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## Research

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# Global warming triggers the loss of a key Arctic refugium

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We document the rapid transformation of one of the Earth's last remaining Arctic refugia, a change that is being driven by global warming. In stark contrast to the amplified warming observed throughout much of the Arctic, the Hudson Bay Lowlands (HBL) of subarctic Canada has maintained cool temperatures, largely due to the counteracting effects of persistent sea ice. However, since the mid-1990s, climate of the HBL has passed a tipping point, the pace and magnitude of which is exceptional even by Arctic standards, exceeding the range of regional long-term variability. Using high-resolution, palaeolimnological records of algal remains in dated lake sediment cores, we report that, within this short period of intense warming, striking biological changes have occurred in the region's freshwater ecosystems. The delayed and intense warming in this remote region provides a natural observatory for testing ecosystem resilience under a rapidly changing climate, in the absence of direct anthropogenic influences. The environmental repercussions of this climate change are of global significance, influencing the huge store of carbon in the region's extensive peatlands, the world's southern-most polar bear population that depends upon Hudson Bay sea ice and permafrost for survival, and native communities who rely on this landscape for sustenance.

## 1. Introduction

Until recently, Canada's Hudson Bay region has remained one of the planet's last Arctic refugia from global warming, largely because of the moderating role of Hudson Bay sea ice resulting in a negative feedback on regional climate [1]. In stark contrast to the rest of the Arctic, the lack of twentieth century warming in this region [2,3] resulted in relatively stable palaeolimnological records. For example, minimal biological change has been observed in numerous well-dated sediment cores including shorter profiles representing the past approximately 200 years [4–6] as well as over the past approximately 1500 years in longer term Holocene records [7,8]. These multi-proxy (e.g. diatoms, chironomids and chrysophytes) palaeolimnological studies, together with dendrochronological records [9], have consistently concluded that stable and relatively cool temperatures have been maintained since the onset of regional neoglaciation approximately 1500 years BP. Unlike the typically pronounced and prolonged warming trend reported throughout the circum-Arctic commencing post mid-1800s [4,10], the eastern Canadian Arctic region (that includes Hudson Bay) was not characterized by a discernible nineteenth century warming trend [7,8], and at most, underwent minimal and unsustainable increases in air temperature [9]. In the mid-1990s, however, detailed climate studies, based on instrumental records, clearly indicate that this region crossed a climate tipping point [3,11–13] with globally important consequences for carbon storage in the region's vast peatlands and for the survival of top predators like the world's southern-most population of polar bears [12].

Almost all circum-Arctic regions have warmed substantially relative to the rest of the world, with striking consequences for freshwater biota [14]. In the

subpolar Hudson Bay region, the recent switch to a warmer climate with increased air and sea surface temperatures (SSTs), reductions in Hudson Bay sea ice extent and changes in sea ice phenology, has further amplified this recent warming trend [3,11]. The rapid transition of this remote subarctic region from an area that has long maintained relatively cool and stable temperatures [1,2] to one of intense warming provides a rare, natural observatory for identifying the effects of global climate change in the absence of direct anthropogenic influences. We anticipate that the abrupt shift towards a warmer climate in the Hudson Bay Lowlands (HBL) may result in appreciable ecological repercussions in lakes and ponds as a consequence of the sharp interface between boreal and Arctic environments. There are early signs that the recent HBL warming is affecting river systems with observable negative consequences on fish populations during particularly warm years. For example, abnormally high summer air temperatures in 2001 produced unusually warm conditions in the Sutton River and its headwater lake (Hawley Lake), causing mass mortality of anadromous brook charr (*Salvelinus fontinalis*) from thermal stress [15]. Such events, extremely rare in northern environments, will probably occur more frequently if rapid warming continues, with dire consequences for aquatic ecosystems on which native communities depend.

Our detailed algal records from dated sediment cores collected in multiple lakes have high temporal resolution (approx. 1–3 years) that enable us to pinpoint the timing of aquatic threshold responses to recent regional warming and to make robust comparisons to instrumental climate records. Given the recent and abrupt nature of temperature increases in the HBL and, owing to the lack of long-term monitoring data for these remote regions, the ecological effects of these striking climate changes on freshwater systems remain largely unknown. In this paper, we use palaeolimnological methods to determine whether the algal communities of lakes in the HBL have responded to the abrupt recent warming trend recorded for this region, and if so, whether these changes were similar to climate-related algal shifts reported in the nineteenth to early twentieth century in other circum-Arctic regions [4]. In addition to recent climate change, we briefly explore potential alternative or synergistic effects of long-range atmospheric nitrogen deposition [16,17] as a possible explanation for the recent algal changes observed in the lakes from this remote subarctic region.

Diatoms (Class Bacillariophyceae) are among the world's most important primary producers [18]. Many diatom taxa have well-defined preferences for a given microhabitat type (e.g. benthic, epiphytic and planktonic) and respond rapidly to environmental changes. This makes diatoms robust environmental indicators that can be used to track climate-induced aquatic changes [19]. Longer and warmer ice-free seasons affect fundamental water column properties (e.g. light, nutrient distribution, thermal stability, and mixing strength and depth) that favour the development of more complex and diverse diatom assemblages, particularly in Arctic systems [4,20], and the growth of planktonic diatoms in lakes throughout the Northern Hemisphere [21]. In addition to diatom compositional changes, neo- and palaeolimnological studies are reporting that planktonic diatom cell size is decreasing with warming in lakes [22] and in oceans [23]. In agreement with palaeolimnological trends, an empirical model derived from long-term historical data

found that small-celled and fast-growing *Cyclotella* and *Discostella* species were favoured with warming as they are able to compete well and expand under longer open water periods and/or intensified stratification [22]. Distinct compositional shifts in diatom community structure, such as the increase in planktonic diatoms at the expense of benthic fragilarioid taxa and/or large, filamentous *Aulacoseira* species, were found to lack coherence among broad-scale ecozones (i.e. Arctic, alpine and temperate) as lower latitude aquatic ecosystems recorded increases in planktonic diatoms approximately 100 years later than in Arctic lakes [21]. This is consistent with the asynchronous nature of climate warming, particularly across the very different temperate and Arctic ecoregions.

The timing of the diatom shifts reported in many Northern Hemisphere lakes, however, overlaps the onset of a variety of environmental stressors (e.g. acidification, eutrophication and chemical contamination), often making it difficult to identify climate warming as the primary driver [24]. Moreover, atmospheric nitrogen deposition has increased in the mid-twentieth century following mass synthesis of ammonia through the Haber–Bosch process [25]. In remote high-latitude and high-altitude regions, long-distance atmospheric deposition of nitrogen has been explored as an alternative or synergistic mechanism to warming for these observed diatom community shifts [16,17]. The remoteness of the HBL in the eastern Canadian subarctic, together with the late onset of recent warming in the region, makes this an ideal, natural test area to examine the potential trigger driving recent widespread algal shifts reported throughout the Northern Hemisphere.

## 2. Material and methods

Sediment cores were retrieved from the deepest parts of Hawley, North Raft and Spruce lakes in August 2009 and from Aquatuk Lake in August 2010 using a Glew [26] gravity corer (diameter 7.62 cm). (See the electronic supplementary material for details on sample collection.) Cores were dated using gamma spectrometry techniques [27] by measuring activities of radioisotopes in selected intervals from each core.  $^{210}\text{Pb}$  dates were estimated for the past approximately 150 years using the constant rate of supply model ([28]; electronic supplementary material, figure S1). Whole-lake production was assessed using visible reflectance spectroscopy that enables quantitative inferences of sedimentary chlorophyll *a*, including primary chlorophyll *a* and all its isomers and phaeopigments [29]. Sediment spectra were obtained using a FOSS NIRSystems Model 6500 series Rapid Content Analyzer (Tidestone Technologies Inc.), operating over the range of 400–2500 nm. Sediment chlorophyll *a* concentrations were inferred using the published algorithm [29].

Diatom samples were prepared for contiguous (0.25 cm) sediment intervals (32–50 samples per core) following standard procedures [30]. A heavy liquid separation technique using sodium polytungstate removed excessive clastic material and concentrated the diatom valves on microscope slides, enabling a minimum count of 350 diatom valves per sediment interval (expressed as per cent relative abundance). Species diversity using Hill's  $N_2$  [31] was calculated on the relative abundance data following square-root transformation.

Climate data (1943–2011) from Churchill (Manitoba) provide the closest, continuous temperature record for the western HBL, and were obtained from Environment Canada (<http://www.cccma.ec.gc.ca/hccd/>). The Winisk (Ontario) climate station, located closer to the Sutton River region, was not used because it was missing a decade of data as a consequence of flooding of the

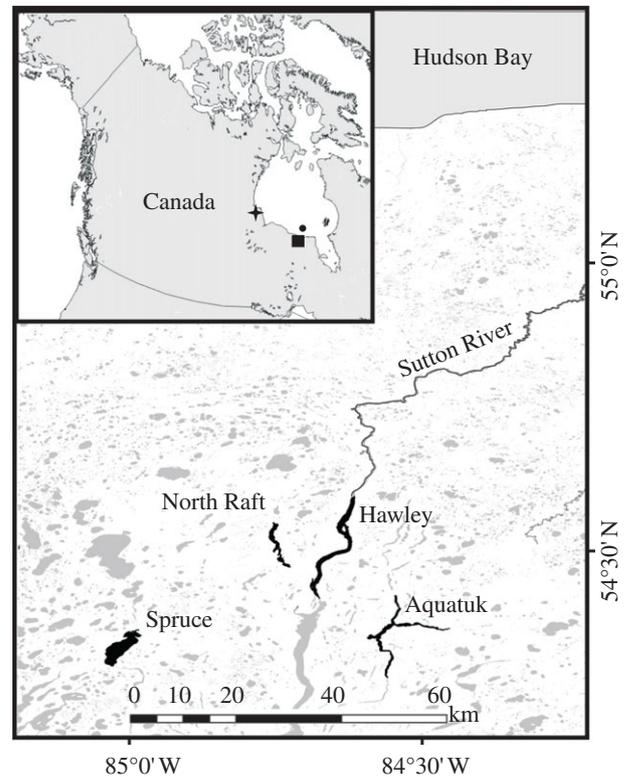
settlement and its subsequent relocation further inland to Peawanuck. Strong correlations between the available data from the Winisk/Peawanuck and Churchill climate stations (annual and seasonal temperature; electronic supplementary material, figure S2) indicate that Churchill temperature trends are representative of the region. SST data from a Hudson Bay location near the Sutton River (85°37' E, 58°35' N) were obtained from National Oceanic and Atmospheric Administration (NOAA) extended reconstruction SSTs (ERSST3b: <http://nomads.ncdc.noaa.gov/las/getUI.do>).

Principal components analysis (PCA) was used to summarize the diatom data using the default options available in the program CANOWIN, v. 4.5 [32]. The critical value (i.e. breakpoint) at which an ecological threshold is exceeded [33] was identified using a two-segment, piecewise linear regression [34]. Breakpoint analyses were applied to our time-series data for the Churchill temperature record, the SST records, as well as the algal records (species diversity, main taxonomic groups, PCA diatom summaries and sedimentary chlorophyll *a*) to estimate the timing of threshold responses.

### 3. Results and discussion

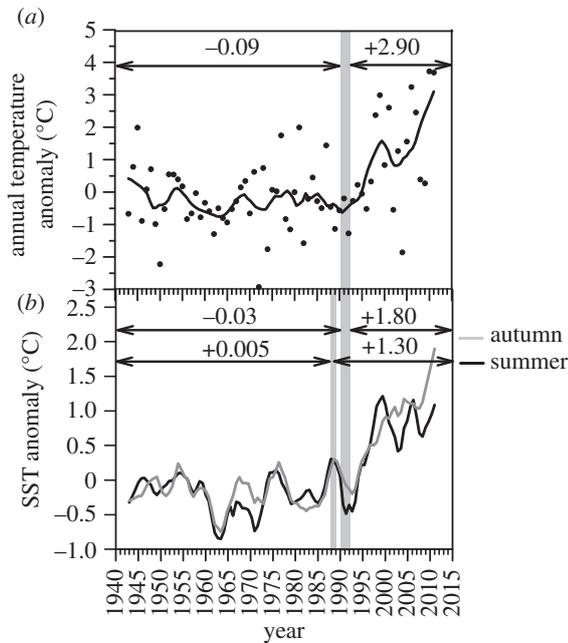
To determine whether the recent and abrupt shift in the regional climate regime of the HBL has altered freshwater ecosystems, we examined long-term environmental trends using biological information preserved in lake sediments. Our regional palaeolimnological records were based on high-resolution algal analyses in four sediment cores (see the electronic supplementary material, figure S3) retrieved from subarctic lakes in the remote Sutton River region of northern Ontario, Canada (figure 1 and electronic supplementary material, table S1). These lakes are situated approximately 100 km inland from the western shoreline of Hudson Bay on discontinuous permafrost at a relatively high elevation (120 m above the surrounding lowlands) near the Sutton Ridges, an outcrop of Precambrian Shield bedrock within an otherwise limestone-dominated region. The study region is approximately 400 km north of the nearest road system, and thus is not impacted by regional anthropogenic disturbances (e.g. roads, towns, agriculture, etc.). These lakes are relatively deep, slightly alkaline, relatively low in water column nutrients (e.g. total phosphorus and nitrate; electronic supplementary material, table S1), and were weakly to moderately thermally stratified at the time of sampling, although stable stratification was observed at Hawley Lake in August 2001 [15]. Radiometric dating of 0.25 cm sediment intervals yielded high temporal resolution (1–3 years per sedimentary interval) for all four diatom records (see the electronic supplementary material, figure S1), allowing us to establish the timing of changes with accuracy and enabling robust (i.e. high number of palaeolimnological samples) comparisons to regional temperature trends.

Air temperature data (1943–2011) from Churchill (Manitoba) recorded a marked warming trend in the annual (figure 2*a*) and seasonal data, but the trend was most pronounced in autumn and winter (see the electronic supplementary material, figure S4). Likewise, SST data from a Hudson Bay location near the Sutton River, and from the same time period, displayed distinct warming trends in the annual record and during the open water season (summer and autumn; figure 2*b*). Applying a two-segment, piecewise linear regression to the regional air temperature and SST data identified a threshold change to higher mean temperatures in the early 1990s (figure 2*a,b* and electronic supplementary material, figure S4).



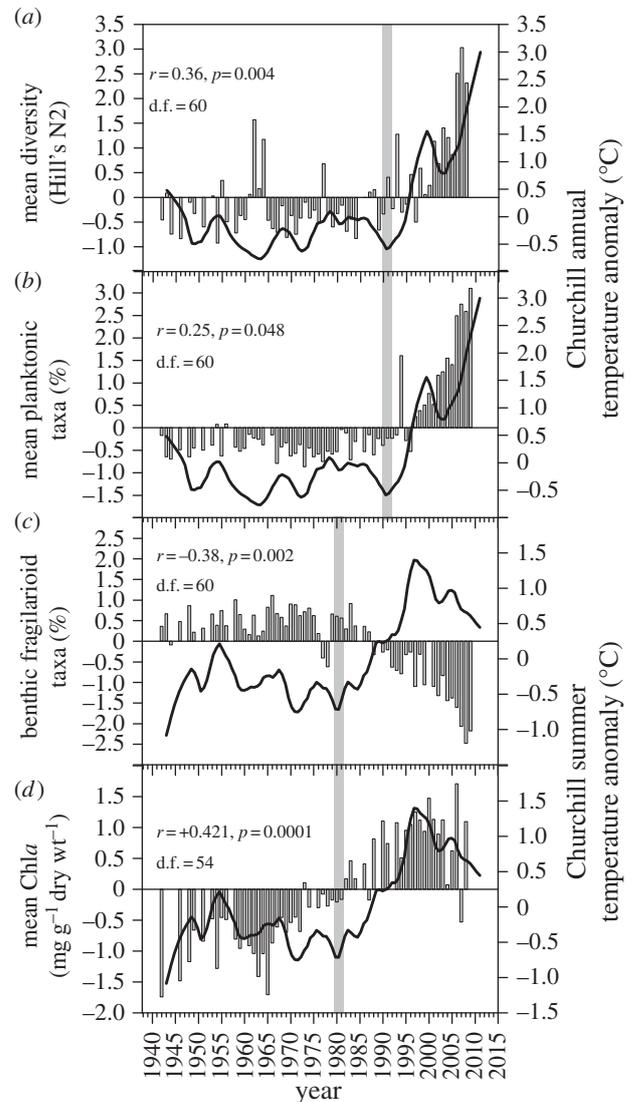
**Figure 1.** Map of study sites. Location of the study lakes in the Hudson Bay Lowlands of subarctic Canada. Inset map: square represents location of study area, star represents Churchill climate station and circle represents location of SST site.

One of the most compelling trends in our HBL palaeolimnological profiles is the synchrony between algal shifts across lakes and regional increases in temperature (figure 3) which is observed in all of our study lakes (see the electronic supplementary material, figure S5). It is important to note that diatoms do not track air temperature changes directly but respond to the effects that warming has on lake properties such as an increase in the ice-free season, changes in thermal structure, diversification of aquatic habitat availability and, in turn, all of the consequent effects that these changes impose on lake water properties, including the distribution and availability of nutrients. Because lakes respond indirectly to temperature trends, it is unrealistic to expect diatoms to respond to warming in a linear fashion. Nonetheless, there are clear threshold-type responses in planktonic diatoms to regional climate warming in HBL lakes (figure 3*b* and electronic supplementary material, figure S5) as observed in diatom records throughout the circum-Arctic [4,24] and the Northern Hemisphere [21]. When taking into account errors associated with estimated  $^{210}\text{Pb}$  dates, differences in the sensitivity of a given lake in response to the onset of warming (discussed in Smol & Douglas [24] and further below), and the indirect response of diatoms to climate, a 'perfect' match between recorded temperatures and diatom taxa would not be expected. What is clearly evident is that, despite the uncertainties inherent in palaeolimnological analyses with variations in sediment quality across lakes, differences in sedimentation rates and dating errors, the timing of change among the study lakes is strikingly similar, as are the relationships between our HBL algal trends and regional instrumental records (figure 3 and electronic supplementary material, figure S5).



**Figure 2.** Step changes in SSTs and air temperatures in the Hudson Bay Lowlands. (a) The mean annual air temperature anomalies from the Churchill (Manitoba) climate station (see figure 1 for location) from 1943 to 2011. (b) SST anomalies from a location ( $85^{\circ}37' E$ ,  $58^{\circ}35' N$ ) proximal to the Sutton River (see figure 1 for location) from 1943 to 2011 from NOAA extended reconstruction SSTs. The SST and air temperature anomalies are relative to the 1971 to 2000 baseline. To improve the clarity of the figure, a LOESS smoother (span = 0.15) was applied to the climate data to highlight trends. Grey-shaded vertical lines represent the breakpoint and standard errors are determined by a two-segment, piecewise linear regression ( $p < 0.0001$ , summer SST =  $1998 \pm 2.9$ , autumn SST =  $1991 \pm 2.7$ , annual air temperature =  $1991 \pm 0.6$ ). Arrows indicate the magnitude of temperature changes (i.e. the slope of a linear regression over the time period of interest) prior to, and following, the identified breakpoints.

An increase in species diversity and the first occurrence and expansion of planktonic diatoms was a common trend in all of our study lakes (figure 3a,b and electronic supplementary material, figure S3), with the predicted variability in the magnitude and nature of the diatom shifts observed across the four HBL lakes (i.e. diatom changes were not expected to be identical in terms of the amount of change and in assemblage composition; electronic supplementary material, figure S3). This variability in diatom responses is to be expected given the site-specific differences in lake morphometry including depth (reviewed in Smol & Douglas [24]). Nonetheless, it is the similarities in the general nature and particularly in the timing of the algal responses across sites that are most notable. For example, comparable in timing to Churchill temperature breakpoints, significant threshold responses (piecewise linear regression) were observed in all of our algal records, both for individual lakes (see the electronic supplementary material, figure S5), as well as the composite trends of the four lakes (standardized using z-scores; figure 3). Declines in epilithic (i.e. attached to rocks) fragilarioid taxa in the early 1980s, which dominated the earlier diatom assemblages of all lakes, were synchronous with the expansion of an assortment of benthic taxa that are characteristic of littoral habitat diversification [24] (see the electronic supplementary material, figure S3) and were similar in timing to an increase in regional summer air temperature in the late 1970s (figure 3c). Benthic fragilarioid taxa are common to many Arctic aquatic systems because



**Figure 3.** Step changes in algal trends relative to regional temperature records. Composite algal trends (standardized to mean variance using z-scores) from the four study lakes (bars) compared to air temperature anomalies (relative to the 1971–2000 baseline) from the Churchill (Manitoba) climate station from 1943 to 2011 (black lines) for: (a) species diversity using Hill's N2; (b) mean planktonic diatom relative abundances; (c) mean benthic fragilarioid diatom relative abundances and (d) mean spectrally inferred, sedimentary chlorophyll *a* (Chla). Grey-shaded vertical lines represent the breakpoint and standard errors are determined by a two-segment, piecewise linear regression for averaged annual air temperature ( $p < 0.0001$ ,  $1991 \pm 0.6$ ) and for averaged summer air temperature ( $p < 0.0001$ ,  $1978 \pm 2.2$ ). Breakpoints and standard errors (lines not shown in figure) for Hill's N2 diversity =  $1998 \pm 0.44$ , planktonic diatoms =  $1994 \pm 0.3$ , benthic fragilarioid diatoms =  $1984 \pm 0.58$  and Chla =  $2000 \pm 3.0$ . The standard deviation and mean for each variable and each lake associated with the z-scores plotted in this figure are provided in the electronic supplementary material, table S2. Results of correlation analysis (Spearman rank) with Bonferroni-adjusted probabilities are given in each panel for the algal trends in relation to the temperature data. For each sedimentary interval in each lake, the average air temperature during the period of its accumulation was calculated, thereby integrating the temperature data with the diatom data [35]. Given the nearly annual temporal resolution of the diatom data in all cores, little difference in correlations was observed between this integrated technique and the raw temperature data.

they compete well under light-limited, ice-covered conditions with short growing seasons [24,36]. The appearance and increased importance of planktonic diatoms (mainly *Discostella*

*pseudostelligera* and *Fragilaria tenera*) in our four HBL lakes in the 1990s occurred concurrently with a regional shift to substantially warmer temperatures in winter and autumn (represented by mean annual temperature) and lagged the benthic fragilarioid decline by an average of approximately 10 years (figure 3*b,c* and electronic supplementary material, figures S3 and S5).

The lag observed between the shifts in planktonic and benthic taxa is consistent with diatom species responses to changing climate [37], and the seasonal progression of ice cover decline on a given lake [19]. Warmer and longer growing seasons in summer lead to the expansion of periphytic taxa that compete with benthic fragilarioid taxa [24,36]. For example, in North Raft Lake, a switch from dominance by epilithic fragilarioid taxa to a greater diversity of benthic diatom species approximately  $1974 \pm 2$  years, most notably small *Navicula* taxa, is close in timing to the regional summer air temperature breakpoint ( $1978 \pm 2.2$  years). As rising temperatures crossed climate thresholds in winter and autumn during the early 1990s, conditions became favourable for the establishment of planktonic diatom growth, including a variety of pennate planktonic taxa (most notably *F. tenera*), as well as several centric planktonic *Cyclotella* and *Discostella* taxa. Once more, using North Raft Lake as an example, a sustained increase of at least 2% above background levels (i.e. 0.5% from approx. 1940s to approx. 1990s) in planktonic *D. pseudostelligera* was observed at approximately  $1993 \pm 2$  years and again is close in timing to the much larger magnitude winter warming with a breakpoint identified at  $1992 \pm 1.5$  years, as well as autumn warming with a breakpoint of  $1991 \pm 0.6$  years (see the electronic supplementary material, figure S4). *D. pseudostelligera* and *Cyclotella comensis* have been known to bloom in autumn in Arctic and alpine lakes, often at the breakdown of summer stratification [37,38]. Substantially warmer winter temperatures have appreciable effects on reducing ice thickness and advancing ice phenology [39] that, in turn, increase lake thermal stability and reduce mixing leading to conditions that are advantageous for planktonic diatom growth [40]. Considering the high temporal resolution of our algal records (rarely seen in high-latitude lakes), we are probably tracking diatom assemblage changes that include seasonal differences in temperature changes in the HBL, adding an interesting facet to this recent threshold response.

In addition to the observed post-1990 taxon-specific diatom compositional changes, a breakpoint analyses applied to the PCA (axis one and two scores) summaries of the assemblage-scale diatom shifts for all lakes likewise indicated that the greatest change occurred in the last few decades (see the electronic supplementary material, figure S5). All lakes showed a notable increase in species richness (between 10% and 48% increase in number of species), and a distinct shift to higher species diversity in the modern sediments (figure 3*a*) that is particularly well expressed in Aquatuk Lake (electronic supplementary material, figure S3*a*). Concurrent with the observed diatom shifts, all lakes underwent pronounced increases in whole-lake primary production (inferred from sedimentary chlorophyll *a* and its diagenetic products), following comparatively low values in the earlier sedimentary intervals of these naturally unproductive lakes (figure 3*d*). These recent increases in lake primary production are consistent with increases observed in other regions of the Arctic that have been linked to warming with decreased ice cover, longer algal growing seasons and new habitat availability [29].

A warmer climate, shorter duration of lake ice cover and changes in ice phenology often lead to fundamental changes to water column properties that are important for phytoplankton growth [41]. As noted earlier, it is well documented that algae respond indirectly to temperature changes through mechanisms such as the physical and chemical changes in lake water properties as a result of warming (e.g. longer open water season and changes in thermal structure including increased stability and weakened mixing, changes in light habitat, changes in nutrient availability and distribution; [24,42]). Differences among lakes in terms of, for example, lake morphometry and physical setting will lead to variation in the magnitude and character of changes in lake water properties in response to warming, and therefore identical diatom responses among lakes would not be anticipated [21] (see the electronic supplementary material, figure S3). Nevertheless, all lakes share a concurrent increase in primary production and increase in species diversity that includes a shift to assemblages characteristic of a more planktonic life strategy from an almost exclusively epilithic fragilarioid diatom assemblage. We note that thermal stratification (although it can be important) is not necessarily required to initiate a change in the diatom communities [24]. However, a lake that has rarely or never experienced thermal stratification for prolonged time periods can produce a pronounced response by the diatoms with the onset of warming and the development of a thermally stratified water column [43,44]. The lakes of the HBL may only be starting to show responses to warming, but these changes are nevertheless clearly expressed in the sedimentary records.

The recent abrupt and coherent changes in the algal communities of these remote lakes are consistent with a response to the warmer climate regime and are the focus of our paper. Nevertheless, diatom summaries (PCA scores) suggest that subtle and gradual changes occur among the diatoms in the earlier parts of the lake records (see the electronic supplementary material, figure S5). These early and gradual trends may suggest that there is a complex response to regional environmental change prior to the crossing of the climate threshold in the last few decades. These gradual diatom trends are more difficult to interpret because the earlier diatom assemblages were dominated by several species and varieties of small benthic fragilarioid taxa, and early changes in PCA axes scores reflect subtle fluctuations among these taxa. Deciphering meaningful ecological differences among this group of fragilarioid taxa has always been a challenge [45–47], making palaeolimnological inferences based on changes among these taxa difficult. In the absence of additional monitoring data or regional stressor information in this remote region, we cannot draw definitive conclusions as to the underlying mechanism for these subtle fluctuations among benthic diatoms, but they probably reflect catchment-scale disturbances or natural variability.

In remote regions, where direct anthropogenic influences are minimal, long-range transport of contaminants provides a potential source of pollution to freshwater systems. For example, industrial-scale mass synthesis of ammonia was made possible by the development of the Haber–Bosch process in the 1930s and its subsequent application as synthetic fertilizers worldwide [48]. Increased atmospheric nitrogen deposition has been proposed as a possible alternative or synergistic explanation to climate change for recent diatom shifts observed in remote lakes [16,49]. Nitrogen deposition rates for regions north of  $60^\circ\text{N}$  latitude are poorly known [50] and direct measurements for the HBL do not exist.

However, global-scale overviews estimate that atmospheric nitrogen deposition rates in the HBL region are extremely low at approximately  $1 \text{ kg N ha}^{-1} \text{ y}^{-1}$  [51]. Moreover, streams and rivers draining into Hudson Bay north of  $52^\circ \text{ N}$  latitude are estimated to have among the world's lowest fluxes of total nitrogen [52] and low total inorganic nitrogen [50]. It is also well understood that the delivery of atmospheric nitrogen to lakes will, in part, be moderated by watershed characteristics. As a consequence, nitrogen retention in the terrestrial system and nitrate export to a lake or stream may vary considerably between catchments [53]. For example, *Sphagnum* peat provides a natural trap for inorganic nitrogen (and the removal of nitrogen through denitrification), effectively reducing nitrogen inputs into freshwater systems [50,54,55].

Although measured data on atmospheric nitrogen deposition and export are lacking for the HBL (as they are in almost all Arctic regions), it is certainly a region that experiences low concentrations of atmospheric nitrogen deposition [51] as well as low fluxes of nitrogen to regional freshwater lotic systems [50,52]. Furthermore, the diatom species changes (both the subtle, gradual fluctuations of benthic fragilarioid taxa in the earlier part of the records and the distinct, abrupt increases in planktonic diatoms in the past few decades) that we record do not suggest a response to increases in nitrogen. These diatom taxa are not known to be nitrogen-sensitive, and the timing of these changes postdate the onset and height of atmospheric nitrogen deposition. Based on the available measurements, these lakes would not be considered to be nitrogen-limited (see the electronic supplementary material, table S1), although we acknowledge that we only have 3 years of discrete nutrient measurements at mid-summer. The low primary production (i.e. sedimentary chlorophyll *a*), together with the compositional changes evident in the diatom assemblages, clearly show that diatoms in our palaeolimnological records are not changing in response to additions of nitrogen. Moreover, the coherency of the diatom responses would not be expected if changes were due to indirect climate/nutrient effects (e.g. release of nitrogen from catchments with warming) because the amount of nitrogen delivered to a lake would be dependent upon a variety of specific watershed characteristics including hydrological pathways and drainage ratios that vary among the study lakes.

## 4. Conclusion

The timing and nature of the algal changes from the HBL palaeolimnological records are consistent with abrupt regional climate warming in the mid-1990s. The recent algal changes that accompanied these warmer conditions are similar to those reported from many other Arctic regions, where the onset of modern warming occurred decades earlier. This provides strong reinforcement that the previously published assemblage shifts were also primarily driven by warming, and not nitrogen deposition or other environmental factors.

The biological threshold responses reported in our study highlight the disappearance of one of the planet's last remaining Arctic refugia as a consequence of warming and provide evidence that we are witnessing the transformation of the Arctic at an exceptional pace. It is likely that lakes in the HBL region are currently experiencing the very beginning stages of warming-induced ecosystem change that are, nevertheless, clearly expressed in the lake sediment records and is unprecedented in the past approximately 1500 years. Continued warming at the rate and magnitude currently underway will undoubtedly lead to more pronounced, directional ecosystem responses with repercussions cascading throughout this subarctic region.

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