used in this study were established using  $^{210}\text{Pb}$  techniques, a widely used approach for dating recent lake sediments that have accumulated over the past c. 150 years (Appleby, 2001, 2008; Smol et al., 2005).

### *Before and after snapshot analysis: comparisons between modern and pre-industrial diatom assemblages*

The original harmonised data set for the before and after snapshot paleolimnological analysis comparing modern and pre-industrial assemblages included 452 diatom taxa in 116 sites. To eliminate rare taxa for numerical analyses, we applied a cut-off criterion where all taxa that represented at least 2% in at least one sample were retained for analyses, effectively reducing the number of diatom taxa in our 116-lake (i.e. 232 samples) snapshot data set to 174. For each of the 116 study lakes with both modern and pre-industrial samples, we used a Bray–Curtis (B-C) dissimilarity coefficient to evaluate differences in diatom assemblage composition between the pre-industrial and the late 20th century samples. The larger the B-C dissimilarity coefficient, the larger the degree of diatom change at that site. To geographically display the trends across the 116 sites, the degree of compositional change was arranged into four categories of B-C dissimilarity coefficients based on distribution quartiles (0–30; >30–40; >40–50; >50), providing a means to visually compare the magnitude of diatom assemblage change across the circum-Arctic region.

Differences between diatom assemblages in modern and pre-industrial samples were explored statistically across all 116 sites, as well as among Arctic zones and lake depths. First, we used a non-parametric, one-way analysis of similarity (ANOSIM) to examine how different diatom assemblages were between modern and pre-industrial samples across all lakes, with time period (modern or pre-industrial) as the single grouping factor. Specifically, ANOSIM was used on a B-C dissimilarity matrix of all samples (including modern and pre-industrial sediment samples for all sites) to determine whether there was stronger pairwise similarity within groups (i.e. among all modern diatom assemblages or among all pre-industrial assemblages) than could occur by chance. ANOSIM calculates a Global *R* value that usually ranges between 0 and 1, with values close to 1 showing stronger differences between groups (modern and pre-industrial assemblages) than within groups. Statistical significance was calculated with an  $\alpha$  of 0.05 using 999 permutations (Clarke, 1993). ANOSIM was run using the PRIMER 6 software package (Clarke & Gorley, 2006).

Second, to assess whether the degree of diatom assemblage change between modern and pre-industrial samples differed among lake depths (pond, shallow, deep) and ecoclimate zones (BF, T, LA, HA), we applied a two-way ANOVA to B-C dissimilarity values calculated for each pair of snapshot samples (i.e. one B-C value for each lake, comparing paired modern and pre-industrial samples, rather than the B-C matrix across sites that was used for ANOSIM). This analysis fit the model: B-C dissimilarity = lake depth + ecoclimatic zone + (lake depth)\*(ecoclimatic zone), where the term (lake depth)\*(ecoclimatic zone) tested whether the effect of lake depth on temporal change in diatom composition was dependent on the ecoclimatic zone.

Lastly, to examine general trends in diatom compositional change between modern and pre-industrial samples, the percent relative abundances of a selection of the most common diatom taxa observed in the 116 sites were visually assessed in a series of 1:1 scatter plots comparing snapshot data from modern and pre-industrial

samples. Sites were classified by both depth (pond, shallow, deep) and ecoclimatic zone (BF, T, LA, HA) categories. Data points that fell below the 1:1 line indicated taxa that were present at higher relative abundances in the pre-industrial samples, whereas points that plotted above the 1:1 line were indicative of an increase in relative abundance since pre-industrial time. To determine whether there were significant differences between modern and pre-industrial relative abundances, a Wilcoxon signed-rank test was applied to the diatom data.

### *Full core paleolimnological analysis*

A total of 80 full sedimentary diatom records spanning the past c. 200 years from across the Arctic were available for this study; primarily from lakes in Canada but also including two lakes in Russia, three lakes in Finland and 12 lakes from Greenland (although the latter were presence/absence data taken from published literature and therefore not included in analysis). We are aware that many more dated diatom profiles have been studied in Europe, but because the data gathering and processing activities of the CBMP were not exhaustive and were necessarily limited by funding support, these additional data could not be included at this time.

A diatom record was included in the analysis if each sediment core met two criteria: (1) it had a sufficiently reliable  $^{210}\text{Pb}$  dating profile (analysed by either  $\gamma$  or  $\alpha$  spectroscopy) to establish a chronology for the past c. 150–200 years; and (2) it was not affected by known human or natural disturbances (e.g. oil sumps, storm surges) within the time frame of interest. We did not include diatom records in three situations: (1)  $^{210}\text{Pb}$  activities were too low to establish a reasonable chronology; (2) the chronology was solely based on a  $^{137}\text{Cs}$  peak; or (3) the dates for the past c. 200 years were solely estimated from age–depth chronologies that used  $^{14}\text{C}$  dating techniques focusing on Holocene-scale trends. Of the original 80 cores, 52 diatom records were deemed acceptable for further analyses as they had sufficient chronological control, included relative abundance data, and were not affected by disturbances (Table 1). In each core, an estimated  $^{210}\text{Pb}$  date was assigned to all sedimentary intervals containing diatom data using a straight-line interpolation between each successive dated interval (Campbell, 1996). When necessary, dates were extrapolated back to c. 150–200 years ago so that each core represented approximately the same age span.

Detrended canonical correspondence analysis (DCCA) estimated the amount of diatom species compositional turnover (as  $\beta$ -diversity) measured in standard deviation units (Smol et al., 2005; sensu Birks, 2007). As biostratigraphical sequences are in a known temporal order, the DCCAs were constrained to sample age (Smol et al., 2005) to estimate diatom compositional changes within the past c. 200 years for each of the 52 diatom profiles. Beta-diversity was used to compare the relative amount of diatom compositional change across our ecoclimatic gradients (BF, T, LA, HA), where higher values indicated a greater magnitude of species turnover. DCCAs were performed using CANOCO 4.5 (ter Braak & Šmilauer, 2002) with the options of detrending by

segments and non-linear rescaling, following the protocols of Smol et al. (2005).

### 3 | RESULTS

#### 3.1 | Contemporary data

##### 3.1.1 | Overall patterns in Arctic diatom species richness and spatial diversity

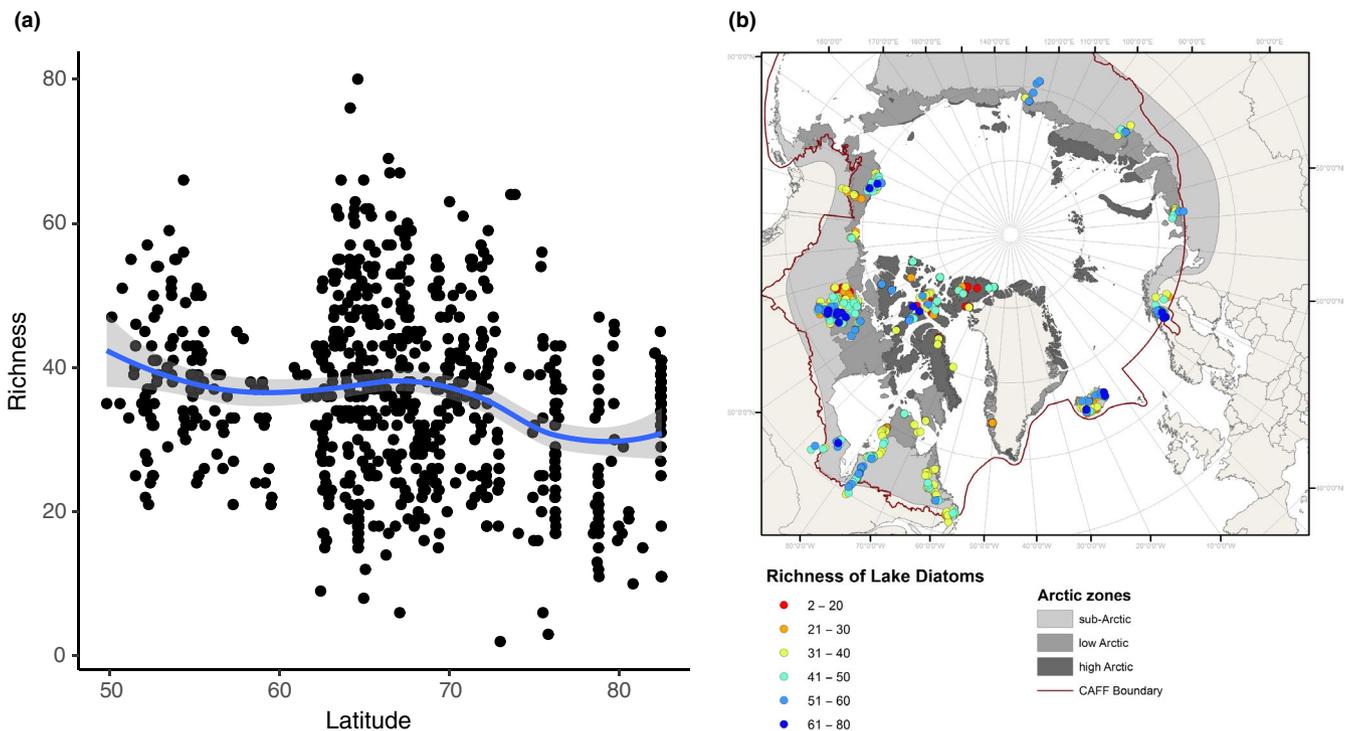
The contemporary diatom dataset incorporated all geographic regions of the Arctic and consisted of 549 harmonised diatom taxa belonging to 139 genera. Sampling intensity was highest between 62°N and 72°N; however, lake surface sediment samples were well distributed across all latitudes (Figure 1). In contrast, there were notable sampling gaps in stream samples, particularly between 75°N and 81°N (Figure 2), and lake and river samples were unevenly distributed longitudinally. In general, taxonomic richness was higher in lake surface sediment samples (mean: 36, range: 2–80,  $n = 727$ ) than in stream scrapes (mean: 25, range 2–78,  $n = 427$ ). Local richness showed a unimodal distribution for stream samples, and decreased slightly at the highest latitudes for both lakes and streams (Figures 1 and 2). Maximum richness of both lakes and streams occurred between latitudes 60°N and 75°N (Figures 1 and 2). Although there was large variation in taxa richness among sites from similar latitudes, taxa accumulation curves corroborate that sites in the ABA High Arctic zone, most of them at latitudes >70°N,

had lower species richness in both lakes and streams than ABA Low Arctic or sub-Arctic sites (Figure 3). However, species accumulation curves did not reach an asymptote for lake or stream samples in any Arctic zone or any habitat, which suggests that sampling effort was insufficient to capture all diversity (Figure 3, Figure S1).

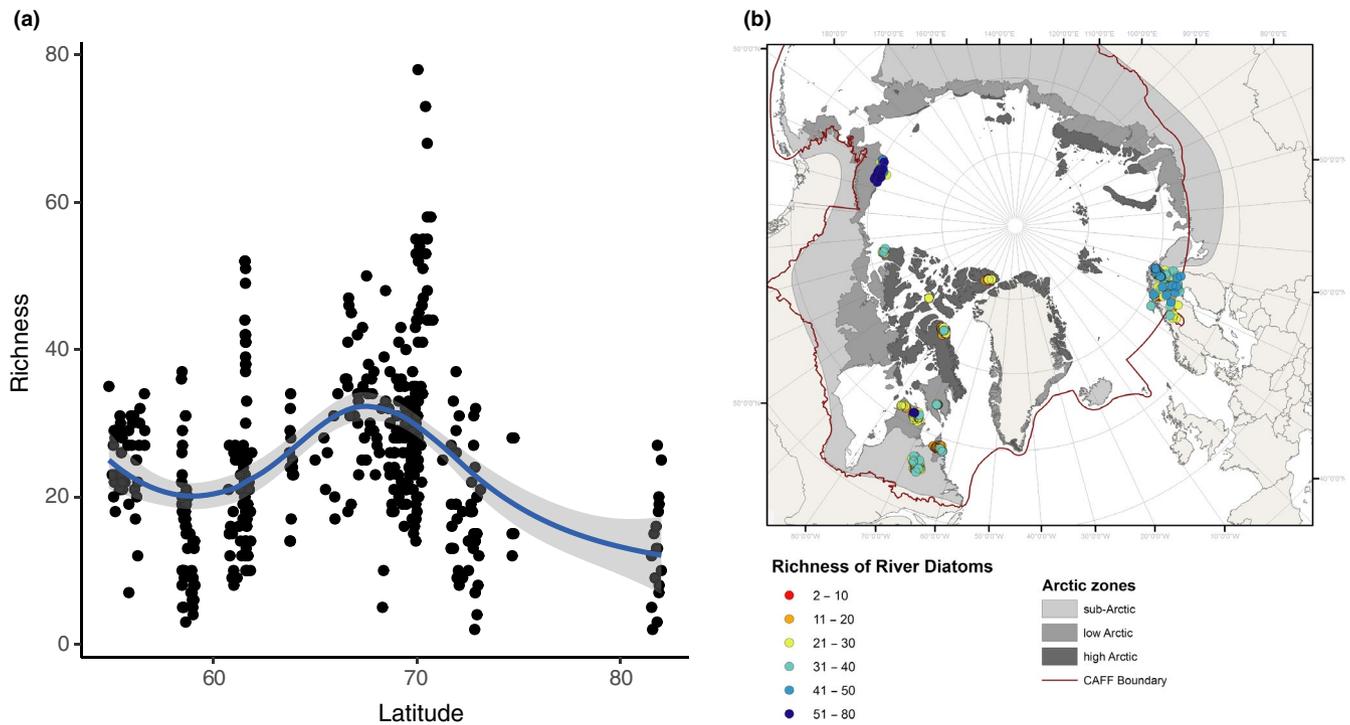
In general, we found that 50% of all diatom taxa in this study were common to all three ABA Arctic ecoregions, but a subset of diatom taxa was exclusive to a given ecoregion (Figure 4). The ABA Low Arctic and ABA sub-Arctic ecoregions shared a relatively high number of taxa for both habitats (Figure 4). There was some evidence of diversity hotspots across the circum-Arctic. High diatom richness was found in lakes from Alaska, lower latitude central Canada, Iceland, Fennoscandia, and Russia (Figure 1). Lake diatom richness was lower in eastern Canada and the Canadian High Arctic. Diatom richness in streams was clearly higher in Alaska and Fennoscandia than in Canada (Figure 2).

##### 3.1.2 | Diatom biotypes across the circum-Arctic

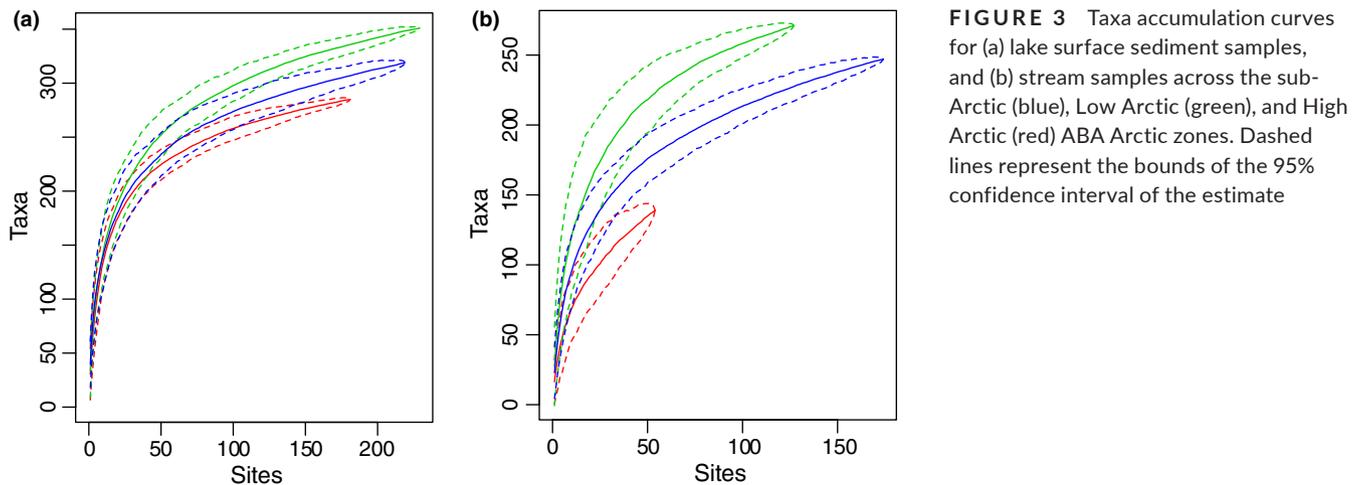
The SOM analysis generated biotypes for lakes and rivers that were indicative of distinct assemblages found in different sites across the circum-Arctic. Self-organising map analysis categorised six clearly distinct biotypes for the lake surface sediment samples (Tables 2 and S3; Figure 5) and four distinct biotypes for the stream habitat samples (Tables 3 and S3; Figure 6). As a general trend, all lake biotypes were evenly distributed longitudinally across the Arctic, and the distribution of diatom assemblages differed significantly among latitudes ( $p < 0.05$ , Kruskal–Wallis rank sum test, Figure 5). In contrast, stream biotypes



**FIGURE 1** Local diatom species richness of Arctic lake surface sediments, showing (a) richness as a function of latitude, and (b) site-specific richness. A LOESS smoother (blue line) with a span of 0.75 and a 95% confidence interval (grey shading) was applied to the data (a) to better highlight the general trend. Coloured circles on the map indicate the species richness at the sampling sites



**FIGURE 2** Local diatom species richness of Arctic diatom assemblages from stream scrapes, showing (a) richness as a function of latitude, and (b) site-specific richness. A LOESS smoother (blue line) with a span of 0.75 and a 95% confidence interval (grey shading) was applied to the data (a) to better highlight the general trend. Coloured circles on the map indicate species richness at the sampling sites



**FIGURE 3** Taxa accumulation curves for (a) lake surface sediment samples, and (b) stream samples across the sub-Arctic (blue), Low Arctic (green), and High Arctic (red) ABA Arctic zones. Dashed lines represent the bounds of the 95% confidence interval of the estimate

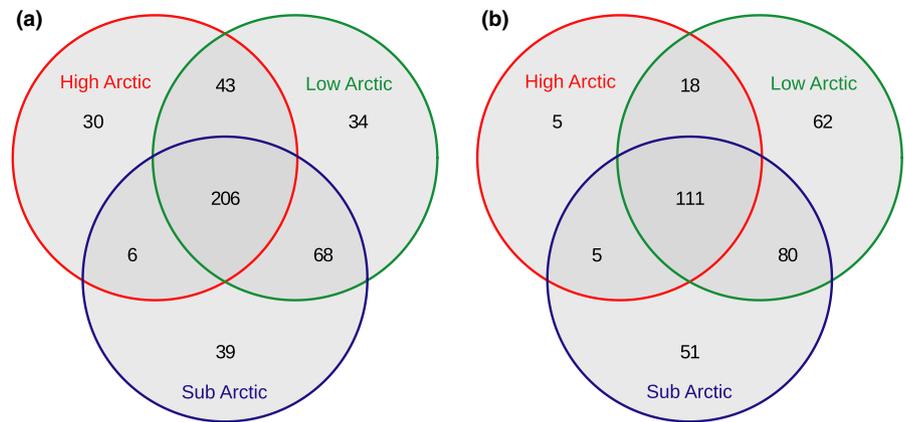
had different distributions both longitudinally and latitudinally across the Arctic ( $p < 0.05$ , Kruskal–Wallis rank sum test, Figure 6).

Lake biotype 5 was found almost exclusively at High Arctic sites ( $>75^{\circ}\text{N}$ ) and its geographic distribution was significantly different from all other lake biotypes (Mann–Whitney test,  $p < 0.05$ , Figure 5). Three lake biotypes (2, 4 and 6) were mainly found at latitudes near  $70^{\circ}\text{N}$  (no significant difference in latitude among these three clusters, Figure 5), and two lake biotypes (1 and 3) were more characteristic of lower-Arctic latitudes below  $65^{\circ}\text{N}$  (no significant difference in latitude between these two clusters, Figure 5). Stream biotypes 2 and 3 were found at higher latitudes (median  $70^{\circ}\text{N}$ ) than biotypes 1 and 4 (median  $62^{\circ}\text{N}$ ; Mann–Whitney test,  $p < 0.05$ ; Figure 6). Some longitudinal patterns were also evident for stream biotypes; for example, biotypes 2 and 4 were more

common to North America, biotype 1 was common to Europe and Eastern Canada, and biotype 3 was more common in Alaska and Europe.

In general, local environmental variables (water chemistry and field observations, including lake depth) and geospatial data (including climate) differed among biotypes. The relatively deep ( $>6$  m), oligotrophic (median TP =  $7.0 \mu\text{g/L}$ ), circumneutral (median pH = 7.4) lakes of biotype 1 (64 sites) were predominantly from northern treeline regions (boreal forest, transition, low Arctic tundra) of Canada and Iceland (Table 2). The *Discostella* complex was identified as a strong indicator and had the highest relative abundance for biotype 1 (Tables 2 and S3). Other small-celled planktonic cyclotelloid taxa, such as the *Cyclotella ocellata* complex, and elongate planktonic taxa, such as *Asterionella formosa* and *Fragilaria*

**FIGURE 4** Taxonomic richness of circum-Arctic diatom assemblages from (a) lake surface sediment samples, and (b) stream scrapes, showing the number of taxa found in one or more ABA Arctic zones. For lake surface sediment samples, ABA High Arctic (HA):  $n = 181$ , ABA Low Arctic (LA):  $n = 229$ , and ABA sub-Arctic (SA):  $n = 258$ . For stream scrapes, HA:  $n = 54$ , LA:  $n = 127$ , SA:  $n = 159$



*tenera*, were also identified as significant indicator taxa for biotype 1 (Table S3). Biotype 2 contained the highest number of samples (236), which were dispersed across all latitudes and countries, and had a wide range of pH (7.1–8.4; median = 7.7), and included a wide range of lake depth (1.3–11 m; median = 3.2 m). Small, abundant, benthic fragiliroid taxa (species belonging to genera *Staurosirella*, *Staurosira*, and *Pseudostaurosira*) were strong indicators of this biotype. Biotype 3 (211 samples) contained sites with moderately deep lakes (median maximum lake depth = 6.1 m), had circumneutral to slightly acidic pH (median = 6.8), and were situated largely within the Low Arctic tundra and sub-Arctic (boreal forest) of Canada (179) and Greenland (24). Several strong indicator taxa were identified for biotype 3, including the *Frustulia rhomboidea* complex, the *Encyonema gaemannii/perpusillum* complex, the *Fragilaria virescens* complex, the *Aulacoseira distans* complex, and the *Aulacoseira perglabra* complex. A highly diverse diatom biotype 4 (26 samples) consisted of sites in Low Arctic tundra and sub-Arctic (boreal forest) zones from Alaska, Canada, Russia, and Iceland. Although no strong indicator taxon (i.e. 0.5 or greater) was identified by ISA, significant indicator taxa ( $p < 0.05$ ) included the *Nitzschia dissipata/recta* complex, the *Fragilaria capucina* complex, the *Sellaphora pupula* complex, and *Hippodonta hungarica*. In this biotype, no taxa reached relative abundances higher than 10%. Biotype 5 (80 samples) was the most distinct and found almost exclusively in the Canadian High Arctic. Biotype 5 differed from other biotypes by being colder (mean annual temperature =  $-16^{\circ}\text{C}$ ), drier (mean annual precipitation = 9.1 mm), and shallower (median of maximum lake depth = 0.3 m). Strong indicators for biotype 5 included *Nitzschia perminuta* and *Caloneis* taxa, and the biotype was further characterised by an assortment of epiphytic diatoms. Biotype 6 (64 samples) from the High Arctic tundra and the sub-Arctic boreal forest zones of Canada, comprised of shallow (median maximum lake depth = 1.9 m), circumneutral to alkaline (median pH = 7.9), lakes and ponds that were higher in nutrients (median TN = 0.642 mg/L, median TP = 11.0  $\mu\text{g/L}$ ), and DOC (median = 9.2 mg/L) in comparison to other biotypes in this study. *Achnanthydium minutissimum* was the only strong indicator taxon of this biotype and the only taxon with relative abundances  $>10\%$ . Several other epiphytic taxa, including the *Encyonopsis descripta/falaisensis/microcephala* complex, *Encyonopsis cesatii*, and *Brachysira vitrea*, had ISA values  $<0.5$  but were statistically significant indicators of biotype 6.

Water chemistry, field observations (including stream substrate), and geospatial data (including climate) differed also among stream biotypes (Table 3). Stream biotype 1 (212 samples) had a wide range in catchment area, including the streams with the largest catchments, and was located in different Arctic regions, though dominated by Low Arctic sites. The sole strong indicator taxon for this biotype was the generalist taxon *A. minutissimum*. Biotypes 2 and 3 on average had smaller catchment areas than 1 and 4, probably indicating that they were comprised of smaller streams than the other types. However, all biotypes had a wide range in catchment area. The stream biotype 2 was associated with the coldest temperatures (mean annual temperature =  $-11^{\circ}\text{C}$ ) and dominated by High Arctic tundra sites with a high pH (median = 8.1). This biotype was characterised by several strong indicator taxa, including the *Synedra cyclopus/Hannaea arcus* complex, the *Diatoma moniliformis/tenuis* complex, and *A. minutissimum*, with the latter having the highest abundances (Tables 3 and S3). Stream biotype 3 was also associated with higher latitudes (many sites in the Scandinavian and Russian taiga) and was characterised by sites with relatively high DOC concentrations and with sand as the predominant substrate. Strong indicator taxa for this biotype included the *Rossethidium pusillum/anastasiae* complex, the *F. tenera* complex, and the *Eunotia incisa* complex. *Achnanthydium minutissimum* and the *R. pusillum/anastasiae* complex were the most dominant taxa. Similar to biotype 1, biotype 4 included samples from a wide range of latitudes from different regions, but was dominated by assemblages from the Low Arctic tundra and had the lowest TN values. The strongest indicator taxa in biotype 4 included *Tabellaria flocculosa*, *Achnanthydium kriegeri*, and the *Psammothidium marginulatum/scoticum/lacus-vulcani/levanderi* complex, and taxa with the highest relative abundances included *A. minutissimum*, the *F. capucina* complex, and *A. kriegeri*.

## 3.2 | Paleolimnological data: assessment of spatial and temporal variability

### 3.2.1 | Before and after snapshot analyses

Mapping of the B-C dissimilarity coefficients displayed a wide spatial variability in the degree of change between modern and pre-industrial diatom assemblages (14–91%) across the 116 study lakes

**TABLE 2** Description of water chemistry, stream substrate, climate and geospatial data for lake surface sediment biotypes characterised by diatom clusters

|   | Biotype  |  |  |  |  |   |
|---|--|--|--|--|--|---|
|   | 1  | 2  | 3  | 4  | 5  | 6   |
| Number of samples                       | 64   | 236  | 211  | 26   | 80   | 64  |
| Latitude (°)                            | 65 <sup>a</sup><br>54–68   | 69 <sup>b</sup><br>59–75                         | 64 <sup>a</sup><br>53–67   | 70 <sup>b</sup><br>64–72                                   | 79 <sup>c</sup><br>76–82                   | 71 <sup>b</sup><br>62–76  |
| ABA High Arctic zone                    | 0 <sup>a</sup>   | 0 <sup>b</sup>                                   | 0 <sup>a</sup>   | 0 <sup>a,b</sup>   | 100 <sup>c</sup>                           | 31 <sup>b</sup>   |
| (% of hydrobasin)                       | 0–0  | 0–100  | 0–0  | 0–100  | 100–100                                    | 0–100   |
| ABA Low Arctic zone                     | 0 <sup>a</sup>   | 19 <sup>a,b</sup>                                | 0 <sup>a,b</sup>   | 69 <sup>a,b</sup>  | 0 <sup>a,c</sup>                           | 0 <sup>a,c</sup>  |
| (% of hydrobasin)                       | 0–100  | 0–100  | 0–100  | 0–100  | 0–0  | 0–70  |
| ABA Subarctic zone                      | 100 <sup>a</sup>   | 0 <sup>b</sup>                                   | 40 <sup>c</sup>  | 0 <sup>b,c,d</sup>   | 0 <sup>d</sup>                             | 0 <sup>b,c</sup>  |
| (% of hydrobasin)                       | 0–100  | 0–100  | 0–100  | 0–100  | 0–0  | 0–100   |
| Terrestrial ecoregion (% of hydrobasin) | >50<br>Iceland-boreal birch forests and alpine tundra & Canadian Shield, boreal forest<br>(64) | Mixed (mainly different tundra regions)<br>(236) | >50 Eastern Canadian Shield boreal forest & Low Arctic tundra (Canada, NWT)<br>(211) | >30 Arctic coastal tundra (north coasts of Alaska)<br>(26) | >80 High Arctic tundra (Canada)<br>(80)    | >70 High Arctic tundra & Canadian Shield, boreal forest<br>(64) |
| Average July temperature (°C)           | 12 <sup>b</sup><br>7–15  | 10 <sup>c</sup><br>4–13                          | 12 <sup>b</sup><br>7–15  | 9.9 <sup>b,c</sup><br>7–14                                 | 2.6 <sup>a</sup><br>2–4                    | 9.7 <sup>c</sup><br>3–15  |
| Mean annual temperature (°C)            | -4 <sup>b</sup><br>(-9)–2  | -9 <sup>c</sup><br>(-16)–0.6                     | -4 <sup>b,d</sup><br>(-10)–0.1   | -9 <sup>c,d</sup><br>(-12)–2                               | -16 <sup>a</sup><br>(-18)–(-16)            | -10 <sup>c</sup><br>(-16)–(-4)                                  |
| Mean annual precipitation (mm)          | 33 <sup>a</sup><br>18–83   | 26 <sup>b</sup><br>11–59                         | 37 <sup>a</sup><br>18–71   | 21 <sup>b,c</sup><br>10–83                                 | 9.1 <sup>d</sup><br>8.7–13                 | 14 <sup>c</sup><br>8.7–27                                       |
| Total nitrogen (mg/L)                   | 0.32 <sup>a,d</sup><br>0.19–0.51<br>(11)   | 0.43 <sup>a,b,d</sup><br>0.25–1.00<br>(21)       | 0.17 <sup>a,c</sup><br>0.09–0.41<br>(74)   | 1.29 <sup>a,b,d</sup><br>0.79–1.79<br>(2)                  | 0.35 <sup>a,b,d</sup><br>0.14–0.76<br>(72) | 0.64 <sup>a,b</sup><br>0.39–1.43<br>(42)                        |
| Total phosphorus (mg/L)                 | 0.007 <sup>a,b</sup><br>0.004–0.017<br>(24)  | 0.01 <sup>a,c</sup><br>0.004–0.023<br>(153)      | 0.007 <sup>a,b</sup><br>0.003–0.017<br>(112)   | 0.01 <sup>a,b,c</sup><br>0.004–0.03<br>(20)                | 0.01 <sup>c</sup><br>0.005–0.078<br>(75)   | 0.01 <sup>a,c</sup><br>0.006–0.02<br>(56)                       |
| Dissolved organic carbon (mg/L)         | 6.5 <sup>b,d</sup><br>0.01–116<br>(24)   | 3.9 <sup>b,c</sup><br>0.013–11<br>(172)          | 1.8 <sup>a,d</sup><br>0.004–13<br>(88)   | 9 <sup>b,d</sup><br>2.8–17<br>(21)                         | 2.6 <sup>c,d</sup><br>0.9–7.5<br>(77)      | 9.2 <sup>b,d</sup><br>3.7–27<br>(56)                            |
| Calcium (mg/L)                          | 3.4 <sup>a</sup><br>0.78–35<br>(47)  | 6.2 <sup>a,b</sup><br>1.7–31<br>(197)            | 0.9 <sup>c</sup><br>0.29–2.7<br>(193)  | 7.2 <sup>a,d</sup><br>2.6–31<br>(23)                       | 23 <sup>d</sup><br>2.6–61.8<br>(74)        | 11 <sup>b,d</sup><br>1.8–32<br>(59)                             |
| pH                                      | 7.4 <sup>b</sup><br>6.6–8.2<br>(32)  | 7.7 <sup>b</sup><br>7.1–8.4<br>(81)              | 6.8 <sup>a</sup><br>5.9–7.9<br>(155)   | 7.4 <sup>b</sup><br>7–7.9<br>(10)                          | 7.7 <sup>b</sup><br>6.7–8.4<br>(71)        | 7.9 <sup>b</sup><br>7.1–8.5<br>(49)                             |
| Maximum lake depth (m)                  | 13 <sup>a</sup><br>6–41<br>(61)  | 3.2 <sup>b</sup><br>1.3–11<br>(186)              | 6.1 <sup>c</sup><br>1.8–18<br>(182)  | 2.1 <sup>b,d</sup><br>1.1–10<br>(24)                       | 0.3 <sup>e</sup><br>0.2–1.1<br>(31)        | 1.9 <sup>d,e</sup><br>0.7–5<br>(39)                             |

(Continues)

TABLE 2 (Continued)

|  | Biotype                    |                                    |  |   |                                    |                                    |
|--|----------------------------|------------------------------------|--|---|------------------------------------|------------------------------------|
|  | 1                          | 2                                  | 3  | 4 | 5                                  | 6                                  |
| Diatom assemblages                       | <i>Discostella</i> complex | <i>Stausirella pinnata</i> complex | <i>Frustulia rhomboides</i> complex  | - | <i>Caloneis</i> spp.               | <i>Achnantheidium minutissimum</i> |
| Strong indicator taxa (ISA) <sup>†</sup> |                            | <i>Stausira construens</i> complex | <i>Encyonema gaeumannii/perpusillum</i> complex<br><i>Fragilaria virescens</i> complex<br><i>Aulacoseira distans</i> complex<br><i>Aulacoseira perglabra</i> complex |   | <i>Nitzschia perminuta</i> complex |                                    |
| Diatom assemblages                       |                            | <i>S. construens</i> complex       | -  | - | <i>Nitzschia perminuta</i> complex | <i>Nitzschia perminuta</i> complex |
| Most frequent taxa (>10%) <sup>†</sup>   |                            | <i>S. pinnata</i> complex          |  |   |                                    |                                    |

Note: For each variable, the median value is in the upper row, and below are the 10th to 90th percentile values. Significant differences (Kruskal–Wallis rank sum test with multiple comparisons) are depicted by superscripted letters. Arctic zone classification follows ABA classification zones (<http://geo.abds.is/geonetwork>). Not all sites had a complete suite of environmental variables; the number of sites with available data is in parentheses. The strong indicator taxa identified by indicator species analysis (ISA, IndVal >0.5) and the taxa with >10% relative abundance are also presented.

<sup>†</sup>See Table S3 for detailed results on the diatom assemblage structure and all indicator taxa for each biotype.

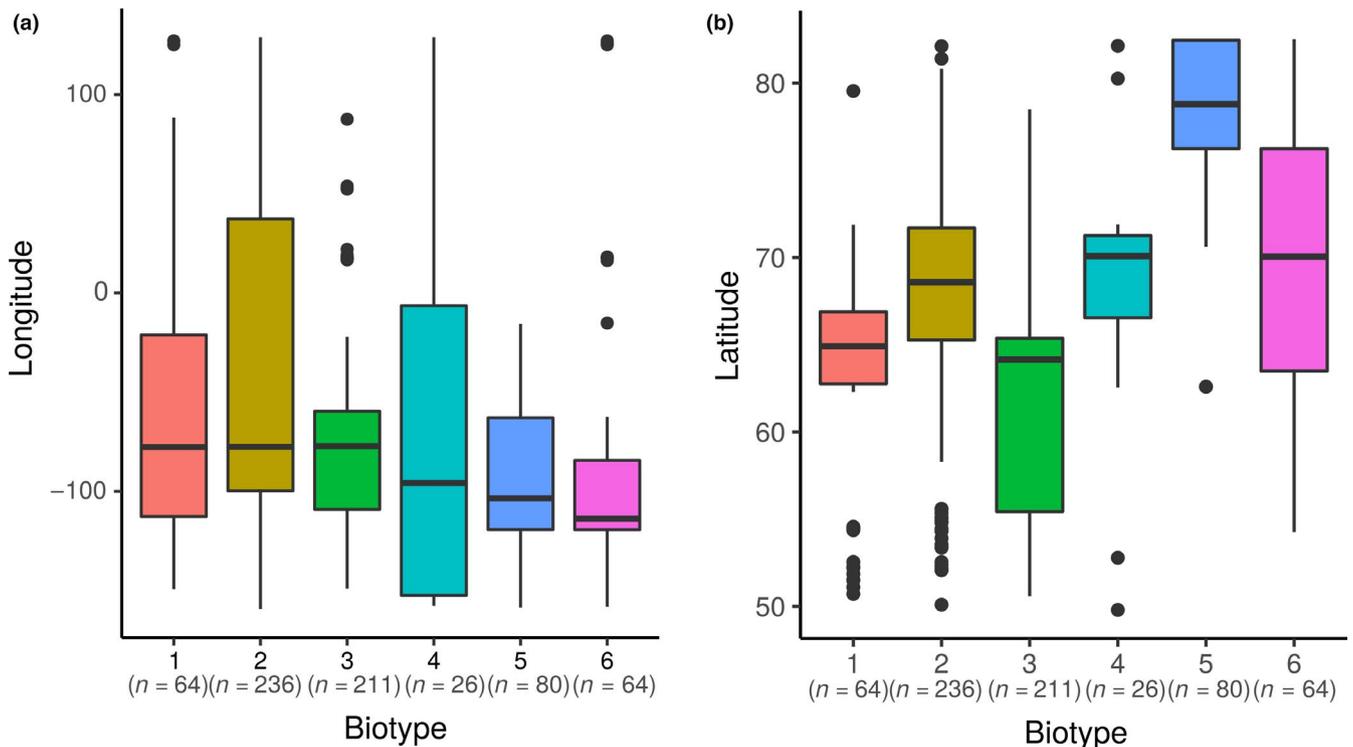


FIGURE 5 Diatom biotypes (self-organising map groups) of lake surface sediment samples versus (a) longitude and (b) latitude. Boxplots show median and interquartile range

(Figure 7). In North America, western (Tuktoyaktuk and Alaska) and High Arctic clusters (Ellesmere Island and other High Arctic islands) displayed some of the greatest differences between modern and

pre-industrial diatom assemblages, followed by lakes from the LA and SA (boreal forest and transition) Canadian regions (NWT and Hudson Bay Lowlands). Lakes located in the central and eastern

**TABLE 3** Description of water chemistry, stream substrate, climate and geospatial data for stream scrape biotypes characterised by diatom clusters

|   | Biotype                                  |   |  |   |
|---|--|---|--|---|
|   | 1  | 2   | 3  | 4   |
| Number of samples   | 212                                      | 60  | 74   | 73  |
| Latitude (decimal °)  | 62 <sup>a</sup><br>55–70                 | 72 <sup>b</sup><br>60–82  | 69 <sup>b</sup><br>67–70   | 62 <sup>a</sup><br>59–73  |
| ABA High Arctic zone (% of hydrobasin)                      | 0 <sup>b</sup><br>0–0                    | 58 <sup>a</sup><br>0–100  | 0 <sup>b</sup><br>0–30   | 0 <sup>b</sup><br>0–100   |
| ABA Low Arctic zone (% of hydrobasin)                       | 0 <sup>b</sup><br>0–100                  | 0 <sup>b</sup><br>0–73  | 0 <sup>b</sup><br>0–100  | 66 <sup>a</sup><br>0–100  |
| ABA subarctic zone (% of hydrobasin)                        | 88 <sup>a</sup><br>0–100                 | 0 <sup>b</sup><br>0–34  | 100 <sup>a</sup><br>0–100  | 0 <sup>b</sup><br>0–65  |
| Terrestrial ecoregion (% of hydrobasin)                     | Mixed<br>(212)                           | >50 High Arctic tundra & Middle Arctic tundra<br>(60)                       | >50 Scandinavian taiga<br>(75)   | Mixed (mainly different tundra regions)<br>(73)   |
| Average July temperature (°C)                               | 11 <sup>a</sup><br>8.5–13                | 7.8 <sup>b</sup><br>1.9–10  | 12 <sup>c</sup><br>9.6–14  | 9.2 <sup>d</sup><br>3.6–12  |
| Mean annual temperature (°C)                                | −3.9 <sup>a</sup><br>−7.1 to 0           | −11 <sup>b</sup><br>−19 to (−5.1)   | −1.3 <sup>a</sup><br>−9.2 to 0.3   | −6.6 <sup>b</sup><br>−15 to (−4.1)  |
| Mean annual precipitation (mm)                              | 42 <sup>a</sup><br>29–57                 | 12 <sup>b</sup><br>11–56  | 37 <sup>c</sup><br>11–46   | 32 <sup>c</sup><br>18–56  |
| Total nitrogen (mg/L)                                       | 0.15 <sup>b</sup><br>0.05–0.45<br>(71)   | 0.15 <sup>b</sup><br>0.04–0.76<br>(49)                                      | 0.22 <sup>b</sup><br>0.12–0.4<br>(22)  | 0.1 <sup>a</sup><br>0.05–0.19<br>(32)   |
| Total phosphorus (mg/L)                                     | 0.004 <sup>b</sup><br>0.001–0.01<br>(73) | 0.005 <sup>b</sup><br>0.002–0.04<br>(53)                                    | 0.02 <sup>a</sup><br>0.007–0.03<br>(40)  | 0.006 <sup>b</sup><br>0.002–0.08<br>(34)  |
| Dissolved organic carbon (mg/L)                             | 2.7 <sup>b</sup><br>0.8–9.5<br>(20)      | 2.4 <sup>b</sup><br>0.4–9.8<br>(48)   | 7.3 <sup>a</sup><br>5.3–16<br>(18)   | 1.8 <sup>b</sup><br>0.4–5.2<br>(25)   |
| Calcium (mg/L)  | 5.4 <sup>a,c</sup><br>1.8–33.8<br>(53)   | 26 <sup>b</sup><br>6.1–63<br>(53)   | 12 <sup>a,b</sup><br>3.9–30<br>(22)  | 2.5 <sup>a,c</sup><br>0.7–20<br>(32)  |
| pH  | 7.1 <sup>b</sup><br>6.7–8.2<br>(53)      | 8.1 <sup>a</sup><br>7.7–8.4<br>(44)   | 6.8 <sup>b</sup><br>6.6–7.2<br>(23)  | 6.9 <sup>b</sup><br>6.6–8.1<br>(23)   |
| Catchment area (km <sup>2</sup> )                           | 329 <sup>a</sup><br>11–10358<br>(105)    | 57 <sup>b</sup><br>14–493<br>(32)   | 37 <sup>b</sup><br>4.3–394<br>(54)   | 153 <sup>a</sup><br>19–4505<br>(33)   |
| Sand substrate (%)  | 0.5 <sup>b</sup><br>0–13<br>(30)         | 1.0 <sup>b</sup><br>0–31<br>(38)  | 74 <sup>a</sup><br>0–95<br>(18)  | 2.2 <sup>b</sup><br>0–12<br>(30)  |
| Diatom assemblages Strong indicator taxa (ISA) <sup>†</sup> | <i>Achnanthydium minutissimum</i>        | <i>Diatoma moniliformis/tenuis</i><br><i>Synedra cyclopus/Hannaea arcus</i> | <i>Rossethidium pusillum/anastasiae</i><br><i>Fragilaria tenera</i> complex<br><i>Eunotia incisa</i> complex | <i>Tabellaria flocculosa</i> complex<br><i>Achnanthydium kriegeri</i><br><i>Psammothidium marginulatum/scoticum/lacus vulcani/levanderi</i> |

(Continues)

Canadian Arctic (lower islands of the Arctic Archipelago, Baffin Island and northernmost Ungava, Québec) experienced the lowest degree of diatom change between pre-industrial and modern assemblages.

Lakes representing Eurasia were too scarce in our snapshot paleolimnological study (Siberia = 2, Finland = 3) to determine the magnitude of diatom assemblage changes since the pre-industrial era for

TABLE 3 (Continued)

|  | Biotype                |  |                               |  |
|--|------------------------|--|-------------------------------|--|
|  | 1                      | 2  | 3                             | 4  |
| Diatom assemblages                     | <i>A. minutissimum</i> | <i>A. minutissimum</i> , <i>Fragilaria</i>   | <i>A. minutissimum</i>        | <i>A. minutissimum</i>   |
| Most frequent taxa (>10%) <sup>†</sup> |                        | <i>capucina</i> complex<br><i>S. cyclosum</i> / <i>H. arcus</i><br><i>D. moniliformis/tenuis</i> | <i>R. pusillum/anastasiae</i> | <i>F. capucina</i> complex<br><i>T. flocculosa</i> complex<br><i>A. kriegeri</i> |

Note: For each variable, the median value is in the upper row, and below are the 10th to 90th percentile values. Significant differences (Kruskal–Wallis rank sum test with multiple comparisons) are depicted by superscripted letters. Arctic zone classification follows ABA classification zones (<http://geo.abds.is/geonetwork>). Not all sites had a complete suite of environmental variables; the number of sites with available data is in parentheses. The strong indicator taxa identified by indicator species analysis (ISA, IndVal >0.5) and the taxa with >10% relative abundance are also presented.

<sup>†</sup>See Table S3 for detailed results on the diatom assemblage structure and all indicator taxa for each biotype.

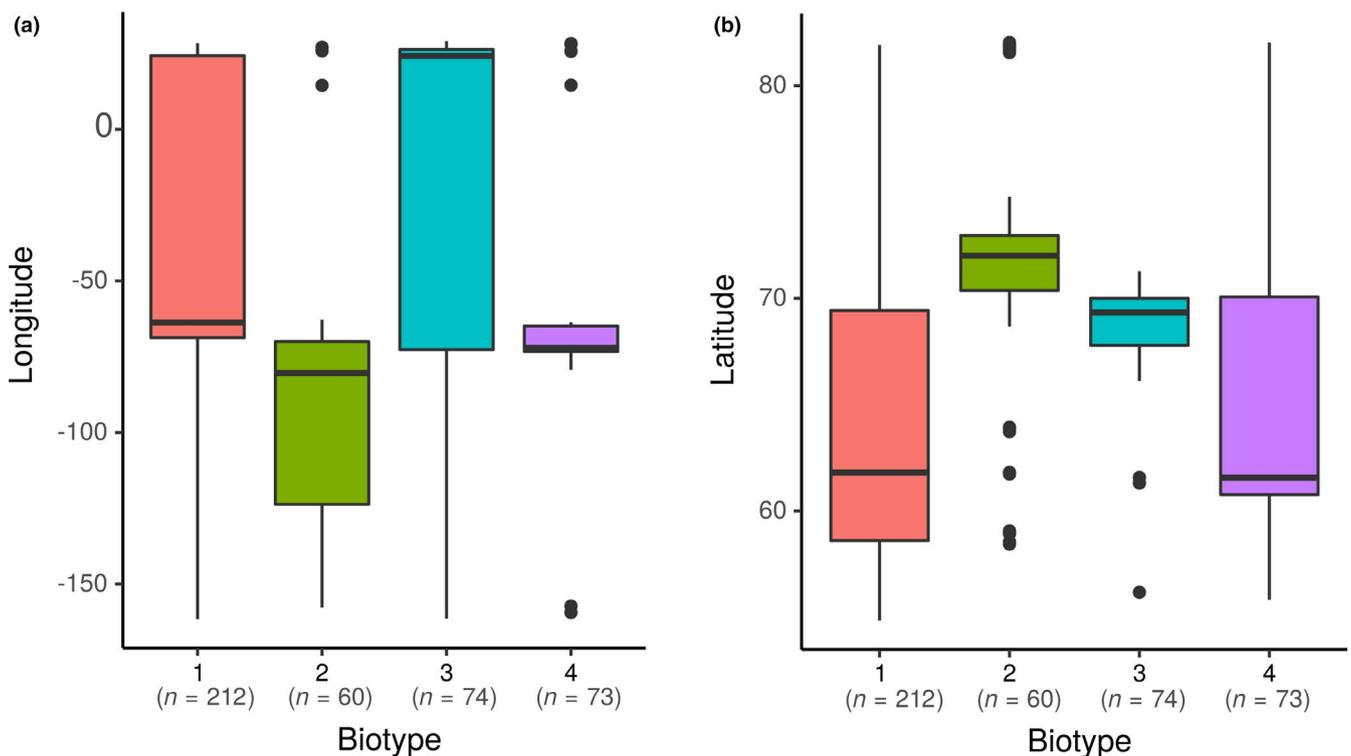
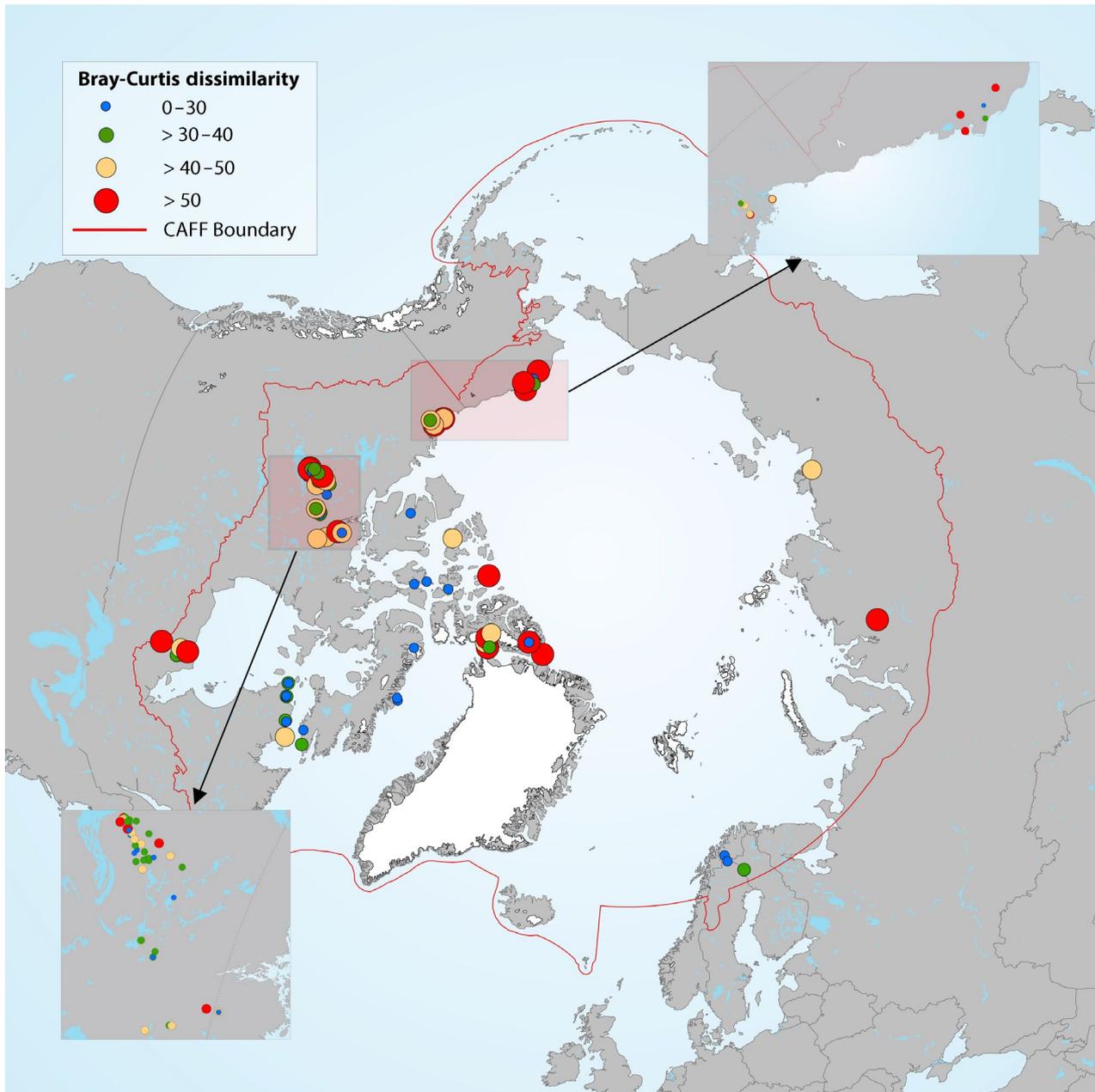


FIGURE 6 Diatom biotypes (self-organising map groups) of stream scrapes versus (a) longitude, and (b) latitude. Boxplots show median and interquartile range

these regions. Despite the notable changes detected in many of the 116 lakes (visualised through mapped B-C coefficients presented in Figure 7), ANOSIM results determined that when samples were averaged across all lakes, the differences between modern and pre-industrial diatom assemblages were minimal ( $R = 0.01$ ,  $p < 0.05$ ). A two-way ANOVA on B-C dissimilarity values for each lake looked more directly at factors affecting the amount of dissimilarity between paired snapshot samples. The results of the ANOVA indicated that lake depth and ecozone did not have a significant effect on the B-C dissimilarity matrix ( $p > 0.05$  for all terms in the ANOVA model). There was strong spatial heterogeneity in the degree of change between modern and pre-industrial samples, which suggests that lake types respond differently to change in different biomes, and there may exist stronger predictors of change that were not included in the analysis.

At the taxon level, there were clear differences between modern and pre-industrial samples in the percent relative abundances of some of the more common diatoms, as shown in the 1:1 scatter plots (Figure 8). In general, deeper lakes (particularly in the BF and LA) contained higher abundances of the planktonic *Discostella stelligera* complex (*D. stelligera*, *Discostella pseudostelligera*) in the modern samples, whereas *N. perminuta* was more common in the modern assemblages of ponds, particularly in the HA (Figure 8). A group of small *Psammothidium* taxa (*P. marginulatum*, *P. scoticum*, *P. lacus-vulcani*, *P. levanderi*) occurred at higher relative abundances in the modern sediments of most lakes, particularly in deeper HA and LA lakes (Figure 8). A group of the more common tycho planktonic *Aulacoseira* taxa (*Aulacoseira subarctica*, *A. perglabra*, *Aulacoseira lirata*) occurred in distinctly higher relative abundances in the pre-industrial samples from

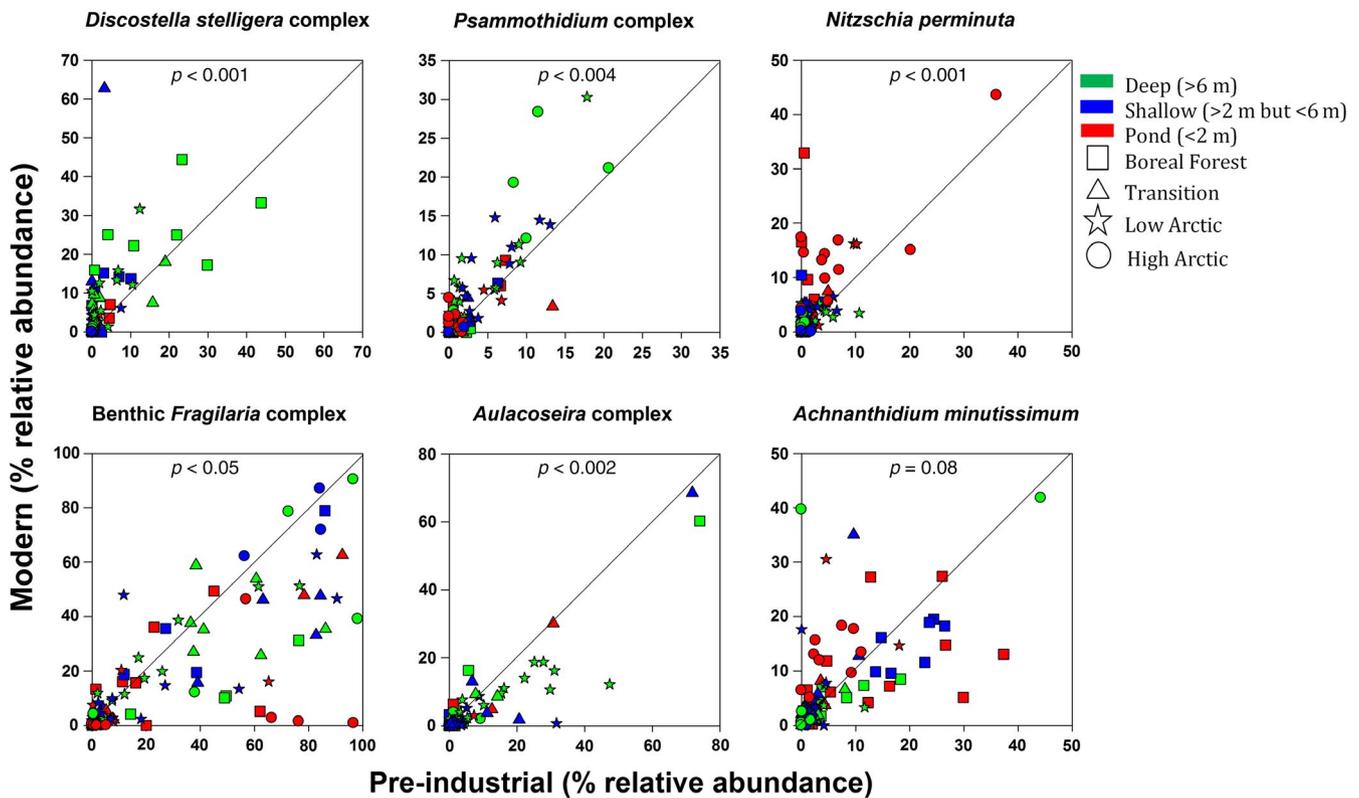


**FIGURE 7** Map showing the magnitude of change in diatom assemblages across the circum-Arctic lakes based on Bray–Curtis dissimilarity coefficients between pre-industrial and modern sedimentary intervals (i.e. before and after snapshots) of the 116 lakes. Boundaries for the Bray–Curtis dissimilarity categories are based on distribution quartiles, where the lowest values (small blue dots) represent the lowest degree of change, and the highest values (large red dots) represent the highest degree of change in diatom assemblage composition between top and bottom samples in each lake

deeper lakes in all ecozones but particularly in the LA (Figure 8). Species of small benthic *Fragilaria* sensu lato taxa (*Staurosirella pinnata*, *Staurosira construens*, *Pseudostaurosira brevistriata*) were the most common diatoms across all zones and all depth categories and occurred in distinctly higher relative abundances (often dominating the assemblages) in the pre-industrial sediments. *Achnanthyidium minutissimum* was common in both the pre-industrial and modern sediments of lakes in all ecozones and in all depth categories, with no clear directional trend when considering all samples together.

### 3.2.2 | Full core analyses: diatom $\beta$ -diversity (species turnover) temporal trends

Beta-diversity values (DCCA: length of gradient, scaled in standard deviation or turnover units) for each lake that had detailed diatom records from  $^{210}\text{Pb}$ -dated sediment cores were used to estimate the degree of diatom compositional change over the past c. 200 years (sensu Smol et al., 2005). The results were mapped to provide an overview of temporal and spatial variability in the amount of species turnover across the circum-Arctic region (Figure 9), with  $\beta$ -diversity



**FIGURE 8** Scatter plots of common diatom taxa and taxonomic groupings showing the relationship between the percent relative abundances recorded in the pre-industrial and modern sedimentary intervals used in the before and after snapshot paleolimnological analysis of the 116 circum-Arctic lakes. Samples that plot above the 1:1 line have higher relative abundances of that taxon in the modern assemblages than in the pre-industrial assemblages. Significant differences between all modern and all pre-industrial diatom assemblages were determined using a Wilcoxon signed-rank test

binned into categories based on the distribution of standard deviation units from all cores, which were also consistent with categories determined by Smol et al. (2005).

High spatial variability in the amount of diatom species turnover in the past c. 200 years was evident from our analyses. Northernmost Québec, Baffin Island, the Central Canadian Archipelago, and northern Finland showed the least amount of change (highest inertia). Sites in the HA and north-eastern NWT showed moderate magnitude of compositional change, whereas the greatest increase in  $\beta$ -diversity was observed in the westernmost cluster of sites, near the Beaufort Sea, the west coast of Hudson Bay, and in the Hudson Bay Lowlands. However, variability in diatom  $\beta$ -diversity among lakes within each of these regions was high, with large changes evident in some lakes and only moderate changes in others.

## 4 | DISCUSSION

### 4.1 | Trends in contemporary diatom assemblages

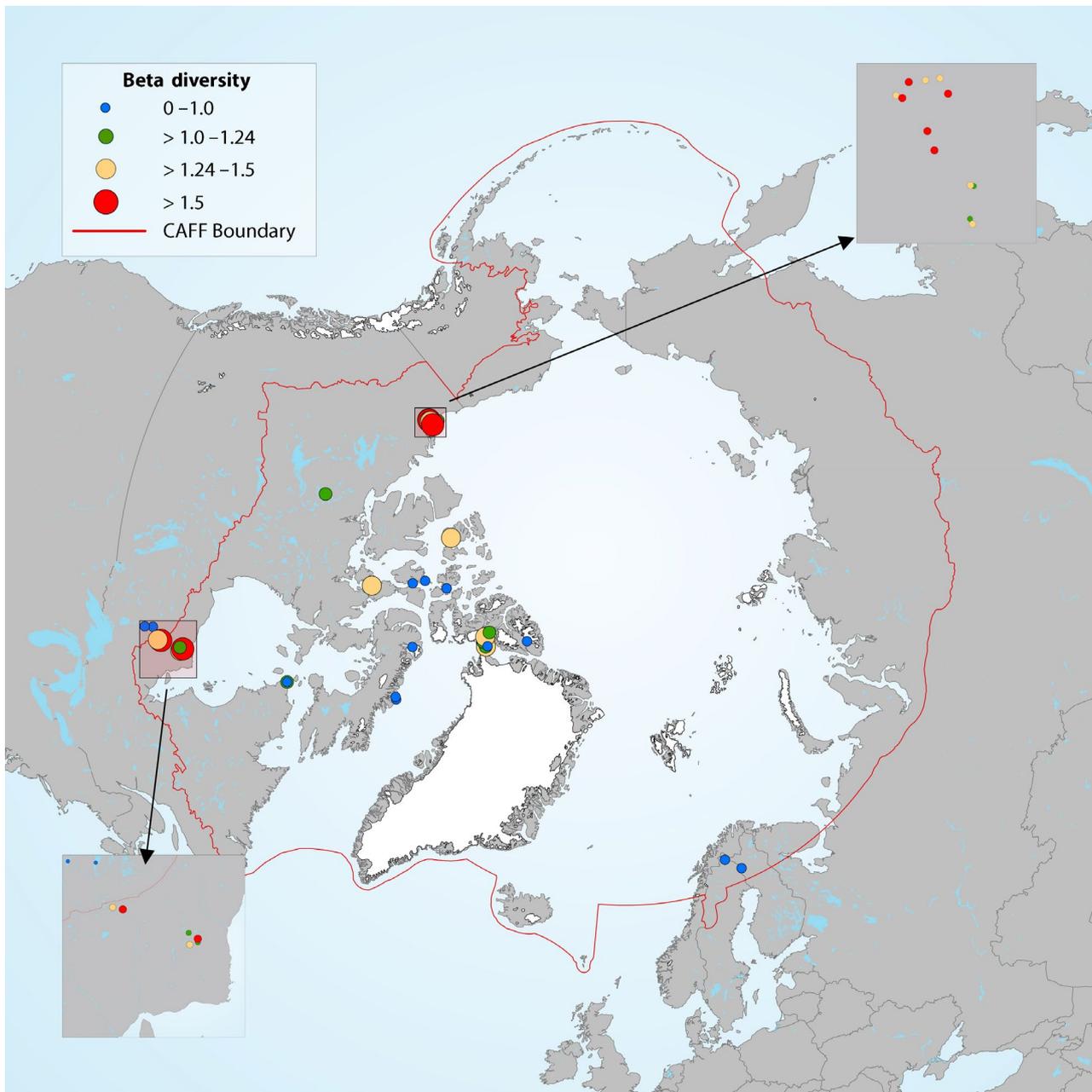
#### 4.1.1 | Diversity

Circum-Arctic trends in diatom species richness provide a first step toward better understanding of: (1) where sampling efforts should

be maximised; and (2) which environmental factors can influence these trends. This baseline information will be important for guiding the development of future monitoring and conservation strategies for these under-studied high-latitude freshwater systems.

Diatom biogeographical and biodiversity trends varied at different spatial scales across the Arctic, as well as between streams and lakes of different depths. Despite this high variability, our findings are consistent with earlier studies showing that both lentic and lotic systems exhibited a subtle decrease in richness with increasing latitude, and an overall unimodal distribution with latitude, with maximum richness occurring between 60°N and 75°N. A combination of factors such as differences in the length of the growing season, ice dynamics, water chemistry, and dispersal limitation probably influences these geographical trends in richness.

In Arctic lakes and ponds, the decreasing trend of biodiversity with latitude has been associated with lower temperatures, a longer ice cover period, and a shorter algal growing season at higher latitudes (Douglas & Smol, 2010; Michelutti, Douglas, et al., 2003a; Wrona et al., 2013). Latitudinal differences in lake ice dynamics can alter species richness as the extent of ice and snow cover affects important drivers of biological communities such as light penetration and mixing regimes (Hobbie, 1980; Rautio et al., 2011; Smol & Douglas, 2007a; Vincent et al., 2013). When ice cover duration is extensive, High Arctic shallow lakes and ponds



**FIGURE 9** Map showing the magnitude of diatom compositional change in the past c. 200 years across the circum-Arctic, as estimated by DCCA for 52 dated sedimentary diatom records. Boundaries for the  $\beta$ -diversity categories are based on DCCA results and expressed as *SD* units of species turnover, where the smallest values (small blue dots) represent the lowest degree of change, and the larger values (large red dots) represent the highest degree of change in diatom assemblage composition

tend to be species-depauperate (often represented almost entirely by pioneering species associated with rocky or sediment substrates). In contrast, when the ice-free season is longer, these shallow systems tend to be much more species-rich, represented by periphytic taxa (Smol & Douglas, 2007a; Smol et al., 2005) associated with the establishment of aquatic macrophytes and mosses (Douglas & Smol, 2010; Michelutti, Douglas, et al., 2003a; Rohde, 1992; Vincent et al., 2013). There are numerous limnological variables that can also be affected by climate-related changes in lakes and streams (e.g. pH, alkalinity, nutrients), providing additional important influences on the richness and composition of diatom

assemblages (Douglas & Smol, 2010; Michelutti, Douglas, & Smol, 2006; Passy et al., 2018; Smol & Douglas, 2007a; Wolfe, 2002). It is likely that diatom richness in circum-Arctic streams is influenced by similar factors as in lakes, but stream system studies are less common (but see Lebourcier et al., 2019; Pajunen, Luoto, & Soininen, 2016). In a recent study using data from stream localities in the U.S.A. and Finland, Passy et al. (2018) showed that a decline in diatom species richness with increasing latitude could be coupled to decreasing temperature and nutrients (total phosphorus concentrations), suggesting that factors other than climate are also important drivers of species richness in high latitude regions.

Diversity at higher latitudes also may be limited by dispersal constraints, including the size of the regional diatom pool, habitat availability, or connectivity between habitats (Hillebrand, 2004; Vyverman et al., 2007).

Although Soininen et al. (2016) previously found a positive relationship between latitude and stream diatom richness, these findings are actually consistent with our study because their most northern sites were in Finland at latitudes that correspond to the maximum richness observed in our study (60–75°N). Our observed unimodal pattern may be due to a combination of factors including differences in glaciation history and resource variability. Our finding of high diatom richness in lakes and streams in Alaska is consistent with earlier studies from the region (Foged, 1971). It has been speculated that because Alaska experienced limited ice extent during the last (and earlier) glaciation, many lakes and streams in the region have been in existence for millennia, which may be a contributing factor to the high number of diatom taxa observed in Alaskan water bodies (Foged, 1971). Sites in this latitude range (60°N to 75°N) were also in general the most variable in terms of diversity for both streams and lakes. Variability of diversity at similar latitudes across the Arctic may be expected given the range in water body types and sizes, diverse catchment characteristics, and settings that collectively can affect diatom species richness. Passy (2010) and Passy et al. (2018) noted the important impact of resource supply, and variability of resource supply, on diatom richness. In our study, we found that where richness was highest, samples covered a wider range of longitudes thereby containing a relatively wide range of habitat and climate conditions. Both Passy (2010) and Soininen et al. (2016) speculated that high levels of iron and other chemical compounds exported by wetlands were driving high richness at their sites. Although sampling effort was insufficient to capture all diversity, our species accumulation curves for both lakes and streams nevertheless showed that species richness in the Low Arctic was higher than in the sub-Arctic. Moreover, diversity hotspots were more prevalent across the Low Arctic than other Arctic zones. Together, these results suggested that the patterns in species richness that we observed reflected differences in local and regional environmental factors rather than differences in sampling effort.

#### 4.1.2 | Biotypes for lake and stream environments

The establishment of current Arctic biotypes identified by SOMs (1) provides context and enables informed assessments of future changes in diatom distributions resulting from continued global change; (2) estimates potential future diatom assemblage distributions so that global monitoring programmes will be better prepared to account for changing biotypes; and (3) determines what the current spatial distribution of diatom assemblages are across the Arctic region and identifies whether there are diatom taxa that are particularly indicative of a given environment (whether they are related to latitude or other factors).

#### *Lake diatom biotypes*

Lake surface sediment biotype 1, characterised by assemblages from deep oligotrophic and circumneutral lakes, were predominantly from the sub-Arctic treeline regions of Canada and Iceland. Planktonic diatoms including small-celled cyclotelloid taxa as well as elongate diatoms that typify this biotype have an ecological advantage over larger, heavier-celled taxa when warmer conditions and longer ice-free periods increase lake thermal stability. The high surface area to volume ratios of these planktonic taxa slow their sinking velocity (Litchman, Klausmeier, Miller, Schofield, & Falkowski, 2006) increasing their ability to compete for limiting light and nutrient resources (Ptacnik, Diehl, & Berger, 2003; Winder, Reuter, & Schadlow, 2009) during periods of weaker water column mixing. In deeper sub-Arctic lakes, these warming-related changes in water column properties have increased the prevalence of planktonic taxa, such as *D. stelligera*, capable of prolific reproduction when conditions are favourable (Rühland et al., 2008, 2015; Saros, Northington, Anderson, & Anderson, 2016; Smol et al., 2005). The lack of High Arctic lakes contributing to diatom biotype 1 is probably due to the thermal inertia of deeper lakes at these higher latitudes (Michelutti, Douglas, et al., 2003a). Extensive ice and snow cover for most (if not all) of the short summer would inhibit the formation of conditions that are ideal for the growth of these planktonic taxa (Rühland et al., 2015).

The largest grouping of diatom samples belongs to biotype 2 comprising a diverse group of lakes and ponds. The small benthic fragilarioid taxa typical of this biotype are one of the most opportunistic and ubiquitous diatom groups reported in the literature (Schmidt, Kamenik, Lange-Bertalot, & Klee, 2004) and are commonly reported in lakes across the circum-Arctic (Douglas & Smol, 1995; Griffiths, Michelutti, Sugar, Douglas, & Smol, 2017; Laing, Pienitz, & Smol, 1999; Lehnher et al., 2018; Pienitz et al., 1995; Rühland et al., 2003; Saulnier-Talbot, Larocque-Tobler, Gregory-Eaves, & Pienitz, 2015; Schmidt et al., 2004; Smith, 2002; Weckström et al., 1997; Zgrundo, Wojtasik, Convey, & Majewska, 2017). The generalist nature of these benthic diatoms results in their occurrence in a wide range of habitats where they are able to tolerate low light conditions, as, for instance, under ice (Lotter & Bigler, 2000) or in turbid waters (Karst-Riddoch, Pisaric, Youngblut, & Smol, 2005).

Biotype 3 occurred in a large number of lakes, predominantly from sub-Arctic regions of Canada (as well as Greenland), that were significantly lower in pH, had lower calcium concentrations, and lower organic carbon content than the other biotypes. Diatom taxa indicative of this biotype, such as the heavy, large-celled tycho-lanktonic *Aulacoseira* taxa, have been commonly reported in deeper, well-mixed, slightly acidic to circumneutral oligotrophic sub-Arctic lakes above the treeline (Petryakova, Herzsuh, Gorodnichev, & Wetterich, 2018; Rühland et al., 2008, 2015, 2003). These tycho-lanktonic taxa probably prevail there because wind-induced mixing is facilitated by the open conditions of the tundra zone (Rühland et al., 2003; Sorvari & Korhola, 1998).

Biotype 4 contained the smallest number of lakes, but with representatives from many countries. This biotype was characterised by the absence of both strong indicator taxa and dominant taxa,

reflecting large differences in environmental variables and diatom composition among lakes. Consequently, it was not clear what distinguished this biotype from the others, and more data are needed before understanding the underlying factors.

Biotype 5 most clearly represented High Arctic sites (predominantly ponds) from Canada, representing the coldest and driest conditions in the dataset. Consistent with the published research from this region, distinct diatom assemblages from surface sediment samples comprised periphytic diatoms, reflecting the low temperatures and short ice-free periods experienced in these high latitude shallow systems. The generalist species *N. perminuta* was the strongest indicator taxon for this biotype and is one of the most ubiquitous diatoms in the Canadian High Arctic as it is present in almost all shallow lakes and ponds (Antoniades, Douglas, & Smol, 2005a; Keatley, Douglas, & Smol, 2008; Lim, Smol, & Douglas, 2007). It often reaches highest relative abundances in Arctic sites that are naturally more nutrient rich than the typically ultra-oligotrophic ponds in other High Arctic regions (Griffiths et al., 2017; Keatley, Douglas, Blais, Mallory, & Smol, 2009; Lim, Douglas, Smol, & Lean, 2001). The aerophilous epiphytes that also characterise this High Arctic biotype (*Pinnularia obscura*, *Pinnularia borealis*, *P. marginulatum*, *Chamaepinnularia soehrensensis*, *Caloneis* taxa, and *Diademsis contenta*) have the ability to withstand periodic shoreline drying during the height of the summer when these shallow systems are exposed to 24-hr daylight, warmer temperatures, and low precipitation (Michelutti, Holtham, Douglas, & Smol, 2003b; Smol & Douglas, 2007a) and have been commonly reported in numerous shallow sites throughout the Canadian High Arctic (Antoniades et al., 2005a; Lim, 2004; Michelutti, Douglas, & Smol, 2007; Michelutti, Smol, & Douglas, 2006).

Biotype 6 is similar to biotype 5, but unlike the High Arctic ponds situated on barren land that characterised biotype 5, the High Arctic shallow systems of biotype 6 largely consist of sites from Mould Bay on Prince Patrick Island (Northwest Territories) that, relative to other High Arctic regions, contain dense vegetation cover and deep soils (Antoniades, Douglas, & Smol, 2003). Ponds and shallow lakes from Mould Bay are also distinct from other High Arctic regions in terms of water chemistry, such as higher concentrations of DOC and nutrients (Antoniades et al., 2003). This provides a plausible explanation for why these atypical High Arctic sites of biotype 6 shared similar diatom assemblages with shallow, sub-Arctic sites in Canada, as the boreal forest ecozone typically has higher concentrations of DOC and nutrients relative to sites north of Arctic treeline (Pienitz, Smol, & Lean, 1997b; Rühland & Smol, 2002; Saulnier-Talbot et al., 2020). Periphytic diatoms that typify biotype 6 include the generalist species *A. minutissimum* as well as *B. vitrea* and a variety of cymbelloid taxa. These taxa have been found to occur in higher relative abundances in sites with relatively high concentrations of DOC and TN from both the boreal forest (Rühland et al., 2003) and the Canadian High Arctic (Antoniades, Douglas, & Smol, 2005b). *Achnantheidium minutissimum* is one of the most widespread, commonly occurring

taxa found throughout the circum-Arctic from the boreal forest (Rühland & Smol, 2002) to the High Arctic (Keatley et al., 2008; Michelutti et al., 2007). Although *A. minutissimum* is regarded as having a wide tolerance for a variety of environmental conditions (i.e. a generalist) and is one of the most ubiquitous diatom taxa worldwide, Antoniades et al. (2005b) suggested that the sensitivity of *A. minutissimum* to increases in UV radiation (Vinebrooke & Leavitt, 1996) may have enabled this taxon to reach higher relative abundances in relatively high DOC systems that offer protection from UV radiation. Biotype 6 encompasses groups of shallow lakes and ponds from both the southernmost and northernmost latitudes of our study range, highlighting the importance that site-specific environmental factors can have on diatom species distribution in these highly complex Arctic landscapes.

#### Stream biotypes

Stream biotype 2, consisting of High Arctic sites, was typified by diatom taxa that reflect the relatively alkaline waters of this cold, dry ecozone. For example, both *H. arcus* and the *D. moniliformis/tenuis* complex have been classified as alkaliphilic to alkalibiontic (Van Dam, Mertens, & Sinkeldam, 1994). *Hannaea arcus* has been reported in Arctic streams and associated with rocky substrates, low temperatures and high velocities (Antoniades & Douglas, 2002), and *Diatoma* taxa have been observed in waters with high conductivity in Arctic regions (Griffiths et al., 2017).

Diatom assemblages in stream biotype 3 were predominantly from subarctic taiga regions of Fennoscandia, as well as Alaska, where pH and calcium concentrations were lower than those observed for stream biotype 2, and DOC content was higher than in all other biotypes. The oligotrophic, sandy streams in this group were characterised and dominated by diatom taxa associated with low pH, high DOC concentrations, and sand. For example, *Eunotia* taxa are unambiguous indicators of low pH values, and are common in humic waters (Lange-Bertalot, Båk, Witkowski, & Tagliaventi, 2011; Van Dam et al., 1994). Similarly, oligotrophic taxa such as the *R. pusillum/anastasiae* complex indicated the low nutrient (both TP and TN) values of this biotype, and the small epipsammic fragilarioid taxa (predominantly the *S. pinnata* complex) reflected the sandy substrate.

Both stream biotypes 1 and 4 comprised assemblages collected in sites located at similar latitudes, however, biotype 4 reflected the Low Arctic tundra, whereas biotype 1 predominantly reflected the sub-Arctic region (i.e. including boreal forest regions). Biotype 1 included assemblages from streams with generally larger catchment areas than biotype 4, whereas assemblages from biotype 4 were generally collected in streams with higher pH and calcium concentrations. Biotype 1 was characterised almost exclusively by the generalist *A. minutissimum* complex that has been reported to be sensitive to low pH values (Van Dam et al., 1994). Biotype 4 was characterised by several taxa more tolerant of low pH, such as *Eunotia* taxa, the *Frustulia rhomboides* complex, the *P. marginulatum* complex, and *T. flocculosa*, with the latter dominant in this biotype.

## 4.2 | Spatio-temporal trends in paleo diatom assemblages

The high variability in the magnitude and nature of changes in diatom assemblages over time reflects the large number of geographically diverse sites in this dataset. Therefore, the significant changes reported in some sites and the relative inertia of response in others will dampen broad-scale trends of change across the circum-Arctic. Furthermore, the 23-year span over which most paleolimnological data were collected must also be considered as certain regions of the Arctic have been sampled both prior to the onset of notable change (and muted diatom response) as well as after (and pronounced diatom response) within a given region. In particular, sedimentary diatom records from the eastern Canadian Arctic, near Hudson Bay in northern Quebec and Labrador, have changed little relative to the rest of the Arctic, largely because the persistence of Hudson Bay sea ice had maintained a cool environment (Smol et al., 2005). However, this is no longer the case as anthropogenic warming in the region has accelerated in recent decades (Hochheim & Barber, 2010, 2014). Diatom records more recently collected from the Hudson Bay Lowlands show one of the largest compositional changes in our study, consistent with a response to this new climate regime (Rühland, Paterson, Keller, Michelutti, & Smol, 2013).

The wide range of lake types comprising the sites studied in the before and after snapshot analysis across the circum-Arctic probably obscured assemblage-scale compositional trends, especially when all samples were assessed collectively. Many lakes did exhibit marked differences in diatom assemblages between pre-industrial and modern samples. Changes were particularly notable at the taxon level, with several diatom taxa showing striking and statistically significant differences between pre-industrial and modern samples that often varied with depth and latitude. For example, one of the most widely observed patterns of change in our dataset was a shift from assemblages dominated by small, benthic *Fragilaria* sensu lato taxa and large, heavy-celled *Aulacoseira* taxa to small-celled, planktonic *D. stelligera*. This trend of greater relative abundances of *D. stelligera* in modern samples was best expressed in the deeper lakes, particularly in the BF zone, as well as in many LA and T sites. This shift among taxa with distinctly different life strategies, particularly in deeper sub-Arctic and Low Arctic lakes, is consistent with warming-related changes in lake ice, stratification and mixing regimes, the depth of the epilimnion, and attendant changes in resource availability including light and nutrients reported in many regions (Rühland et al., 2008, 2015; Salmaso, 2005; Saros, Strock, McCue, Hogan, & Anderson, 2014; Winder & Sommer, 2012).

Other notable taxonomic differences between the modern and pre-industrial sediment samples also tie in well with the spatial trends observed in our contemporary lake sediments (biotypes). In particular, relative abundances of *N. perminuta* and the *Psammothidium* complex are notably higher in the modern sediments of ponds, particularly from the HA ecozone, consistent with this common taxon

characterising contemporary lake biotype 5. The ubiquitous nature of *A. minutissimum* frequently reported in the literature, and highlighted in lake biotype 6 of our contemporary dataset, is also reflected in our snapshot paleolimnological analysis, where it is one of the most common taxa recorded in both modern and pre-industrial sediments. It occurred in higher relative abundances in modern sediments of the HA ponds than in the corresponding pre-industrial samples. Recent warming and longer ice-free periods (Hochheim & Barber, 2010, 2014; Prowse et al., 2011; Prowse & Brown, 2010) have been reported to be the main driver of phytoplankton dynamics (Hodgson & Smol, 2008) and of changes in diatom assemblage composition throughout the circum-Arctic (Prowse et al., 2011; Rantala et al., 2017; Smol & Douglas, 2007a; Thompson et al., 2005). Our observation of an increase in the variety of epiphytic diatoms in the modern samples replacing low diversity assemblages dominated by epipelagic and epilithic fragilarioid diatoms in pre-industrial assemblages is consistent with a decrease in ice-cover extent and duration, resulting in an increase in the availability of habitats and plant substrates for benthic diatoms to exploit (Antoniades et al., 2005a; Douglas, Smol, & Blake, 1994; Griffiths et al., 2017).

Many of the taxon-specific trends examined in our 116 before and after snapshot analyses are also relevant to our full core paleolimnological analysis, but for these dated diatom profiles, we focused on the variability in the magnitude of species turnover over the past c. 200 years across the circum-Arctic. Our full core paleolimnological analysis indicated highly variable degrees of diatom species turnover in the past c. 200 years, both across and within the different geographical zones. This is to be expected with such a large spatial coverage of lakes as large changes in some lakes will be dampened by the relative inertia in others. Again, many lakes in this dataset experienced considerable compositional change over time. We observed varying degrees of change within and among the different geographic regions, indicating inter- and intra-regional variability. For example, the Canadian High Arctic region showed a wide range in the magnitude of species turnover from some of the smallest to some of the most marked compositional changes over the past c. 200 years. Although accelerated Arctic warming with longer ice-free periods and extended growing seasons across the circum-Arctic affect the types and availability of habitat (Douglas et al., 1994; Griffiths et al., 2017), and, in deeper lakes, changes stratification and mixing regimes (Rühland et al., 2015; Sorvari et al., 2002), site-specific differences across the circum-Arctic were numerous. Factors including lake depth and setting (shadiness, exposure, windiness) that can strongly affect ice cover dynamics (Griffiths et al., 2017; Keatley et al., 2008; Prowse & Brown, 2010), as well as differences in the degree of vegetation cover and soil development (Antoniades et al., 2003; Griffiths et al., 2017), probably explain some of this variability in diatom compositional turnover ( $\beta$ -diversity). Site-specific differences can affect Arctic lake systems and phytoplankton dynamics in numerous ways (e.g. Antoniades et al., 2003), but change in lake ice cover is one of the most pronounced and widespread (Rantala et al., 2017; Smol & Douglas, 2007a; Thompson et al., 2005). For example, deep HA lakes with extensive ice cover can register muted

and delayed responses to regional warming compared to nearby shallow lakes and ponds that experience a more dynamic ice cover (Antoniades et al., 2007; Michelutti, Douglas, et al., 2003a; Perren et al., 2012; Rühland et al., 2015). Even lakes that are almost limnologically identical and separated by <20 m were found to have strikingly different changes in diatom assemblage composition due to substantial contrasts in the degree of ice cover due to shade (Keatley et al., 2008), highlighting the important role of ice cover on diatom dynamics in high latitude lakes.

Our study of 52 dated diatom profiles exhibited the same overall regional pattern of diatom compositional turnover as the 42 diatom records reported by Smol et al. (2005), despite the fact that there was little overlap in samples between studies (four profiles in common). This is an important finding that speaks to the generality and strength of these regional trends that were not specific to a particular set of lakes. The easternmost regions of the Canadian Arctic, which have not warmed as much as the west and far north, showed the lowest degree of compositional turnover. At sites located in the central High-Arctic islands (in eastern and southern Baffin Island, as well as in northernmost Ungava [Québec], across the Hudson Strait)  $\beta$ -diversity values were smaller compared to the relatively large compositional turnover estimated for sites in Alaska. In contrast, the southernmost sites (the cluster of lakes and ponds in the southwestern Hudson Bay region, Hudson Bay Lowlands) showed high degrees of change in the most recently retrieved cores (c. 2010) from this region (in both snapshot and full core paleolimnological analyses). Warming in the Hudson Bay region only crossed a major climate threshold in the mid-1990s related to changes in Hudson Bay sea ice phenology and positive feedback responses, leading to rapid and pronounced increases in air and sea temperatures (Bhiry et al., 2011; Hochheim & Barber, 2010). These Hudson Bay Lowland sites with relatively high compositional turnover were collected decades after some of the records reported in the Smol et al. (2005) study. It is possible that some of the sedimentary records from Labrador and the northern Québec region (eastern Canadian Arctic) that showed minimal change in diatom composition (i.e. low  $\beta$ -diversity) at the time of their retrieval, that were highlighted in Smol et al. (2005), may now be starting to show signs of response to post-1990s warming, as observed in the Hudson Bay Lowlands (Rühland et al., 2013).

### 4.3 | Future biomonitoring

The assessment of spatial and temporal trends in Arctic freshwater biota, as well as any changes in their physical and biogeochemical habitats in response to a warming climate, requires a large-scale and harmonised monitoring programme. Efforts are now being made to establish harmonised and coordinated monitoring for circum-Arctic freshwaters by the Freshwater Group of the Circumpolar Biodiversity Monitoring Plan (Culp, Goedkoop, et al., 2012a; Culp, Lento, et al., 2012b; Lento et al. 2019). Knowledge of the spatial distribution of diatom assemblages (at the finest possible taxonomic level) across

this large geographic scale, in both lakes and streams, is essential to ensure sufficient coverage of biodiversity and to determine the composition of contemporary diatom assemblages that typify Arctic freshwater environments. The large-scale spatial trends observed in this study were supported by published regional diatom studies across the circum-Arctic.

Although this study is the result of many decades of data collected across a wide geographic region, much more work is needed to better understand diatom assemblage structure and spatial distributions and improve interpretation of current and future changes in the circum-Arctic. For example, with the present level of sampling effort, we did not attain full species richness in any Arctic zone, and latitudinal and longitudinal gaps in data coverage remain. We found that both monitoring and research efforts have focused on lakes, and documentation of Arctic biodiversity changes in streams is comparatively underrepresented. Overall, routine monitoring is lacking in many Arctic countries, which precludes a routine assessment of the status and trends in lakes and streams. However, each country encounters its own distinct set of challenges; for example, most of the vast Arctic regions of North America and the High Arctic regions of Norway (Svalbard) are only accessible by air, making research and data collection challenging and costly (Mallory et al., 2018). In comparison, many European Arctic regions are accessible by road, making the establishment of a monitoring programme more realistic, but causing human pressures on these sensitive ecosystems.

Future biomonitoring must also ensure to maintain harmonisation and a high degree of taxonomic precision across this large diatom dataset, which is challenging but important to more accurately depict species diversity trends. Biodiversity studies at the species scale can reduce information gaps on diatom ecology and taxonomy (Antonelli, Wetzel, Ector, Teuling, & Pfister, 2017), thereby increasing our understanding of the mechanisms underlying spatial differences. Taxon harmonisation for a central database (such as the Circumpolar Diatom Database [Pienitz & Cournoyer, 2017] or the European Diatom Database [Battarbee, Juggins, et al., 2001b]) is challenging as it requires integrating differences in diatom identification among laboratories. Although not an option at present, future monitoring efforts may be aided by the use of DNA metabarcoding, which can provide a means to facilitate more rapid assessments and possibly overcome some of these problems. Until such time, we recommend that circum-Arctic freshwater diatom harmonisation and identification activities should encompass establishing circum-Arctic diatom intercalibration, including a harmonised view on species, handling of difficult complexes, and routine ring-tests with follow-up workshops.

## 5 | CONCLUSIONS

Dominant diatom taxa differed within and between the habitats studied (lake surface sediment samples and stream scrapes), but at the circum-Arctic scale, differences in diatom assemblage composition were gradual rather than marked or abrupt species turnovers. In

addition, the dominant diatom taxa were those commonly reported in other regions of the world. Collectively, these trends are consistent with the observation that polar aquatic systems are not dominated by taxa endemic to these high latitudes (Antoniades, Hamilton, Douglas, & Smol, 2008; Smol et al., 2005; Wrona et al., 2013).

The species richness maximum at c. 60–75°N for lakes and rivers, plus the high variation in local richness at the same latitudes, are probably a reflection of the large variation in both local and regional environmental factors. Regional hotspots for diatom diversity were particularly evident in streams of Alaska and Fennoscandia, as well as some lower-latitude regions of the circum-Arctic, and there was a trend towards lower richness in High Arctic lakes and in eastern Canadian Arctic streams relative to other areas. The study of contemporary diatom assemblage data revealed that clear differences in diatom composition (biotypes) were rarely due to strictly latitudinal attributes. Region-specific differences in geology, setting, and lake morphometry were important factors affecting the modern distribution of diatom assemblage composition. Although there were considerable environmental ranges within a given biotype, there were some notable differences that often distinguished these groupings including temperature and precipitation, pH and calcium, DOC, nutrients, lake depth, percentage of sand as substrate and catchment area. These large variations in site characteristics underscore the complexity of the circum-Arctic, with differences among regions within an Arctic zone often as great as differences in other Arctic zones (e.g. the lush vegetation and thick soil cover of Prince Patrick Island in the Canadian High Arctic share similarities to boreal forest regions of the Canadian sub-Arctic).

Using a different set of lakes from the Smol et al. (2005) meta-analysis, our paleolimnological synthesis of sedimentary diatom records corroborates the conclusions made 15 years ago, clearly showing that the effects of global warming are evident in these remote, high-latitude ecosystems. Indeed, one of the more extreme consequences of accelerated climate change has recently been observed in the Canadian High Arctic, with the complete desiccation of ponds that had been in existence for millennia (Smol & Douglas, 2007b). These paleolimnological data track diatom compositional change from 19th century to the present, establishing that our modern baseline biotypes are already on a trajectory of change in response to anthropogenic warming.

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## CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

For the purpose of this assessment, the Arctic was considered to include the areas covered by the ABA and CAFF boundaries, whichever was more inclusive for a particular area (Culp, Goedkoop, et al., 2012a). We used existing lotic and lentic Arctic diatom data compiled for the CBMP Freshwater Database, which is stored in the Arctic Biodiversity Data Service (Table S1; www.abds.is, CAFF (2019)).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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