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Climate warming is shifting northern aquatic ecotones

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Abstract:

Northern ecosystems are undergoing major changes in response to amplified warming, including range migrations due to changing environmental constraints on species distributions. The circumpolar Arctic's abundant freshwater ecosystems are highly sensitive to increasing temperatures as well as the effects of warming-induced changes in terrestrial catchment vegetation and soils. Here, we examine a 1400 km-long transect in Arctic and Subarctic Canada and show northward shifts in aquatic ecotones over the past ~25 years in response to accelerated regional warming.

Main

Temperatures in the Arctic are rising at an average rate of up to four times the global average, as warming is amplified by feedback mechanisms including surface albedo reductions and poleward energy transport[1]. Arctic and subarctic ecosystems are therefore disproportionately affected by climate change[1]. Temperate species are expected to propagate into northern ecosystems as climates become more conducive to their survival, with consequent disruptions to trophic networks[2]. At the landscape scale, ongoing changes affect interspecies relationships and favor new species associations with far-reaching effects, including the transmission of zoonotic and vector-borne diseases, which may either amplify or act antagonistically to expected biogeographic patterns[3,4]. Potential consequences include the loss of ecosystem services, reduced community stability and reduced biodiversity[4]. Warming also affects the Subarctic and Arctic's abundant lakes and ponds, causing rising water temperatures and shifts in ice phenology that result in longer open-water seasons and changes in light penetration, water column stability and stratification regimes[5–8].

Changing climates, including temperature and precipitation increases, also cause compositional changes in vegetation (Fig. 1), the most apparent being the expansion of deciduous shrub communities within the northern treeline zone (i.e., shrubification)[9].

This increase in primary productivity has occurred in biomes from boreal forest to shrub tundra[10]. Although the spatial patterns and magnitude of greening remain uncertain and vary between studies, northern Quebec and Labrador have consistently been highlighted as regions of pronounced greening in studies using remote sensing and other methods[10-12].

Aquatic resource availability may also be modified by associated alterations to soil microbial activity, nutrient cycling and hydrology. Ongoing changes in catchment vegetation and their downstream effects on lakes intensify the stress on lake biota due to rapidly shifting conditions[5]. The greening of lake catchments also contributes to the so-called 'browning' of their waters (i.e., increasing allochthonous dissolved organic carbon (DOC) concentrations) through higher inputs of organic matter from watersheds, particularly where trees were previously sparse[13]. Moreover, permafrost thaw increases the depth of the carbon-rich active layer and thus mobilizes allochthonous carbon[14,15]. Combined with shrub densification, these processes have complex feedbacks that can increase DOC inputs to lakes[16]. Permafrost thaw also affects the connectivity to the drainage network by altering landscape water storage and promoting land cover transition[17], that increase both surface and subsurface runoff[18,19]. Higher precipitation also intensifies catchment runoff, leading to greater terrestrial inputs (carbon, nutrients and ions)[20,21]. This increase in connectivity between lakes and watersheds, affect the primary productivity of aquatic ecosystems[22].

Ecotones are highly dynamic regions that integrate characteristics of two adjacent biomes. Because of their transitional nature they manifest relatively rapid biological changes[23]. In this study, we define aquatic ecotones at the landscape scale, as latitudinal transition zones between groups of lakes that differ in their biological, physical, and chemical characteristics[24]. This transition can reflect broader ecological boundaries, such as a shift between boreal and subarctic ecozones, and are inferred based on abrupt changes in aquatic community composition (diatom assemblages) along the latitudinal gradient[24]. The positions of these aquatic ecotones, and how they shift over time, can provide key information about the impacts of climate change on freshwater ecosystems[25].

Initial studies of a ~1100 km latitudinal transect in Nunavik, Canada, near the eastern margin of Hudson and James bays, showed close relationships between the positions of

Figure 1: Representation of temporal trends of climatic and limnological variables across study lakes. Each panel (a-c-e-g) represents the evolution of one variable from 1995 to 2022 for all lakes (individual lines), with color gradients indicating latitude (from red = southern to blue = northern). The right subpanels (b-d-f-g) display the corresponding spatial arrangement of lakes, colored by latitude. The horizontal red lines show 2021-22 breakpoint positions, while the black dotted lines show the 1995 breakpoint positions. Panels (a) and (b) show changes in precipitation (mm), respectively, panels (c) and (d) depict changes in summer and spring temperature (°C), panels (e) and (f) depict changes in frost-free days, and panels (g) and (h) depict changes in NDVI (Landsat 5). The bold black line in each left panel represents the median trend across all lakes.

terrestrial and aquatic ecotones in the late 20th century[26]. Temperatures in this subarctic region began to increase markedly only in the mid-1990s[27], whereas warming began much earlier in most other Arctic regions[1]. By using ecotone data that immediately predated the onset of recent temperature increases, we exploited a unique opportunity to study climate-induced ecosystem changes by revisiting and lengthening the same transect (to ~1400 km; Fig. 2). We then assessed changes in lakes, their catchments and their biota, as well as any shifts in ecotone positions, following 27 years of pronounced warming.

We studied 69 lakes distributed along a transect stretching from 49.80°N to 61.99°N, spanning four vegetation types from two major bioclimatic domains: boreal forest and tundra (see supplementary Table 1 and methods). At each site, we measured water chemistry and examined assemblages of diatoms, a commonly used bioindicator group at the base of the aquatic food chain, to identify aquatic ecotone locations from significant changes in the relationship between β-diversity and latitude[24,26].

Figure 2: The ~1400 km transect and the 69 study lakes. The magnified parts of the map highlight the sensitive ecotone vegetation zones and the lakes located near these dynamic areas. Map created by the authors using ArcGIS Pro version 3.1.0 (Esri, https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview).

The three aquatic ecotones identified in 2021-22 data were analogous to those identified in 1995, reflecting augmented diatom species overturn in response to limnological conditions that were closely linked with terrestrial vegetation transitions (Fig. 3)[26]. The southernmost ecotone (~52-53°N) corresponded to the change from boreal forest to subarctic forest, while an intermediate ecotone reflected the shift from subarctic forest to forest tundra (i.e., 55-56° N). The northernmost ecotone (~ 59° N), which occurred in the tundra, was not associated with a specific vegetation change, and its northern boundary was not detected. In all cases, the ecotone boundaries shifted polewards in the 27 years since the sites were first sampled, with a minimum northward displacement of 68 km.

The pronounced northward shifts of ecotone boundaries between 1995 and 2021-22 (between 68 and 148 km; Fig. 3, supplementary Table 2) were consistent with theoretical northward species displacements due to warming. Significant changes in temporal β-diversity indicated that exceptional changes in community composition occurred in lakes associated with ecotone positions (supplementary Table 1; Fig. 3).

Figure 3: Aquatic ecotones defined from diatom assemblages for 1995 and 2021-22, shown by black hatched areas in (a) and yellow/red shading in (b), respectively. Black (1995) and red (2021-22) lines represent cumulative β-diversity, with lakes having significant temporal β-diversity index (TBI) shown with one/two yellow stars ($p<0.1/0.01$, respectively; Table S1). Vertical arrows show northward displacements of ecotone positions between 1995 and 2021-22. Photos show the same lakes and illustrate vegetation changes over the study period. (c) DOC concentration differences between 1995 and 2021-22; (d) vegetation and (e) permafrost zones.

Important changes in species turnover also occurred within ecotones, as illustrated by a 25% drop in the β-diversity difference within the boreal forest/subarctic forest ecotone (Fig. 3). This suggests biotic homogenization in aquatic ecosystems, similar to that observed for terrestrial vegetation in the Fennoscandian boreal zone[28]. By contrast, species turnover within the subarctic forest/forest tundra ecotone was 50% greater in 2021-22 than in 1995, likely reflecting stronger greening than in other biomes due to shrub expansion[12] and consequent changes in water chemistry and ecosystem diversity. Although both the boreal forest/subarctic forest and subarctic forest/forest tundra ecotones experienced similar climatic changes, in particular increases in temperature and precipitation (Fig. 4), divergent ecological responses in the 23 lakes located in the two different ecotones suggest that climate variables alone cannot explain the observed patterns. Although our data do not allow us to isolate the specific mechanisms underlying these changes, the contrasting patterns in species turnover that occurred despite similar climatic trends suggest a role for vegetation dynamics, such as greening intensity or species expansion. The well-known relationship between catchment vegetation and aquatic DOC concentrations, combined with earlier studies that showed DOC to be the primary variable controlling diatom variance in lakes of our study region, provide the mechanism linking vegetation changes to ecotone shifts[29].

No aquatic ecotones were observed near the northern treeline, where vegetation undergoes dynamic changes, suggesting that vegetation densification is not the main driver of ecotone positioning. This observation is supported by the lack of a significant relationship between changes in the Normalized Difference Vegetation Index (NDVI) and ecotone locations (Wilcoxon $p = 0.5$). In contrast, changes in summer precipitation (Wilcoxon $p = 0.03$) and temperature (Wilcoxon $p = 0.02$) were significant in the 12 lakes situated close to ecotone breakpoints (less than 60 km) when compared to those farther away. This spatial association suggests a potential influence of climatic factors on ecotone shifts. However, further research integrating mechanistic studies and long-term temporal analyses is necessary to establish clear causality.

The multiple ecological consequences of amplified warming in circumpolar regions include changes in species ranges, as well as the loss or transformation of habitats, resulting in northward migration of species over time and the increasingly evident disruption of food webs[2]. Larger, longer-lived organisms are more likely to have difficulty adapting and disappear, while the short generation times and rapid dispersal of microorganisms imply greater adaptive capacity[30]. Our results show that aquatic microbial biogeography is responding rapidly to climate warming and warming-induced landscape changes.

DOC concentrations significantly changed in 2021-22 relative to 1995 in most of our lakes, but this change was less consistent than expected (Fig. 3). Carbon concentrations in northern lakes are closely linked with vegetation and permafrost, and control multiple ecosystem processes in subarctic aquatic ecosystems; various studies have shown DOC increases due to climate warming[23,31]. However, DOC concentrations decreased in some of our lakes (Fig. 3), even where the NDVI highlighted vegetation greening (Fig. 1). Although there was no statistically significant relationship overall between DOC and summer precipitation changes (Spearman's $p = 0.09$), at the local scale changes in precipitation, combined with individual catchment characteristics, may modify the delivery of DOC to lakes. Some of the DOC changes we observed may not indicate a general decrease of DOC over time but rather highlight potential limitations of snapshot sampling in remote regions, which in water samples may be influenced by weather events before the time of sampling, and may not capture the full range of variability in conditions. As such, using 1-cm surface sediment samples that correspond to approximately five years of accumulation, allows the detection of biological shifts that are otherwise difficult to interpret in systems lacking long-term monitoring.

While these ecological shifts can be related to environmental changes such as precipitation, temperature, freezing conditions, and vegetation, we found that the position

Figure 4: Representation of changes in temperature and precipitation and their relation to ecotone positions in 2021–2022. Subpanel a) shows differences between the 1990–1995 and 2017–2022 periods in summer precipitation (mm) vs. latitude, and b) shows differences in summer temperature (°C). The horizontal dotted lines indicate the positions of ecotones in 2021–2022.

of aquatic ecotones in 2021–2022 was significantly associated with changes in summer precipitation and temperature. The most favorable conditions for ecotone shifts appear to occur in areas where summer temperatures have strongly increased, while precipitation increases have remained relatively low between the 1990–1995 and 2017–2022 periods (Fig. 4). However, the extensive latitudinal range of the transect complicates generalization, as the environmental drivers of ecotone shifts are heterogeneous at the local scale. Based on our data, we suggest that northward ecotone shifts result from local combinations of environmental changes, with vegetation changes influencing the southern ecotones and permafrost thaw processes prevailing at the northern ecotones (Fig. 3). Regardless of the precise mechanisms, the striking northward ecotone shifts we observed demonstrate the sensitivity of northern biota to amplified warming and illustrate extensive aquatic community responses to ongoing ecosystem perturbations.

Methods

Site description

In northern Quebec, the boreal forest covers the territory from 51-55°N and is separated at 52°N into closed spruce-moss forest to the south and subarctic forest with spruce-lichen woodland to the north. The tundra biome occurs north of 55°N and is distinguished by four distinct vegetation types: the forest-tundra, a mosaic of shrubby heathlands covering 70% of the landscape and with isolated tree stands, is present from 55-58°N; at the northern limit of the forest-tundra zone is the treeline. Beyond this point shrub tundra is found, which is divided into erect shrub tundra from 58-61°N and prostrate shrub tundra north of this latitude. Our study covers all these biomes.

Lake sediment and water sampling

The study area comprises 69 lakes, 58 of which were sampled in 1995, and spans a ~1400-km long transect along the eastern coast of northern Quebec, extending from 49.80°N in the south to 61.99°N in the north. All were sampled using the same protocols as in 1995, including the 11 new lakes: five that extended the transect's northern limit and six that refined ecotone positions near critical vegetation transitions: one near treeline and five that filled/completed a spatial gap between 54°N and 55°N in the 1995 transect near the forest-tundra/shrub tundra transition.

The lake resampling was carried out during two consecutive summers, and all methods replicated those of the original study[29]. Thirty-four lakes were sampled in late June 2021, and 34 that were not accessible in 2021 due to pandemic-related access restrictions in Nunavik were sampled in June-July 2022. All new lakes were selected following the original criteria: no inflows, roughly circular in shape, and shallow to moderate depth (< 11 m). Sites were accessed on foot from roads where possible, while those beyond road networks were accessed by helicopter. For both access modes, the sampling followed the same sequence: limnological variables were measured *in situ* and water samples were taken just below the surface for chemical analyses, then short surface sediment cores were retrieved at the deepest known part of the lake using a gravity corer, and the top 1 cm, representing the last few years of accumulation, was subsampled on site and placed into a sterile bag and kept cool and in the dark until further analyses in the laboratory.

Sample preparation

Surface sediments were freeze-dried before being treated following standard techniques to oxidize organic matter. Diatoms (class Bacillariophyceae) are known to respond rapidly to changes in limnological conditions due to their short life cycles and taxon-specific preferences for diverse environmental conditions. These characteristics and easy identification to fine taxonomic levels mean that they are ideally suited for biomonitoring and environmental change studies[23]. Counts and identifications were made using an optical Zeiss Axio Imager A2 microscope at 1000x magnification under oil immersion. Identifications were made to the lowest taxonomic level possible (species/morphotype) using reference literature and taxonomically standardized with 1995 identifications based on the photographic plates available in the reference flora for northern Quebec[29]. A minimum of 500 diatom valves was counted per slide and counts were converted to relative abundances prior to statistical analyses.

Environmental data

The positions of vegetation ecotones and permafrost transitions were extracted from existing databases[12,32]. Climate data, including precipitation, temperature, and freeze–thaw days, were retrieved from the ClimateData.ca data portal published by Environment and Climate Change Canada, for each lake at both annual and seasonal scales for the period 1985-2022. The available data are downscaled historical daily observations at ~10 km resolution, interpolated using the Australian National University Spline (ANUSPLIN) method. NDVI values were calculated for each lake using imagery from Landsat 5 (1990-2022) and Sentinel-2 (2017-2022) satellites via the Google Earth Engine platform. For Figure 1, which presents long-term vegetation dynamics from 1990 to 2022, NDVI values were derived exclusively from Landsat imagery due to its consistent availability during this period. To facilitate comparison with more recent vegetation conditions, Sentinel-2 data from 2017 to 2022 were incorporated, leveraging its higher spatial resolution and improved data quality. We acknowledge that integrating data from two different satellite sensors may introduce cross-sensor biases. However, by using aggregated median NDVI values over space and time, we minimized sensor-specific variability and focused on broad vegetation trends despite the lack of fully harmonized data.

The map was created by the authors with ArcGIS Pro version 3.1.0, using data from the open data repository of Données Québec[33].

Statistical analysis

All taxa that reached a relative abundance of at least 1% in at least one lake were included[29]. Outliers were detected based on the modified interquartile range (MIQR)[34]; Lake Q2 was identified as an outlier. The change in its DOC concentration, which increased by 8.00 mg/L between 1995 and 2021–22 compared to the transect median of 0.53 mg/L (supplementary Table 1). This exceptionally high value was accompanied by distinct diatom assemblages and highly divergent water chemistry (with decreases of more than 50% of small *Fragilaria* taxa, as well as concentrations of Al of 1500.7 µg/L, K of 1168.4 µg/L, Fe of 1997.0 µg/L, and Ti of 72.9 µg/L in 2021-22, suggesting that the lake represents an ecologically unique system or one that has undergone major anthropogenic modifications that are not attributable to climate change alone. In fact, logging took place in this lake's catchment, as reflected by the large amount of dead wood and decomposing material in and around the lake. Moreover, sampling of this very shallow lake had to be conducted near the shore due to strong winds on the day of sampling. The lake is also located close to a large peatland, but its increase in NDVI was much lower (−50%) than that observed in nearby lakes, which is consistent with the effects of these disturbances. Given the strong influence of this lake on multivariate analyses and its ecological distinctiveness, we chose to exclude it from the main analyses (in accordance with standard statistical procedures) to avoid skewing patterns that are otherwise consistent across the remaining lakes. It was therefore removed from subsequent statistical analyses.

To detect ecotone positions, we used β-diversity as an indicator of diatom compositional change[24]. Principal Coordinates Analysis (PCoA), using chord distance, was applied to estimate changes in community turnover with latitude, and eigenvalues indicated that chord distance extracted a high portion of the variability in species composition (supplementary Table 3). The square root of sums of the first four coordinates of the PCoA was cumulated from north to south, scaled to zero mean, and used to calculate cumulative β-diversity. Piecewise linear regression was used to identify the number and positions of significant breaks in the cumulative β-diversity slope (i.e., ecotones), with the number of significant breaks being that which minimized the Bayesian information criterion. The temporal β-diversity index (TBI) was calculated to identify lakes with exceptional community changes over time [35].

All environmental variables and DOC concentrations were first tested to verify whether they exhibited significant statistical changes between the two periods, 1990–1995 and 2017–2022. Following this verification, Wilcoxon tests were applied to assess whether the change in each environmental variable differed significantly depending on whether the lake was located near a breakpoint or not (more than 60 km from the breakpoint).

Data availability

The limnological and environmental data on which this paper is based will be made available in the *Borealis repository* upon acceptance of the manuscript. Diatom samples from this research will be deposited in the CANA Phycology Collection and will be accessible through the archives of the Canadian Museum of Nature, National Museum of Natural History of Canada (Ottawa).

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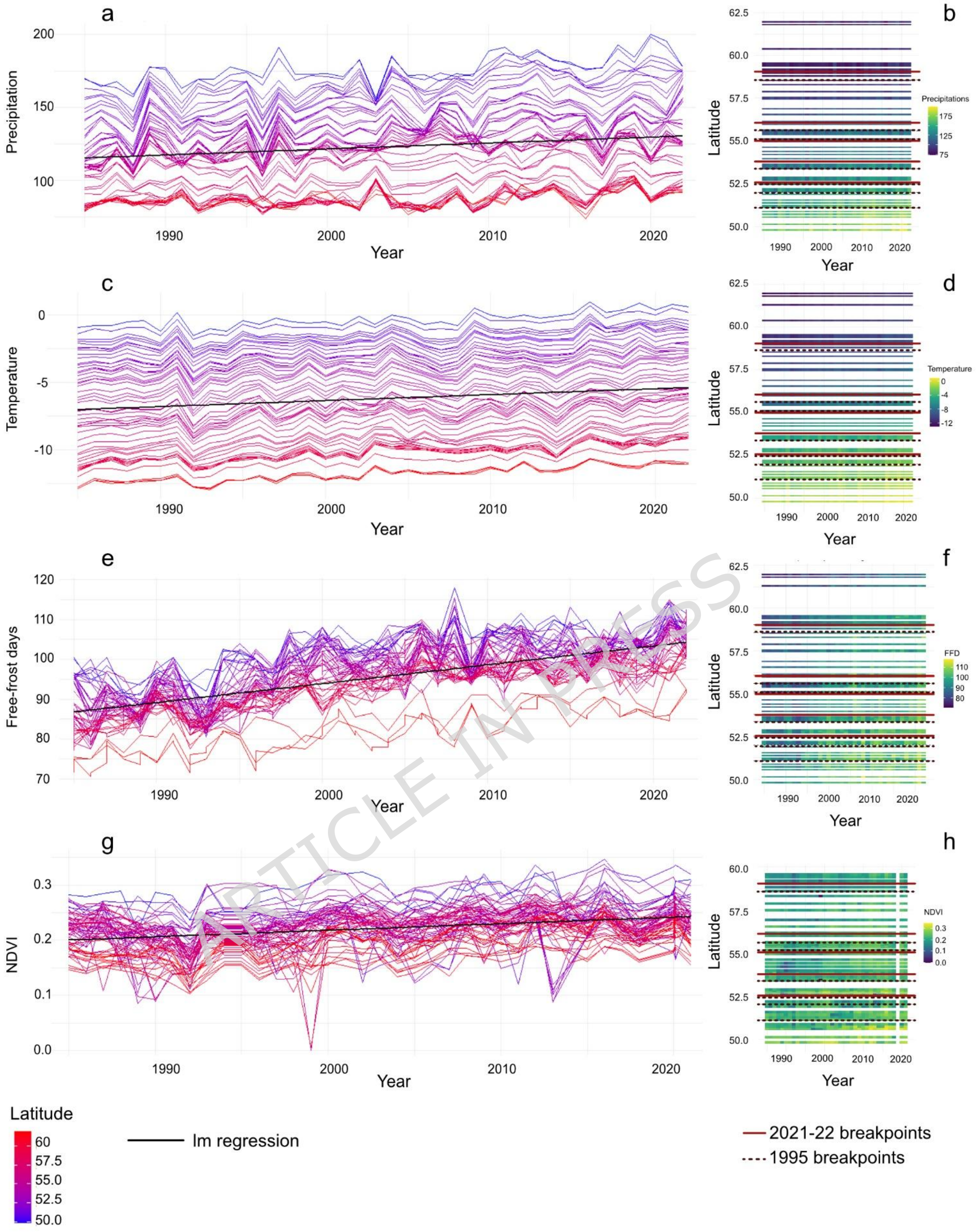
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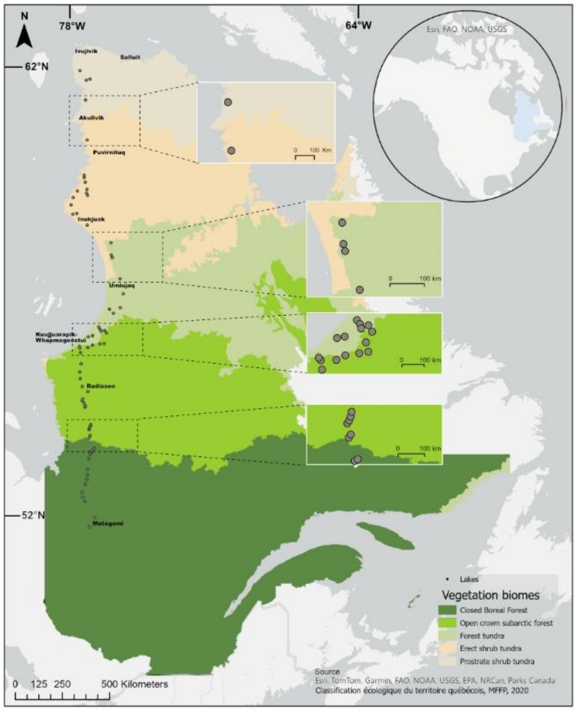
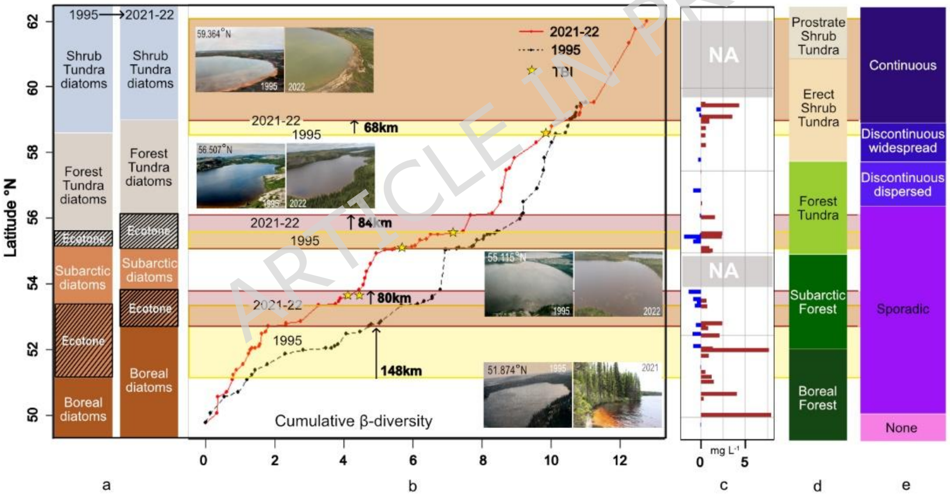
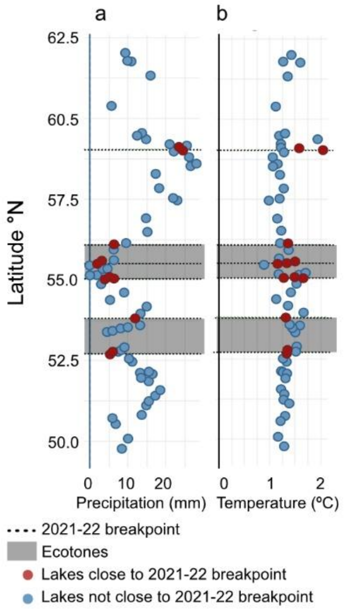


Source
Esri, TomTom, Garmin, FAO, NOAA, USGS, EPA, NRCan, Parks Canada
Classification écologique du territoire québécois, MFFP, 2020




a
b
62.5
60.5
57.5
55.0
52.5
50.0
Latitude °N
0
10
20
Precipitation (mm)
0
1
2
Temperature (ºC)
2021-22 breakpoint
Ecotones
Lakes close to 2021-22 breakpoint
Lakes not close to 2021-22 breakpoint