



Cyclotella Antiqua, a benthic algae species.
Photo: Kathleen Rühland

4.2. Algae from Benthic Samples

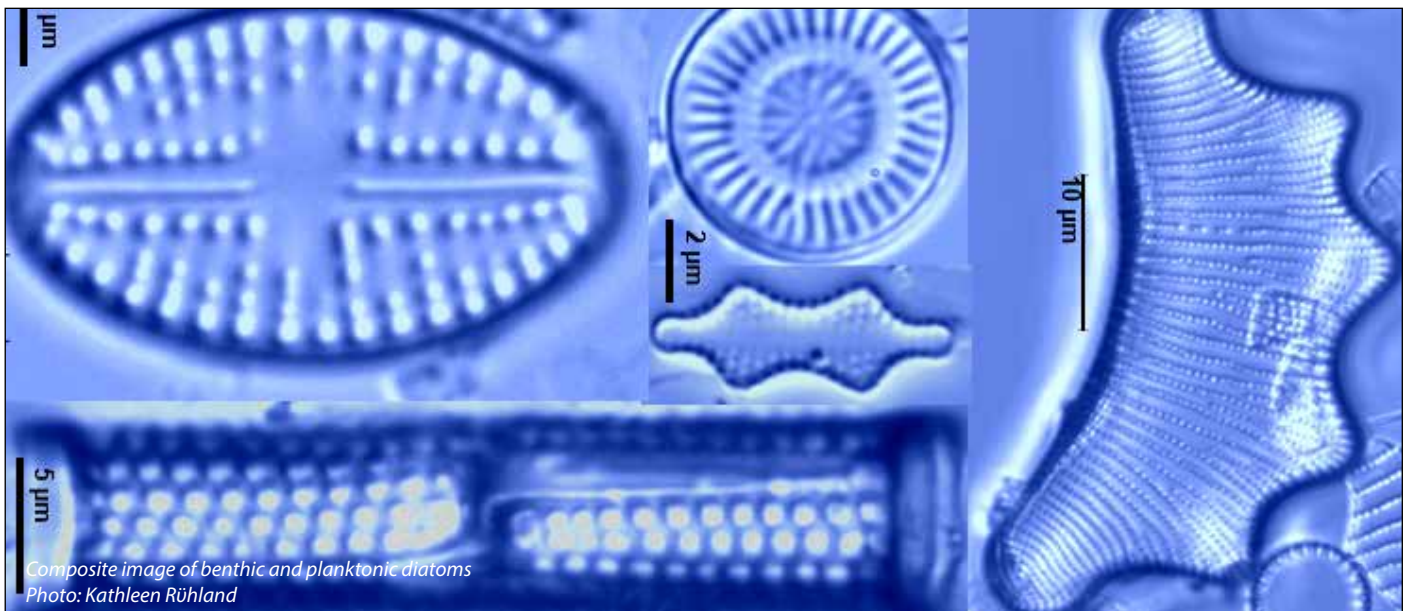
4.2.1. Introduction

Benthic algae are here defined in terms of the habitat in which samples were collected (e.g., lake sediments or streambeds), and thus include taxa collected from benthic habitats, regardless of whether they are otherwise defined as planktonic or benthic species. This definition allows for the comparison of all monitoring data collected by a particular method, without a need to classify species as benthic or planktonic. The Benthic Algae FEC describes primary producers that mainly occur in aquatic habitats, and includes both diatoms (class Bacillariophyceae) and soft algae (non-diatoms such as cyanobacteria, green algae, etc.). Algae from benthic samples are a heterogeneous group, ranging in size from micrometer-long small diatoms, cyanobacteria, or green algae to meter-long filamentous green algae. In benthic habitats, algae generally form a slippery, millimeter thick biofilm or thicker algal mats of around a centimeter. Benthic algae are important in food webs, and are often the main primary producers in open and shallow river stretches or lakes in the Arctic (refer to, e.g., Stevenson and Pan 1999, Wetzel 2001).

Studies of Arctic fresh waters have revealed that lake and stream benthic algae mats are commonly dominated by cyanobacteria, diatoms, and green algae (Conjugatophyceae and Chlorophyceae) (Wrona et al. 2013). Periphytic algal assemblages in Arctic streams are commonly composed of similar classes of algae, though assemblages are dominated by diatoms and cyanobacteria in the Canadian high Arctic (Lento et al. unpublished). In general, these algae provide important nutritional benefits to higher trophic levels, with diatoms in particular having substantial amounts of important fatty acids (Torres-Ruiz et al. 2007). Grazing of algae by herbivores can be affected by algal traits (e.g., morphology), nutritional value that can be modified by algal composition and environmental factors (Müller-Navarra et al. 2000, Ravet et al. 2003), as well as by invertebrate and fish predation on herbivores.

Most algae species in Arctic freshwaters are not restricted to polar regions, and their distributions reflect local geology and water chemistry conditions rather than thermal

preferences (Wrona et al. 2013). Biomass of algae from benthic samples in lakes and rivers declines with increasing latitude, which may reflect the shorter growing season at high latitudes (Wrona et al. 2013). Arctic diatom diversity in both lakes and rivers is predicted to be affected by pH, nutrients, and metals, as found in temperate regions (Smol and Stoermer 2010). Additionally, lake diatom assemblage composition is expected to be driven by differences in the thickness and seasonal duration of ice cover, as these can affect light levels, length of the stratification period, and change across the 10°C July isotherm (Pienitz et al. 2004). In high Arctic regions, shallow, small water bodies might be most sensitive to the effects of climate change, and might display the most pronounced community shifts (Pienitz et al. 2004). Large-scale assessments of algal distributions from benthic samples in Arctic lakes and streams have not been previously done, and thus the broad-scale effect of climate change and human development on this FEC is unknown. In Arctic regions, diatom sampling is preferred over sampling the full assemblage (diatoms and non-diatoms) because of the greater ease of processing and identification of diatoms. Moreover, research on algae from benthic samples in Arctic lakes and rivers generally considers only diatoms or estimates biomass of the entire biofilm through bulk chlorophyll assessment. Thus, a broad-scale assessment of algal biodiversity from benthic samples using existing data must focus on the diatom component of these samples. Diatoms are advantageous for monitoring because they are sessile and thus cannot escape impacts, they grow quickly, react readily to environmental changes, and integrate impacts over a period of weeks. They are often the dominant algal group in benthic samples, are ubiquitous, and are diverse (> 100 taxa possible per cm²). Sample collection is simple, and the glass diatom frustule is preserved well over time (and in sediments), facilitating species-level identification. Diatom ecology and taxonomy is well-studied, and environmental preferences of species are well known, including the response to stressors such as eutrophication, acidification, pollution, salinisation and toxicants (Pienitz et al. 2004, Smol and Stoermer 2010, Villeneuve et al. 2013). These characteristics make diatoms valuable indicators of environmental change in freshwater ecosystems.



4.2.2. Objectives and Approach

Circumpolar assessment of contemporary diatom assemblages was completed for lake surface-sediment samples (i.e., top sediments or tops of cores) and river benthic scrapes. For this analysis, stations were grouped by ecoregion, which are terrestrial regions with similar geography and climate (Olson et al. 2001). Alpha diversity was assessed for each ecoregion by rarefying to a standard set of stations, while beta diversity was estimated within ecoregions and broken down into its components, i.e., turnover and nestedness. Diatom assemblages in lake surface sediments and shoreline scrapes, as well as in river benthic scrapes were also evaluated spatially to study contemporary biodiversity and compositional patterns. This was done both on a circumpolar scale and across a latitudinal (temperature) gradient, and for comparisons between North America and Europe. In addition, paleolimnological data (full lake sediment cores and tops/bottoms of cores) were used to assess long-term changes in biodiversity of lake diatom assemblages. The top-bottom approach is commonly applied in paleolimnological studies in order to assess change between two periods of time in a study set including a large number of lakes (e.g., Rühland et al. 2003). The results provide a before-and-after snapshot of lake conditions, often between the pre-industrial period and the late 20th century, when most lakes have experienced some form and degree of anthropogenic impact.

Diatom data were collected from both national monitoring programs and academic research studies, as routine monitoring of diatoms is limited to only a few countries (e.g., Sweden, Finland). Samples included those for which diatom assemblage structure was analyzed from prepared slides and where at least 300 diatom valves were enumerated under the microscope. Diatom nomenclature was harmonized at the genus or species level across the circumpolar region, and taxonomic differences due to variability in laboratory analysis methods were minimized by grouping some taxa into species complexes.

4.2.3. Overall Patterns and Trends

4.2.3.1. Circumpolar Diversity

4.2.3.1.1. Lakes

Lake diatom stations were arguably the most evenly distributed across the circumpolar region of all the FECs, although coverage was patchy in Russia and stations were lacking in the High Arctic of Greenland or Svalbard (Figure 4-7a). Ten ecoregions across the Arctic had sufficient numbers of samples to allow for comparison of rarefied richness estimates at 40 stations. Among these ecoregions, the highest alpha diversity was found in the Arctic Coastal Tundra in Alaska, with an average of 239 taxa (harmonized to include species complexes) in 40 stations, which was significantly higher than all other ecoregions (Figure 4-7b). High alpha diversity was also evident in northern Canada (Middle Arctic Tundra and High Arctic Tundra) and Iceland (Iceland Boreal Birch Forests and Alpine Tundra), where on average over 205-215 taxa were found in 40 stations (Figure 4-7b). Russia and Fennoscandia had slightly lower, but not significantly different alpha diversity levels (in the Taimyr-Central Siberian Tundra and Scandinavian Montane Birch Forest and Grasslands). The lowest alpha diversity was found in southern Greenland, in

the Kalaallit Nunaat Low Arctic Tundra, which both had only 28 taxa on average in 40 stations (Figure 4-7b), whereas the southern ecoregions in Canada had low to moderate levels of alpha diversity (126 to 178 taxa in 40 stations).



Similar patterns were evident when rarefied taxonomic richness was compared across all 19 ecoregions at a level of 10 stations. The Arctic Coastal Tundra, Middle Arctic Tundra, and Iceland Boreal Birch Forests and Alpine Tundra remained high alpha diversity ecoregions, but the Scandinavian Montane Birch Forest and Grasslands had similar richness to these ecoregions when only 10 stations were considered (Figure 4-7c). The highest diversity was in the Southern Hudson Bay Taiga in Canada, with an average of 155 taxa in 10 stations; however, this ecoregion did not differ significantly from those in the range of 135-150 taxa. The High Arctic Tundra was in a lower alpha richness class when only 10 stations were considered, and was similar to the Scandinavian and Russian Taiga and the other Russian ecoregions (East Siberian Taiga, Taimyr-Central Siberian Tundra, and Northwest Russian-Novaya Zemlya tundra), where 120-130 taxa were found on average in 10 stations. The Kalaallit Nunaat Low Arctic Tundra continued to have the lowest alpha diversity across all regions, but low richness was also found in a mountainous Alaskan ecoregion (Brooks-British Range Tundra) and in eastern and southeastern Canadian ecoregions (Baffin Coastal Tundra, Eastern Canadian Forests, and Eastern Canadian Shield Taiga), where average alpha diversity ranged from 65 to 98 taxa in 10 stations (Figure 4-7c).

Beta diversity β_{SOR} ranged from 0.50 to 0.88 when averaged across hydrobasins in an ecoregion, which indicated that there was generally moderate to high dissimilarity in community structure among stations within hydrobasins. The highest dissimilarity among stations ($\beta_{\text{SOR}} = 0.88$) was found in the Kalaallit Nunaat Low Arctic Tundra, which had the lowest alpha diversity. Thus, despite the low number of taxa, stations in the ecoregion were highly dissimilar. Furthermore, lake beta diversity was dominated by the turnover component in all ecoregions, which indicated that there was a high degree of species replacement across stations (Figure 4-7d), and a low contribution of nestedness to beta diversity (ranging from 3% to 23%, but at 15% or lower for 16 ecoregions). This suggests that spatially-extensive sampling is necessary to capture the majority of species across these ecoregions.

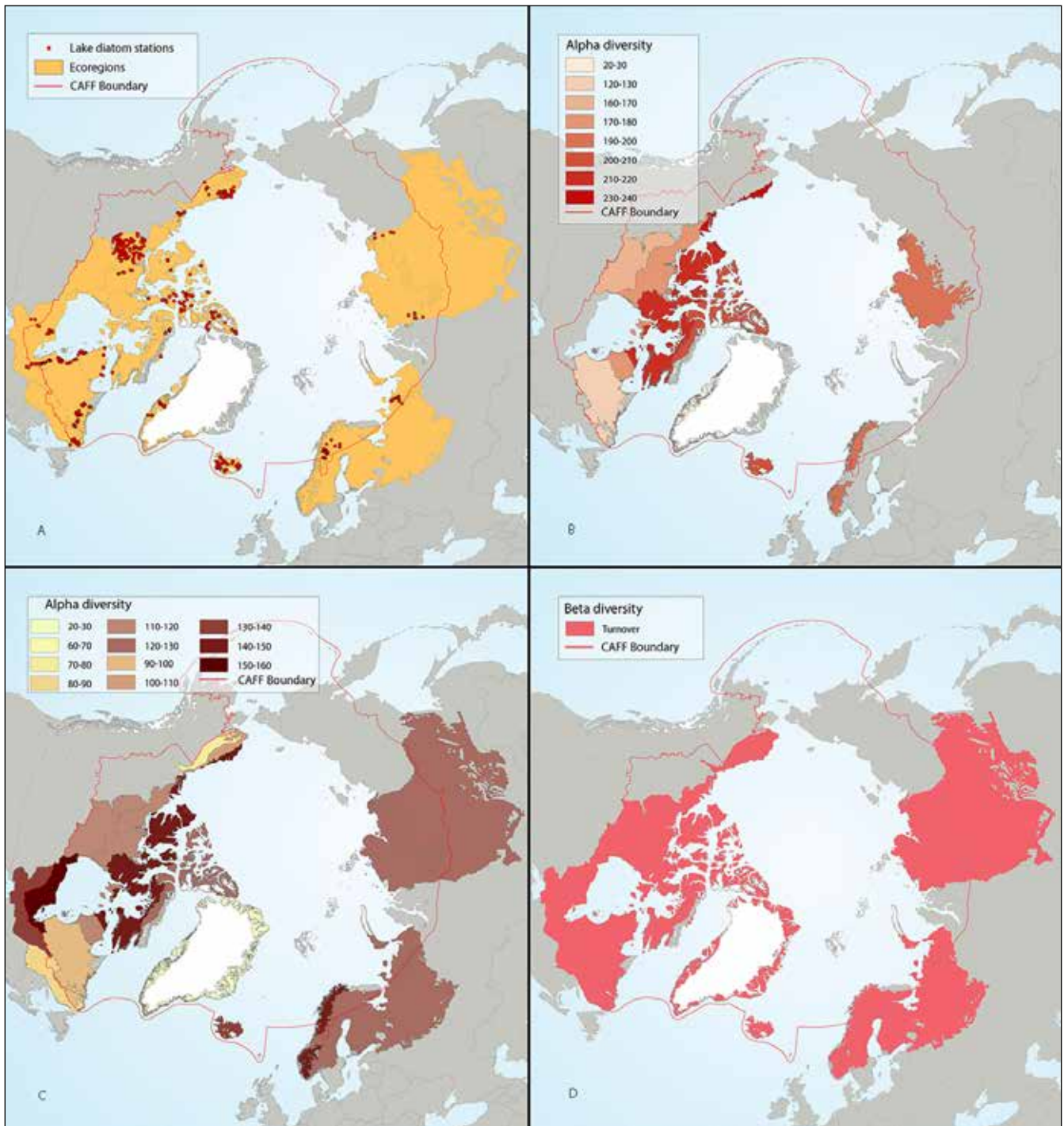


Figure 4-7 Circumpolar assessment of lake diatoms, indicating (a) the location of lake diatom stations, underlain by circumpolar ecoregions; (b) ecoregions with many lake diatom stations, colored on the basis of alpha diversity rarefied to 40 stations; (c) all ecoregions with lake diatom stations, colored on the basis of alpha diversity rarefied to 10 stations; (d) ecoregions with at least two stations in a hydrobasin, colored on the basis of the dominant component of beta diversity (i.e. species turnover, nestedness, approximately equal contribution, or no diversity) when averaged across hydrobasins in each ecoregio.



4.2.3.1.2 Rivers

River diatom data included large gaps in Russia, Iceland, and in the western Canadian low Arctic and sub-Arctic regions (Figure 4-8a). Eight ecoregions had a sufficient number of stations to allow for comparison of richness rarefied at the level of 40 stations. Among these, there were distinct and significantly different groupings of ecoregions with similar alpha diversity. The highest alpha diversity was in the Arctic Coastal Tundra in Alaska, which on average had 252 taxa in 40 stations (Figure 4-8b). The Fennoscandian ecoregions

(Scandinavian and Russian Taiga, and Scandinavian Montane Birch Forest and Grasslands) were similar in alpha diversity, which ranged from 180 to 197 taxa. The northern Canadian ecoregions of the Middle Arctic Tundra and High Arctic Tundra had similar alpha diversity at 115-116 taxa on average in 40 stations (Figure 4-8b). Finally, the lowest richness was found in the eastern and southern Canadian ecoregions (Torngat Mountain Tundra, Eastern Canadian Shield Taiga, and Low Arctic Tundra), which ranged from 91 to 95 taxa on average in 40 stations.

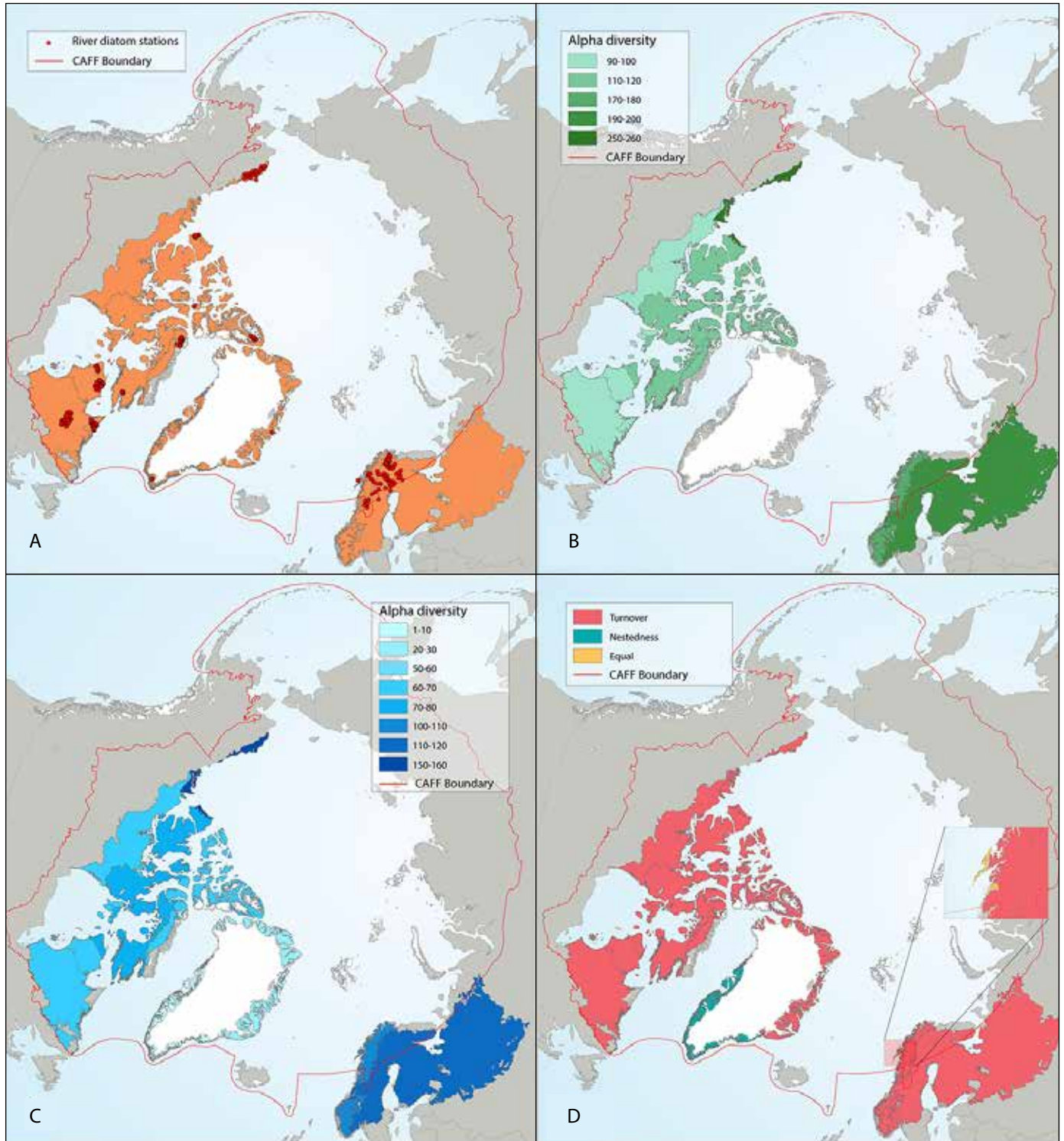


Figure 4-8 Results of circumpolar assessment of river diatoms, indicating (a) the location of river diatom stations, underlain by circumpolar ecoregions; (b) ecoregions with many river diatom stations, colored on the basis of alpha diversity rarefied to 40 stations; (c) all ecoregions with river diatom stations, colored on the basis of alpha diversity rarefied to 10 stations; (d) ecoregions with at least two stations in a hydrobasin, colored on the basis of the dominant component of beta diversity (species turnover, nestedness, approximately equal contribution, or no diversity) when averaged across hydrobasins in each ecoregion.

Comparison of richness values rarefied to 10 stations allowed the inclusion of two additional ecoregions in Greenland and one in Fennoscandia. Both of the Greenland ecoregions had the lowest alpha diversity estimates across the study area (Figure 4-8c). The Kalaallit Nunaat Low Arctic Tundra had an average of 3 taxa in 10 stations, whereas that for the Kalaallit Nunaat High Arctic Tundra averaged 28 taxa in 10 stations, with both values being significantly lower than those for the remaining ecoregions (Figure 4-8c). The Scandinavian Coastal Conifer Forests had low alpha diversity, similar to the Torngat Mountain Tundra, which is also a coastal ecoregion. Comparing the remaining ecoregions at only 10 stations (rather than at 40) resulted in less clear groupings of ecoregions in the low to moderate classes of alpha diversity (e.g., those ranging 52–72 taxa in 10 stations), with some shifts in the similarity of ecoregions. For example, High Arctic Tundra became more similar to the Low Arctic Tundra than to the Middle Arctic Tundra (Figure 4-8c). The observation that groupings of ecoregions were less evident when only 10 stations were sampled emphasizes the importance of sampling a sufficient number of stations in order to capture the range of species present and, consequently, accurately characterize alpha diversity within ecoregions.

Beta diversity within an ecoregion was highly variable for river diatoms, as β_{SOR} ranged from 0.2 (indicating strong similarity among stations in an ecoregion) to 0.81 (indicating strong dissimilarity among stations). Seven of the ecoregions had moderate dissimilarity among stations, with β_{SOR} between 0.5 and 0.65. The lowest beta diversity was in the Kalaallit Nunaat Low Arctic Tundra ($\beta_{\text{SOR}} = 0.2$) and the Scandinavian Coastal Conifer Forests ($\beta_{\text{SOR}} = 0.37$). In contrast, the highest beta diversity was in the Torngat Mountain Tundra ($\beta_{\text{SOR}} = 0.81$) and the Scandinavian Montane Birch Forest and Grassland ($\beta_{\text{SOR}} = 0.75$). Interestingly, one of the lowest beta (Scandinavian Coastal Conifer Forest) and the highest beta (Torngat Mountain Tundra) ecoregions had similar alpha diversity estimates at 10 stations (56 and 52 taxa, respectively). These ecoregions also differed with

respect to the dominant component of beta diversity, as the Torngat Mountain Tundra was dominated by taxonomic turnover (90% of beta), whereas the Scandinavian Coastal Conifer Forests had more similar contributions of turnover and nestedness (64% and 36% of beta, respectively; Figure 4-8d). Across all ecoregions, turnover generally remained the dominant component of beta diversity. However, in the Kalaallit Nunaat Low Arctic Tundra, beta diversity was completely due to nestedness (Figure 4-8d), which reflected the low richness and low number of stations in this ecoregion.

4.2.3.2. Regional Diversity

Circumpolar analysis of ecoregions showed high biodiversity in both lakes and rivers along the northern Alaskan coast, in the Canadian Arctic Archipelago, and in Fennoscandia. At the site scale, lake stations with high alpha diversity were found throughout the circumpolar region (Figure 4-9), whereas clusters of high diversity river stations were somewhat more evident in Alaska and Fennoscandia (Figure 4-10). However, data were more spatially limited for rivers, which may have affected the distribution of taxonomic hotspots. Differences in diversity across the circumpolar regions may be related to a number of factors, including time since glaciation, underlying geology type, and site-specific substrate and nutrient conditions. For example, a number of samples from Alaska were collected in marshy habitats with sandy substrates and high levels of organic material, which may have led to different taxonomic composition than would be expected in rocky habitats. Furthermore, northern Alaska and the Arctic Archipelago are primarily underlain by sedimentary and sedimentary/volcanic bedrock, in contrast to the non-sedimentary bedrock underlying the southern Canadian Arctic regions. These geological differences may have contributed to contrasting diversity across these regions, as diatom species composition is strongly affected by underlying geology through its effect on water chemistry (Grenier et al. 2006).

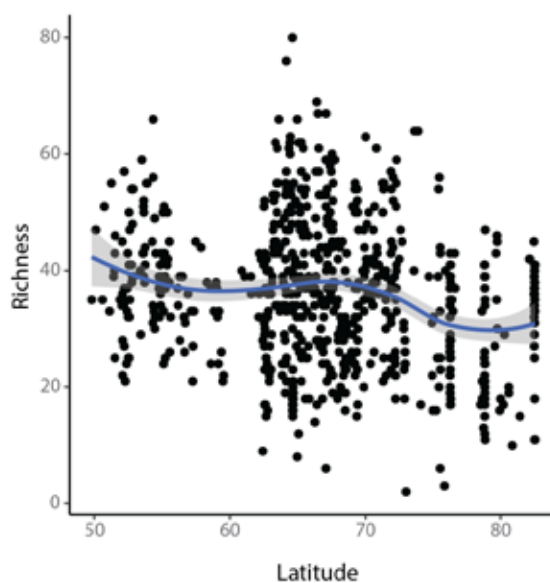
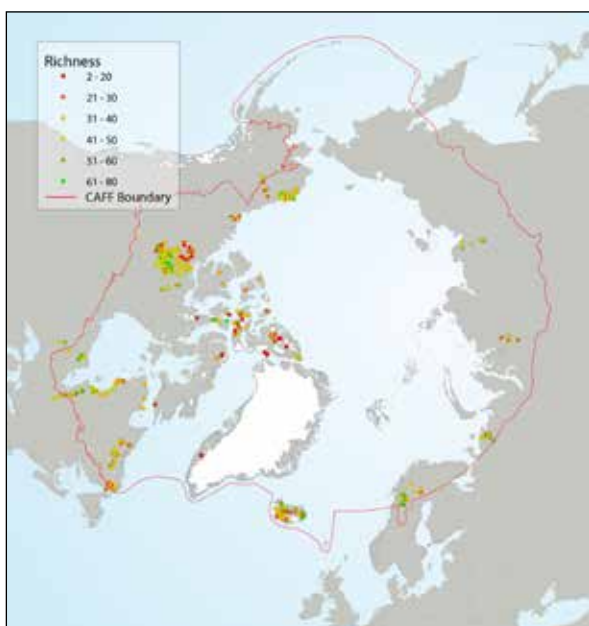


Figure 4-9 (left) Global species richness of diatom communities in Arctic lakes, with stations over the global mean taxonomic richness in red, and (right) local species richness of diatom communities in Arctic lakes across a latitudinal gradient.

Samples with the highest diatom richness, for both lakes and rivers, were generally in the latitude range of 60-75°N (Figure 49, Figure 4-10). However, the decline in richness outside this latitudinal range was small, and partly due to the fact that fewer samples were collected at the highest latitudes (above 75°N), particularly in rivers. Taxa accumulation curves indicated that an asymptote was not reached for either lake or river samples in any Arctic zone (sub-, low, or high Arctic; Figure 4-11), which suggests that raw richness estimates were affected by sampling effort. Taxa accumulation curves for lakes were similar until approximately 100 samples, above which high Arctic lakes had significantly lower taxonomic richness than sub- or low Arctic samples (Figure 4-11).

Similar results were observed for lakes, though the species accumulation curve for the low Arctic appeared to reach a richness value that was significantly higher than the estimate for the sub-Arctic (with no overlap of 95% confidence intervals for the two regions) at around 225 samples. Differences among Arctic zones were more evident for river data. The high Arctic had significantly lower taxonomic richness than the other two zones at 50 samples, whereas the low Arctic reached significantly higher richness than the sub-Arctic at approximately 75 samples. Patterns in lakes and rivers across Arctic zones were thus similar, but differences were stronger and more evident for river samples.

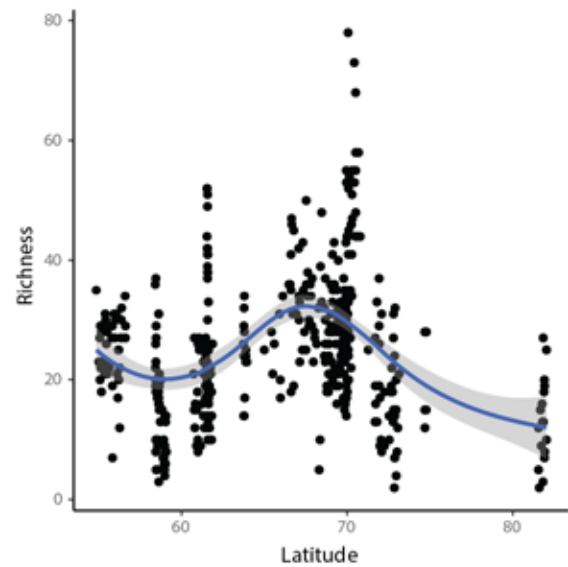
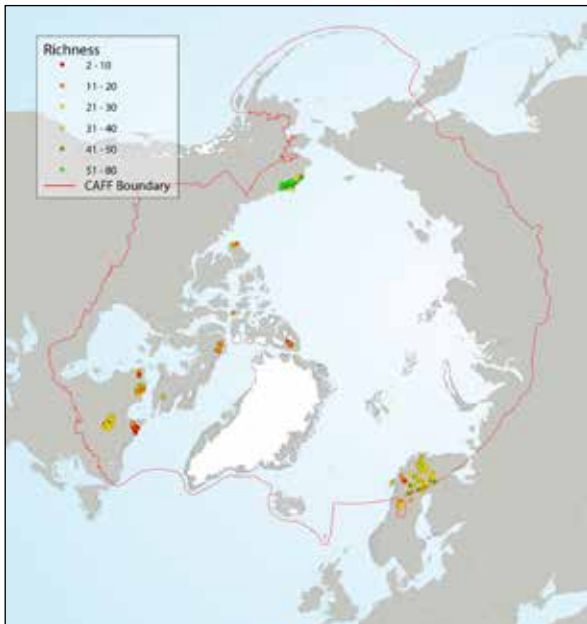


Figure 4-10 (left) Global species richness of diatom communities in Arctic streams, with stations over the global mean taxonomic richness in red, and (right) local species richness of diatom communities in Arctic streams across a latitudinal gradient.

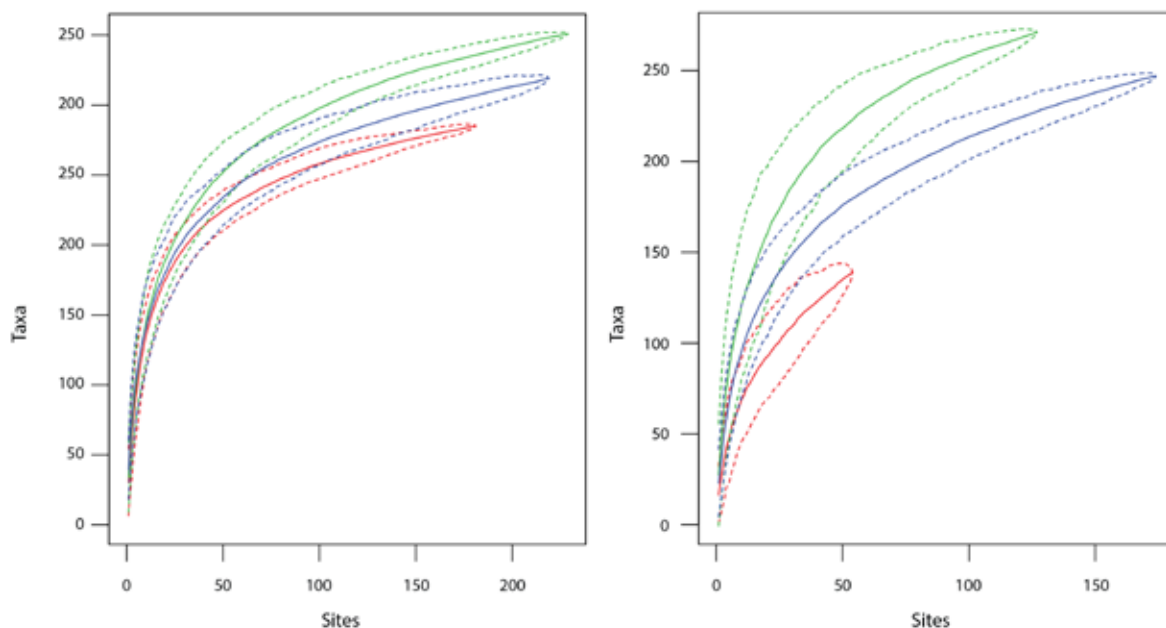


Figure 4-11 Taxa accumulation curves for (left) lakes and (right) rivers in the high Arctic (red), low Arctic (green), and sub-Arctic (blue) zones.

4.2.3.3. Compositional Patterns

Diatom taxa that were found to dominate the samples from across the circumpolar region are generally also common in other regions of the world, consistent with the suggestion that most algal species are not limited to the polar regions (Wrona et al. 2013). Within the studied regions, among-site differences in diatom assemblages were small, resulting in gradual shifts in composition across regions rather than clear thresholds of change. Many of the taxa that were present across the Arctic have an ecological preference for low nutrient levels and neutral pH, though a number of the identified taxa display a wide range of tolerances to environmental conditions and can be found in nutrient-rich conditions.

Diatom samples were grouped into biotypes with self-organizing maps (SOMs) to determine natural groupings of sites based on assemblage structure similarity and to evaluate spatial distributions of taxa. There were gradual changes between groups of sites rather than sharp differences, which indicated that there were no profound shifts in species taxa composition among regions. Clusters of samples did not differ significantly between North America

and Europe/Russia, which indicated that taxa composition was not linked to longitudinal position (Figure 4-12). Instead, some of the similarity among sites was related to latitude, with apparent clusters of taxa associated with high latitude and low temperatures, particularly for the most spatially extensive dataset of lake top sediments (Figure 4-12).

Lake top sediment samples were characterized by six SOM clusters (biotypes), one of which represented a diatom assemblage that only occurred at very high latitudes ($>70^{\circ}\text{N}$) and cold temperatures ($< -15^{\circ}\text{C}$ degrees annual average). This cluster was also characterized by a high number of unique species, contributing to the distinction of these northern samples. There were four SOM biotypes found for rivers, two of which were associated with high latitudes ($>70^{\circ}\text{N}$). Of the high latitude biotype in rivers, only one was associated with cold temperatures ($< -7^{\circ}\text{C}$ annual average degrees). Lake shoreline samples were collected only at lower latitudes and thus did not allow for assessment of compositional differences between Arctic zones. Shoreline samples were characterized by three SOM biotypes, one of which was associated with higher latitudes than the others ($>60^{\circ}\text{N}$) and colder temperatures (approximately $< -7^{\circ}\text{C}$ annual average degrees).

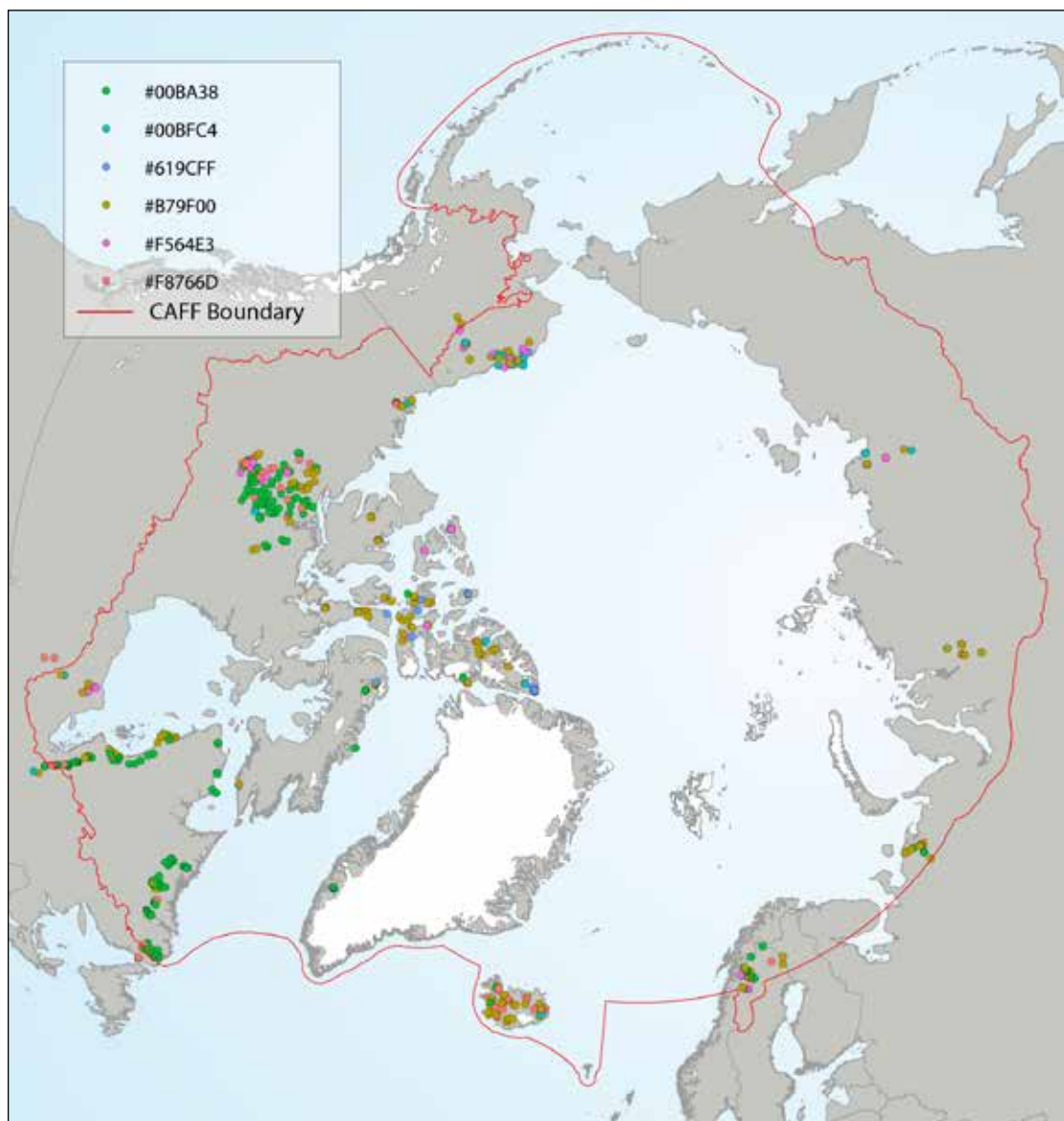


Figure 4-12 Diatom groups from Self Organizing Maps (SOMs) in lake top sediments, showing the geographical distribution of each group (with colors representing different SOM groups).

4.2.3.4. Temporal Trends

4.2.3.4.1. Lake sediment core top-bottom analysis

Analysis of differences between the tops and bottoms of lake cores was completed for 116 lakes, only 5 of which were located outside of North America. We divided the lakes into four categories based on geographical location, climate and vegetation (Boreal forest = BF, transition zone = T, Low Arctic = LA, High Arctic = HA). For certain analyses, sites were also categorized into 3 depth categories: ponds (< 2m), shallow lakes (2.1–6 m) and deep lakes (> 6.1m). Figure 4-13 illustrates the number of lakes per geographic zone for each of the depth categories.

The dataset for the top-bottom analysis included 452 diatom taxa, many of which were rare (e.g., found in low numbers at a single station). To eliminate rare taxa and reduce noise, only taxa that represented at least 2% in at least one sample were retained for the analysis, which reduced the number of species in the data set from 452 to 174. We then used the Bray-Curtis (B-C) dissimilarity coefficient to evaluate the difference in assemblage composition between ~1800 CE and contemporary sediments within each study lake. High values of this coefficient (which ranges from 0 to 100%) indicate strong dissimilarity between samples, whereas low values indicate that samples are similar. Mean values of the B-C dissimilarity coefficient were compared to assess if depth (pond, shallow, deep) and geographical zone (BF, T, LA, HA) influenced similarity between the bottoms and tops of cores.

B-C dissimilarity coefficient analysis showed a very wide range of similarity between tops and bottoms of cores among the stations (Bray-Curtis ranging between 14% and 91%; geographical distribution presented in Figure 4-14). Although the number of lakes outside North America was limited, the results suggested that systems in northern Siberia have changed more over time than those in northern Finland. In North America, western and high Arctic clusters (Tuktuyaktuk, Alaska, Ellesmere Island and other high Arctic Islands) displayed the largest change between now and c. 200 years ago. These were followed by the central Canadian sites (NWT and Hudson Bay lowlands). Finally, lakes in the

central and eastern Canadian Arctic (lower islands of the Arctic Archipelago, Baffin Island and Northernmost Ungava) showed the least change in diatom assemblages in the past c. 200 years.

In North America, continent-wide long-term climatic changes, such as deglaciation, are known to follow a west-east spatio-temporal gradient (Dyke 2004). This is also true of recent climatic warming, evidenced by the degree of change observed in biotic assemblages over the past c. 200 years (Smol et al. 2005). The low degree of change in many eastern Canadian lakes may reflect the temperature stability that has been noted in this area, as the easternmost regions of the Canadian Arctic have not warmed as much as the west and the far north (Prowse et al. 2006a). At sites on central high Arctic islands including Victoria, Prince of Wales and Devon, in eastern and southern Baffin Island, as well as in northernmost Ungava, across the Hudson Strait, changes in diatom assemblages over the past 200 years have remained minor. This is likely to change in the near future, as climate warming and long-distance atmospheric deposition of pollutants increasingly encroach into the region (e.g., Saulnier-Talbot et al. 2015).

The highest latitudes in the Canadian Arctic region have some of the largest temporal variability among stations. This region includes some of the lakes with the largest change over the last c. 200 years, but also includes stations that have recorded very low levels of change. The duration of ice cover is the main environmental variable that has been driving the changes in diatom assemblage composition in this region (Griffiths et al. 2017), with the ice-free season changing from almost none to several weeks per summer. However, not all lakes in the Canadian Arctic region are subject to homogeneous decreases in ice-cover (Keatley et al. 2008), which can explain the large variation in temporal patterns among lakes at high latitudes. Temporal shifts in diatom communities may be less evident where there has not been a change to ice cover duration due to lake morphometry (e.g., deeper lakes, such as Elison Lake; Smol and Douglas 2007, Keatley et al. 2008), localized conditions (e.g., Skeleton Lake, where shading and shelter from wind have sustained ice

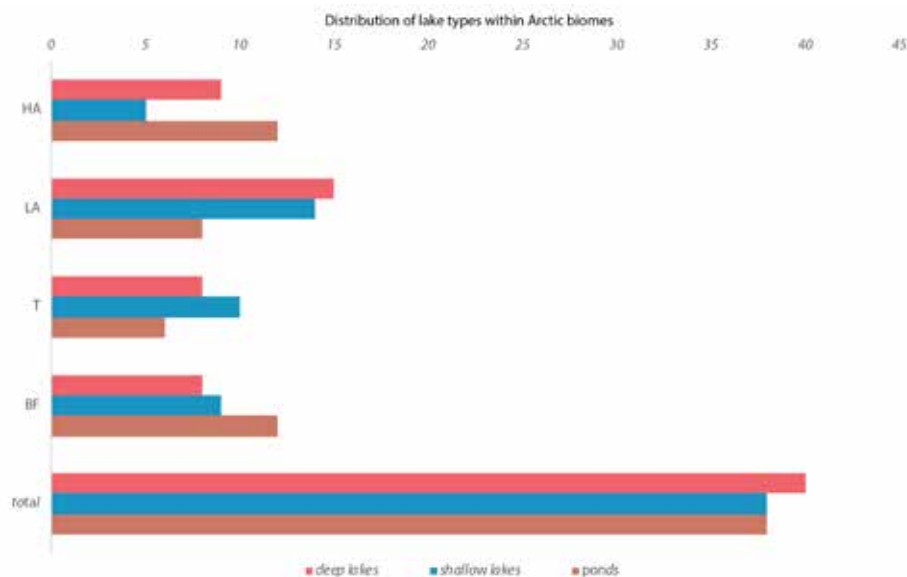


Figure 4-13 Number of deep lakes (light speckled grey), shallow lakes (solid dark grey) and ponds (dark speckled grey) in each geographical zone (BF, T, LA, HA). BF = Boreal Forest, T = Transition Zone, LA = Low Arctic, HA = High Arctic.

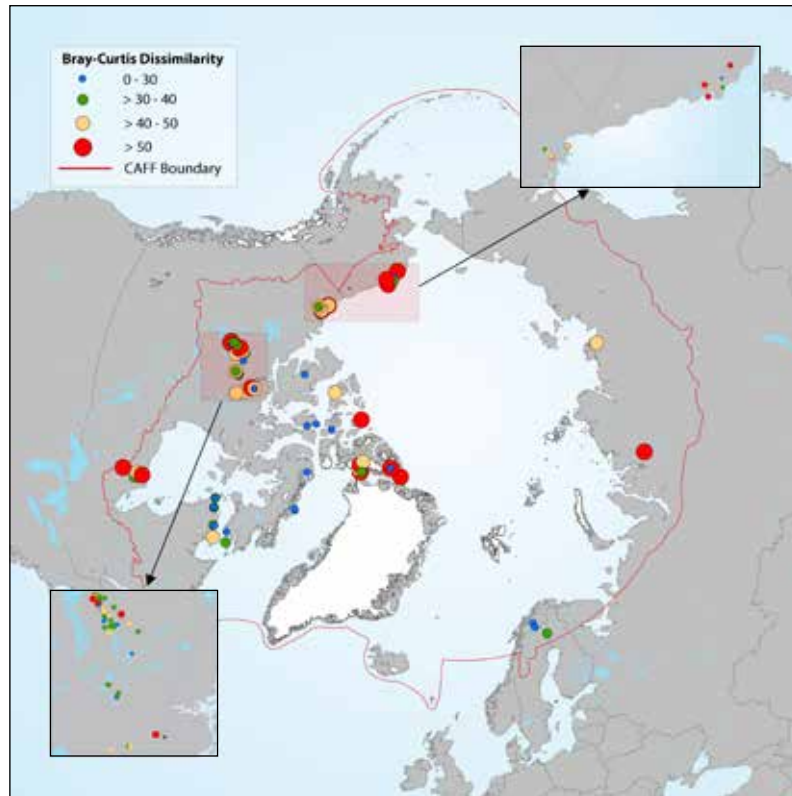


Figure 4-14 Map showing the magnitude of change in diatom assemblages between bottom (pre-industrial) and top (modern) section of the cores, estimated by Bray-Curtis (B-C) dissimilarity. Boundaries for the B-C dissimilarity categories are based on distribution quartiles (0-30%, 30-40%, 40-50% and >50%), where the lowest values (blue dots) represent the lowest degree of change in diatom assemblage composition between top and bottom sediment core samples in each lake.

cover; Keatley et al. 2008)(e.g., Skeleton Lake, where shading and shelter from wind have sustained ice cover; Keatley et al. 2008), or where the climate signal is dampened by other impacts (e.g., Eider Pond, which is dominated by the effects of bird colonies; Michelutti et al. 2010).

In some areas of the Arctic, there were clear shifts in taxa that contributed strongly to dissimilarity between bottom and top core samples. The large change recorded in the Russian sites reflected a transition in the assemblages from small *Fragilarias sensu lato* to epiphytic taxa (especially *Achnanthydium minutissimum*) in one lake, and from a strong dominance of *Aulacoseira humilis* (over 50% of the assemblage) to a more diverse assemblage dominated by small *Fragilarias sensu lato* in the other lake. Changes in the diatom assemblages of lakes located in the Central Canadian Arctic (continental NWT and Hudson Bay Lowlands) were characterised by a switch from a predominance of small, benthic *Fragilaria sensu lato* species to planktonic taxa such as *Discostella stelligera* (Rühland et al. 2003), reflecting changes in the length of the ice-free season and in stratification of the water column (Saros et al. 2016). Temporal change within lakes showed a high degree

of similarity across this region. In contrast, in the subarctic Hudson Bay lowlands, temporal change was highly variable between lakes. In this region, diatom assemblages also responded to climatic warming and decreased ice-cover with an increase in planktonic species, relative to the pre-1850 period (Rühland et al. 2014).

Geographic zone and depth did not have a significant effect on B-C dissimilarity (two-way ANOVA; $p > 0.05$). However, mean within-zone and -lake type B-C dissimilarities suggested that ponds have changed more than shallow and deep lakes and that changes in boreal forest and transition zones are more pronounced than in the low Arctic and high Arctic. Ponds in the boreal forest and in the high Arctic changed more than those in the transition and low Arctic zones; shallow lakes in the transition and low Arctic zones changed more than in the boreal forest and high Arctic; and deep lakes in the boreal forest and transition zones changed more than those in the low Arctic and high Arctic zones (Table 4-1). This strong spatial heterogeneity suggests that different lake types respond differently to change in different biomes.

Table 4-1 Lake depth categories that have changed the most in each geographic zone.

Zone	Ponds	Shallow lakes	Deep lakes
Boreal Forest	X		X
Transition Zone		X	X
Low Arctic		X	
High Arctic	X		

4.2.3.4.2. Identification of Sentinel Species

A SIMPER analysis (similarity percentage) was conducted using the Top-Bottom data to identify individual taxonomic groups that contributed most to the observed differences between pre-industrial and present-day assemblages. This multivariate analysis quantifies the contribution of each variable in a group and can help to identify the variables responsible for the differences between groups (here, fossil versus modern samples). For selected indicator taxa, we plotted the bottom vs. top relative abundances to evaluate the concordance between past and modern data (1:1 plot). The distribution of relative abundances along the 1:1 line indicates the shifts in abundance of these taxa between past and present (below the 1:1 line indicates higher abundances in fossil samples while above the 1:1 line indicates higher abundances in modern samples).

A number of diatom taxa showed large changes in relative abundances between bottom and top samples of the cores. In the boreal forest, the most striking assemblage change was from a predominance of small *Fragilaria sensu lato* to the planktonic species *Discostella stelligera* in all the deep lakes and in most shallow lakes. This was also the case in many low Arctic lakes, and to a lesser degree was also visible in the transition lakes. In the high Arctic, there was a change from small *Fragilaria sensu lato* to a more diverse assemblage dominated by other small benthic taxa such as *Achnanthes minutissima*, which were found at higher relative abundances in modern samples than in fossil samples for ponds. Ponds in the boreal forest showed a shift to lower relative abundances of *Nitzschia fonticola* in modern compared with fossil sediments. *Pseudostaurosira brevistriata* similarly declined in modern samples relative to fossil samples in lakes of all sizes in the transition zone.

When samples were pooled across all Arctic zones and lake sizes, there was evidence that the *Discostella* complex showed a higher relative abundances in modern sediments than in fossil sediments (Figure 4-15), indicating a major temporal shift in the prevalence of this group. Increased relative abundance in modern sediments was also evident for *Psammothidium marginulatum/scoticum/levanderi* (Figure 4-15). Whereas both of these groups increased in dominance in modern sediments, there were other taxonomic groups that became less prevalent in modern samples, including *Aulacoseira perglabra* complex and *Staurosirella pinnata* complex (Figure 4-15). Such a shift in taxa could indicate changes in lake stratification over time in response to climatic changes.

4.2.3.4.3. Downcore Analysis

Diatom composition was analyzed along the length of the core (downcore) to evaluate gradual temporal changes in assemblage structure and biodiversity since the early 19th century. This analysis provided a representation of ecological reorganization that was similar, albeit more in-depth, to the analysis of top and bottom core samples. Only cores that had robust chronologies were retained for this analysis (a total of 52). Samples along the length of the core were compared in multivariate analysis (Detrended Correspondence Analysis) to obtain a measure of beta diversity, which indicated the degree of dissimilarity across the c. 200 years of sediments analyzed from the core. The years in which the sediments were sampled varied considerably. As such, some cores may have been retrieved before the beginning of significant warming in certain areas of the study region, affecting the degree of change between recent and past.

Sediment core analysis results showed high variability in beta diversity across downcore samples, which indicated

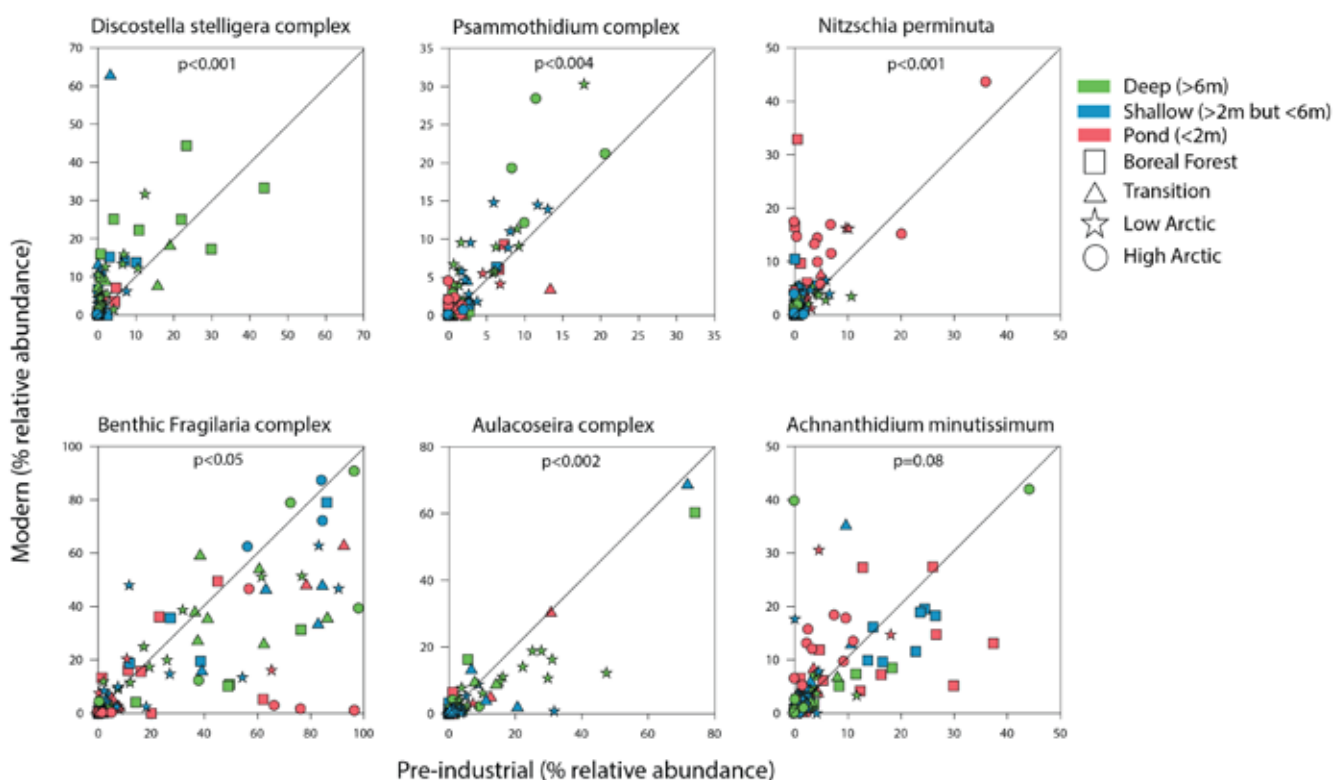


Figure 4-15 Comparison of the relative abundance of select diatom taxonomic groups between core bottoms (pre-industrial sediments; x-axis) and core tops (modern sediments; y-axis) with a 1:1 line to indicate whether there were higher abundances in fossil samples (below red line) or modern samples (above red line).

that rates of change in diatom assemblage composition were not the same across the sampled lakes. Nevertheless, some regional trends were observed. The areas that showed the least change since c. 1800 (lowest beta diversity) included northernmost Québec and eastern Baffin Island in Canada, the Central Canadian Archipelago and northern Finland (Figure 4-16). Sites in the Canadian high Arctic and northeastern Northwest Territories, Canada showed moderate overall change, whereas the largest changes were observed in the westernmost cluster of sites, near the Beaufort Sea in Canada, and southernmost sites (southern Hudson Bay; Figure 4-16). Variability in relative change among lakes was high at these sites. However, these results are similar to those obtained by Smol et al. (2005).

4.2.4. Gaps in Knowledge and Monitoring

Lake top sediment samples covered a large extent of the circumpolar region, but this coverage was primarily due to academic research, and thus does not represent repeated monitoring. Additional data from academia do exist (for example, additional samples are available from paleolimnological training datasets for Europe, including samples on Svalbard and on the Kola Peninsula in Russia), and these could be integrated into the CBMP database for future assessments. Any further assessment of diatoms from lake sediments must rely primarily on academic data, as these samples are not generally part of monitoring programs, with the exception of monitoring by industry and local- or regional-scale government monitoring (e.g., the province of Québec in Canada). However, the advantage of diatom samples in lakes is that long-term changes can be inferred from collecting sediment cores, thus compensating for the lack of routine monitoring activities.

River samples were more sparse, and were lacking from Russia, Iceland, Greenland, Svalbard, and central and western Canada. Although river algae monitoring takes place in some Arctic countries (e.g., Norway, Sweden, Finland), it is limited elsewhere in the circumpolar region (though some local- or regional-scale government monitoring occurs, e.g., the province of Québec in Canada). Furthermore, even in countries where monitoring occurs, the samples may not always be comparable if they focus on non-diatoms (e.g., in Norway) or do not follow comparable procedures (e.g., if they do not digest samples, thus potentially obscuring diatom taxa and making species-level identification impossible). Obviously, there is a clear need to increase the spatial scope of river diatom monitoring in order to capture the full variability in biodiversity across the circumpolar region.

Paleolimnological data for lakes similarly had gaps, in particular across most countries outside North America, resulting from the need to acquire downcore and top-bottom core data from academic sources, as this work is not conducted as part of routine monitoring. In some cases, core data were obtained from published research, but critical information on dates and/or depths may have been missing, or data were obtainable as presence/absence only, when analysis focused on relative abundances. Additional paleolimnological data repositories exist and could be accessed to improve data coverage, particularly for Europe where there was little collection of data of this type. Furthermore, it would be beneficial to make a targeted effort to approach paleolimnological researchers who have not been involved in the CBMP process, to request access to full core data that could fill the gaps in spatial coverage and allow for a broader assessment of long-term trends.

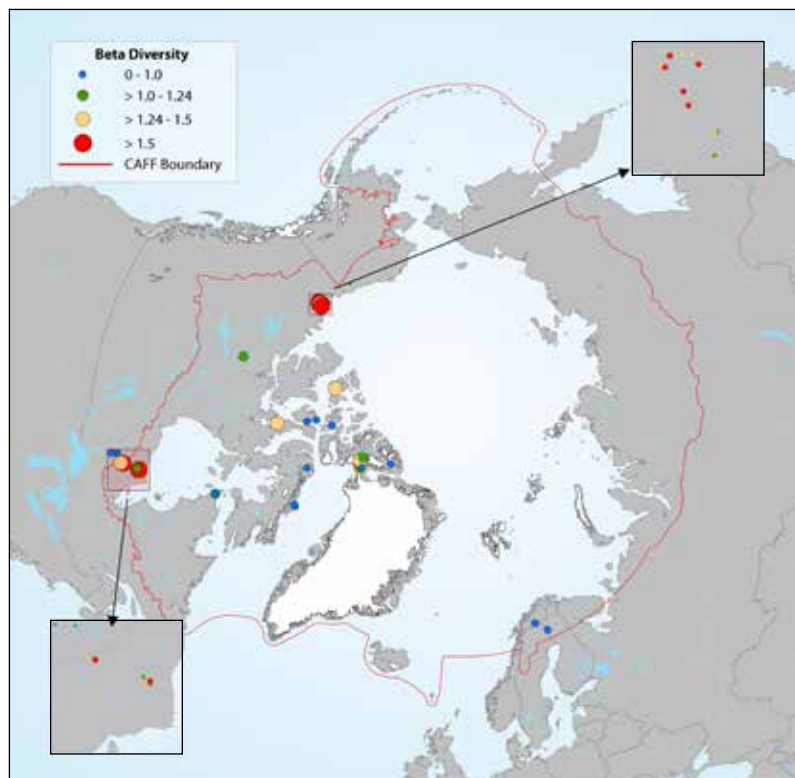


Figure 4-16 Map showing the magnitude of change in diatom assemblages for downcore samples, with beta diversity used as a measure of the compositional differences between samples at different depths along the core. Boundaries for the beta diversity categories are based on distribution quartiles (0-0.1, 0.1-1.24, 1.24-1.5, >1.5), where the lowest values (blue dots) represent the lowest degree of change in diatom assemblage composition along the length of the core in each lake.