

Improving the framework for assessment of ecological change in the Arctic: A circumpolar synthesis of freshwater biodiversity

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Abstract

1. Climate warming and subsequent landscape transformations result in rapid ecological change in Arctic freshwaters. Here we provide a synthesis of the diversity of benthic diatoms, plankton, macrophytes, macroinvertebrates, and fish in Arctic freshwaters.
2. We developed a multi-organism measure of α diversity to characterise circumpolar spatial patterns and their environmental correlates, and we assessed ecoregion-level β diversity for all organism groups across the Arctic.
3. Alpha diversity was lowest at high latitudes and elevations and where dispersal barriers exist. Diversity was positively related to temperature, and both temperature and connectivity limited diversity on high latitude islands. Beta diversity was highly variable among ecoregions for most organism groups, ranging from 0 (complete similarity) to 1 (complete dissimilarity). The high degree of dissimilarity within many ecoregions illustrates the uniqueness of many Arctic freshwater communities.
4. Northward range expansion of freshwater taxa into Arctic regions may lead to increased competition for cold-stenothermic and cold-adapted species, and ultimately lead to the extinction of unique Arctic species. Societal responses to predicted impacts include: (1) actions to improve detection of changes (e.g., harmonised monitoring, remote sensing) and engagement with Arctic residents and Indigenous Peoples; and (2) actions to reduce the impact of unwanted changes (e.g., reductions of CO₂ emissions, action against the spread of invasive species).
5. Current Arctic freshwater monitoring shows large gaps in spatial coverage, while time series data are scarce. Arctic countries should develop an intensified, long-term monitoring programme with routine reporting. Such an approach will allow detection of long-term changes in water quality, biodiversity, and ecosystem services of Arctic freshwaters.

KEYWORDS

aquatic assemblages, biomonitoring, climate change, α diversity, β diversity

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1 | INTRODUCTION

Humans are impacting the Earth's environment through large-scale land-use changes, fossil fuel burning, extensive deforestation, and resource extraction, thereby affecting natural ecosystem processes and climate at an unprecedented rate (IPCC, 2021). The Arctic region is particularly vulnerable to these pressures, as increases in temperature and precipitation (Bitanja & Andry, 2017; IPCC, 2021; Serreze & Barry, 2011) are leading to glacier melt (Zemp et al., 2015), permafrost thaw (Kokelj et al., 2015), shorter winter ice duration (AMAP, 2019; Meridith et al., 2019), and increased vegetation growth (Elmendorf et al., 2012; Jenkins et al., 2020). Moreover, the Arctic is increasingly subjected to land use modification (e.g., agriculture, urbanisation) and resource exploitation (e.g., mining, hydropower) that result in altered erosion rates, increased water withdrawal, and contaminant release, among others (e.g., Cherry et al., 2017; Gregor et al., 1998). The recent climate report from the Intergovernmental Panel on Climate Change (IPCC, 2021) indicates that there is high confidence that warming in the Arctic will continue to exceed twice the global rate. The cumulative effects of increased warming and human activities contribute to the transformation of Arctic landscapes, including freshwater habitats.

Across the circumpolar region, alterations to freshwater habitats and biodiversity in response to climate change and development are already visible (Heino et al., 2020). For example, historical data and paleolimnological records indicate that the period of ice cover on Arctic lakes and rivers has decreased, with a pattern of later freezing and earlier ice break-up being strongly associated with air temperature changes (Lento et al., 2019; Prowse et al., 2011). In this special issue, Svenning et al. (2022) used historical fish catch records to show that increasing temperatures are associated with long-term shifts in the relative proportions of Arctic charr and brown trout in Norway and Iceland. Furthermore, Kahlert et al. (2022) analysed paleolimnological records of diatoms and found large changes in taxonomic composition of Arctic lakes over the last c. 200 years. Environmental change in the Arctic is also evident from water quality data collected over the last 50 years, and trends are expected to continue as climate change progresses and human activity accelerates (Huser et al., 2022). Landscape-level processes driven by warming and development in the Arctic can be traced in the runoff of the rivers that drain these landscapes, and are expected to result in a loss of both habitat and abundances of cold stenothermic species (IPBES, 2019; Lento et al., 2019), favour the northward migration of species (Pecl et al., 2017), and contribute to changes in the genetic diversity of key fish species (Östergren et al., 2021). Unfortunately, our ability to detect and track such abrupt and irreversible change in Arctic freshwater biota is limited by a lack of coordinated monitoring and assessment (Heino et al., 2020).

During the last decade, the freshwater group of the Circumpolar Biodiversity Monitoring Program (CBMP-Freshwater), part of the Conservation of Arctic Flora and Fauna (CAFF) biodiversity working group of the Arctic Council, has worked on the implementation of their circumpolar freshwater monitoring plan (Culp et al., 2012). The

first stage of implementation included the gathering of existing biodiversity data from all Arctic countries and subsequent assessment of the current status and trends in Arctic freshwater. Such an analysis is necessary to analyse spatial patterns in biodiversity, identify diversity hotspots, establish baselines for monitoring continued change, and identify gaps in the coverage of Arctic freshwater monitoring. CBMP-Freshwater has collected existing data from government, industrial and academic research sources to produce a circumpolar database of freshwater biodiversity and supporting variables (CBMP-Freshwater database, housed at the Arctic Biodiversity Data Service, www.abds.is; see Lento et al., 2019). Collected data were harmonised and integrated (see Culp et al., 2022 and special issue papers listed below for details), and selected biotic and abiotic data for lakes (Figure 1a) and rivers (Figure 1b) were used to assess baselines of biodiversity of key organism groups and ecological change in Arctic freshwaters. Special issue papers included circumpolar assessments for water quality (Huser et al., 2022) and specific organism groups including plankton (Schartau et al., 2022), benthic diatoms (Kahlert et al., 2022), macroinvertebrates (Lento, Culp et al., 2022) and fish (Laske et al., 2022); smaller-scale regional assessments of multiple groups for North America (Lento, Laske et al., 2022), Iceland/Norway (Svenning et al., 2022), Fennoscandia (Brittain et al., 2022; Lau et al., 2022), and Russia (Fefilova et al., 2022); but did not include a circumpolar-scale assessment of multi-organism diversity patterns. In addition, Knopp et al. (2022) provided a systematic review of documented Indigenous Knowledge of freshwater biodiversity.

In this paper, we provide a novel synthesis of the data from the special issue papers, including all organism groups and all regions of the Arctic. We develop a multi-organism measure of α diversity to characterise circumpolar spatial patterns and contrast ecoregion-level β diversity for all groups across the circumpolar region. Furthermore, we identify spatial patterns and hotspots of biodiversity across organism groups and summarise the major environmental correlates of biodiversity patterns and predicted drivers of change. The analyses in this paper complement the special issue papers by providing a broad-scale assessment of the data that integrates and synthesises the findings in those papers. Additionally, we discuss the need for development of coordinated and harmonised long-term circumpolar freshwater monitoring to build a framework for science communication and decision support.

2 | ALPHA DIVERSITY

A primary objective of this paper was to use estimates of α diversity (taxonomic richness at local scales) from assessments of single organism groups in the special issue and develop an estimate of α diversity that was integrated across multiple organism groups over the circum-Arctic scale. As sampling effort was uneven within and among regions, the papers in this special issue used rarefaction, or the estimation of taxonomic richness at the same number of sites in each region using species accumulation curves (and extrapolation of curves as needed; see Colwell et al., 2012 for details), to control for

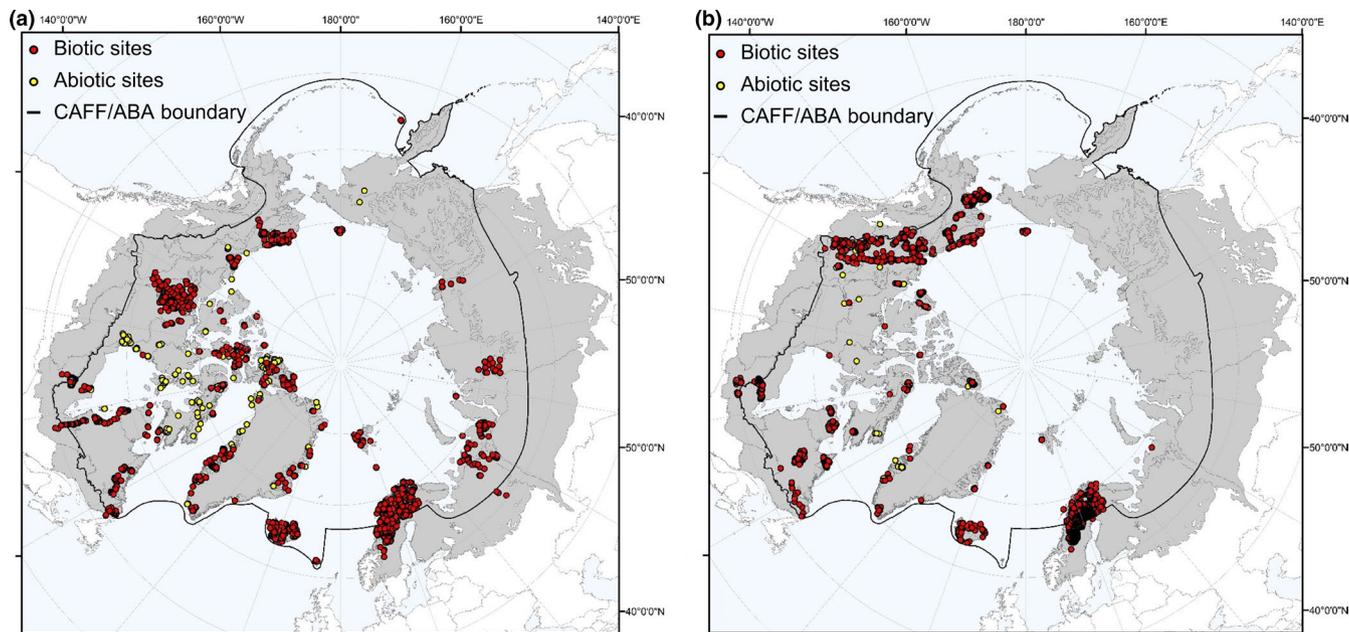


FIGURE 1 Circumpolar sample sites in lakes (a) and rivers (b) with biotic (red points) or abiotic (yellow points) data included in analyses in special issue papers. Ecoregions that are wholly or partly located within the Arctic boundary (as defined by the combination of the Conservation of Arctic Flora and Fauna [CAFF] and Arctic Biodiversity Assessment [ABA] boundaries) are indicated in grey. Biotic site points are layered over abiotic sites. Site locations can be found on abds.is. Country layer (white) and ocean layer (light blue) from www.naturlearthdata.com; ecoregion layer from *Terrestrial Ecoregions of the World* (Olson et al., 2001); CAFF and ABA boundaries from abds.is

differences in sample frequency. Rarefaction was done at the catchment or ecoregion scale (using *Terrestrial Ecoregions of the World*; Olson et al., 2001) to provide standardised, and thus comparable estimates of local-scale diversity. Rarefaction was completed using EstimateS (Colwell, 2013).

To develop a measure of multi-organism α diversity, we integrated the rarefied estimates (diversity at 10 sites within each ecoregion) for each organism group in lakes (phytoplankton, benthic diatoms, macrophytes, zooplankton, benthic macroinvertebrates, and fish) and rivers (benthic diatoms and macroinvertebrates, and fish). Because diversity is naturally higher in primary producers (e.g., diatoms) than in higher trophic levels (e.g., fish), we first standardised the rarefied α diversity estimates for each ecoregion by subtracting the mean rarefied diversity estimate for the organism group (averaged across all ecoregions) and dividing by the group's standard deviation. In this way, rarefied diversity for each group was converted to Z-scores, allowing for a standardised comparison across organism groups. As not all groups were sampled in every ecoregion, we could not sum the standardised diversity estimates for each ecoregion, but instead calculated average standardised diversity (lake average Z ranged from -1.25 to 1.2 ; river average Z ranged from -1.67 to 2.0). This allowed for a circumpolar comparison of standardised estimates of α diversity (averaged among organism groups) that were less affected by local sampling frequency or natural differences in species richness among trophic levels. Average standardised diversity estimates for each ecoregion were classified separately for lakes and rivers as low ($Z < -0.5$), average ($-0.5 < Z < 0.5$), or high diversity ($Z > 0.5$).

We used simple linear regression to analyse the relationship between standardised estimates of multi-organism α diversity in ecoregions and temperature, with separate regressions for lakes, rivers, and lakes and rivers combined. In this analysis, the maximum long-term average (1970–2000) August air temperature (data from WorldClim Version 2; worldclim.org/version2), summarised for the ecoregion, was used as a proxy for the warmest temperatures found in each ecoregion. Spatial connectivity was visualised in regression plots with different symbols for ecoregions based on whether they were completely found on the continental mainland, on islands, or whether there were both mainland and islands within the ecoregion. Analyses were completed in R version 4.0.2 (R Development Core Team, 2015) and graphs were created using the package *ggplot2* (Wickham, 2016).

2.1 | Circum-Arctic patterns in multi-organism α diversity

Spatial patterns in average standardised diversity reflected latitudinal, elevational, and geographic constraints. In both lakes and rivers, low diversity was commonly found at high latitudes, and high elevations, and on islands (Figure 2). For lakes, this pattern was paralleled by low diversity in Greenland, Iceland, Faroe Islands, Svalbard, and islands of northern Russia (Figure 2a), whereas rivers also showed low diversity in northern and eastern regions of the Canadian Arctic Archipelago, coastal areas of Norway, and on Wrangel Island (Figure 2b). Areas of the Arctic with high standardised diversity were similar for both lakes and rivers, and included

ecoregions at the warmer, lower latitudes of North America and ecoregions in Fennoscandia and western Russia that are warmed by the Gulf Stream. These high-biodiversity regions also have generally good spatial connectivity, allowing for movement of taxa, and hold the source populations for northward migrating species. Although these relatively warm and highly connected regions represent the biodiversity hotspots in the Arctic, it is the low-diversity regions (high latitude, high elevation, and remote islands) that best represent the unique communities of Arctic freshwaters, which are dominated by cold stenotherms and cold-water adapted species of the north.

Regional and group-specific α diversity results described in the special issue largely support these broader multi-organism patterns. In circumpolar assessments, α diversity was lowest at the highest latitudes for benthic diatoms (Kahlert et al., 2022), plankton (Schartau et al., 2022), benthic macroinvertebrates (Lento, Culp et al., 2022), and fish (Laske et al., 2022), and showed general declines with increasing latitudes. This latitudinal decline was strongest and most consistent for benthic macroinvertebrates, both at circumpolar and regional scales (Lento, Culp et al., 2022; Lento, Laske et al., 2022). Hotspots for biodiversity varied among taxonomic groups, but commonly included Fennoscandia, low-latitude and low-altitude regions of Canada, and coastal regions of Alaska. Regional analyses of biodiversity patterns for single organism groups in the special issue papers did differ in some cases from the multi-organism, circumpolar patterns presented here. These results are not necessarily contradictory, but are likely to be a consequence of the

combined effects of differences in spatial scales of the studies and region-specific conditions. Warming has not been uniform across the Arctic regions (Hansen et al., 1999) and responses to warming will therefore differ among regions (Lento, Culp et al., 2022, but see also Taylor et al., 2020). Such heterogeneity in responses underscores the need for both regional and circumpolar assessment of diversity change in response to climate warming.

2.2 | Potential drivers of α diversity

Temperature and spatial connectivity were identified in the special issue as two main factors that constrain Arctic freshwater α diversity (see Laske et al., 2022; Lento, Culp et al., 2022; Schartau et al., 2022), and our broad-scale multi-organism assessment of average standardised diversity corroborated these findings (Figure 2). Low diversity was observed in cold regions at high latitudes and high elevations and where there are barriers to dispersal (on islands and around mountain ranges). The positive relationship between diversity and temperature is consistent with the hypothesis that diversity is limited where temperatures are low because the physiological tolerance for cold temperatures is exceeded for most taxa (e.g., Currie et al., 2004). However, because the northernmost borders of the North American and Eurasian continental mainland are at approximately 68°N, and many high-latitude regions of the Arctic are islands, it is difficult to disentangle the effects of low temperature from those caused by geographic disconnection.

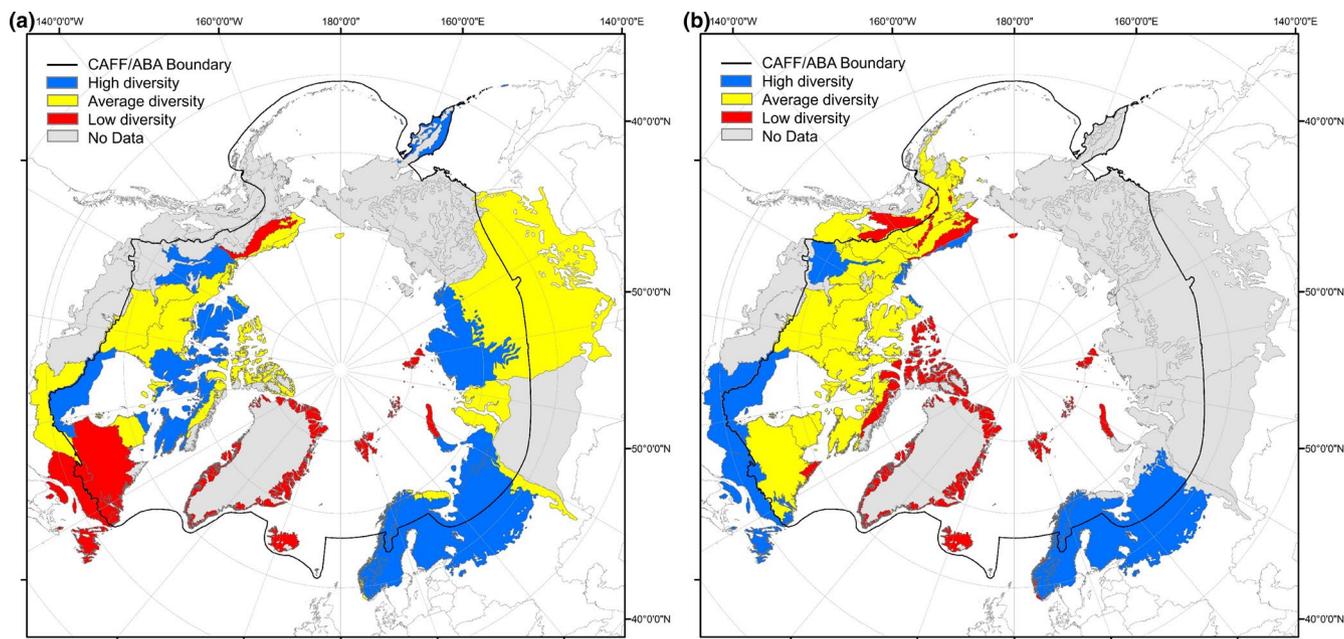


FIGURE 2 Alpha diversity of (a) lakes and (b) rivers in ecoregions across the circumpolar region, with ecoregions characterised based on average standardised taxonomic richness estimates as low ($Z < -0.5$), average ($-0.5 < Z < 0.5$), or high diversity ($Z > 0.5$). Standardised rarefied taxonomic richness was averaged for all organism groups sampled in the ecoregion (averaged across one or more of phytoplankton (lakes only), benthic diatoms, macrophytes (lakes only), zooplankton (lakes only), benthic macroinvertebrates, and fish). The black line marks the combined Conservation of Arctic Flora and Fauna (CAFF) and Arctic Biodiversity Assessment (ABA) boundaries of the Arctic, and ecoregions that intersect the boundary but had insufficient data for analysis are indicated in grey. Country layer (white) and ocean layer (light blue) from www.naturalearthdata.com; ecoregion layer from Terrestrial Ecoregions of the World (Olson et al., 2001); CAFF and ABA boundaries from abds.is

To separate the confounding effects of temperature and geographic connectivity on α diversity, we explored the relationship between multi-organism diversity and temperature for ecoregions distinguished as being on islands, on the mainland, or a combination of mainland and island. This analysis showed a significant positive relationship between diversity and temperature for both lakes and rivers, although the relationship was stronger for rivers (Figure 3, Table 1). Multi-organism diversity was lower in island ecoregions than in mainland ecoregions across the temperature gradient (Figure 3c), which suggests a direct additive effect of low temperatures and a lack of spatial connectivity on diversity in these ecoregions. Where connectivity is higher (i.e., mainland regions), species richness is most susceptible to a large-scale gradual increase following continued warming as warming affects the distribution and competitive success of species and results in gradual species replacements. For example, Svenning et al. (2022) described the gradual change in salmonid species composition in northern European rivers, including the gradual replacement of the cold stenotherm species Arctic Char with brown trout that are competitively superior in warmer waters. These unique long-term catch statistics show this change quantitatively, and similar shifts in fish species composition are part of documented observations by Indigenous Peoples in other regions of the Arctic (Knopp et al., 2022). This implies that many poor dispersers among cold stenothermic or cold-adapted species may approach extinction at the northernmost edge of the continental mainland when temperatures increase beyond their upper tolerance range.

High variability in the relationship between diversity and temperature in the middle of the temperature gradient probably reflects a stronger response of diversity to other environmental variables. Besides temperature and spatial connectivity, water chemistry was also found to be an important diversity correlate, particularly for diatoms. Low diatom diversity in lakes in northern Quebec and Labrador in eastern Canada is likely to be a consequence of the historically stable cold temperatures in that region (Prowse et al., 2006) and the influence of the soft waters of lakes on the Precambrian Shield in this region (Huser et al., 2022; Kahlert et al., 2022). Conversely, high diatom diversity in lakes was found elsewhere in the Arctic, particularly in the Middle Arctic ecoregion of Canada (resulting in high average standardised diversity at lower latitudes of the Canadian Arctic archipelago; Figure 2a), where geology supports favourable water chemistry conditions for diatoms. Benthic diatom/algae assemblages are the primary basal resource in Arctic lakes and rivers (Vadeboncoeur et al., 2002), supplying consumers with a high-quality food resource (Parrish, 2009). Continued warming (Prowse et al., 2011; Schartau et al., 2022) and declines in water N/P ratios (Bergström et al., 2020) will disadvantage diatoms and relative to cyanobacteria, which lack the highly unsaturated fatty acids that are typical for diatoms and promote organism growth and reproduction (Parrish, 2009). These qualitative shifts in the biochemical composition of basal resources have strong repercussions for the trophic transfer efficiency of aquatic food webs (c.f. Brett & Müller-Navarra, 1997), ultimately affecting fish production. Indirect effects of warming on community composition and species distributions will

be mediated by gradual landscape transformations, such as permafrost thaws and the increased vegetation growth or shrubification, that will modify hydrological patterns, nutrient, and sediment runoff, thereby modifying the physical and chemical habitat of aquatic flora and fauna (Chin et al., 2016; Huser et al., 2022). Examination of the response of freshwater biota to changes in the physical and chemical habitat will therefore become more important as the direct and indirect impacts of warming and development are felt.

3 | BETA DIVERSITY

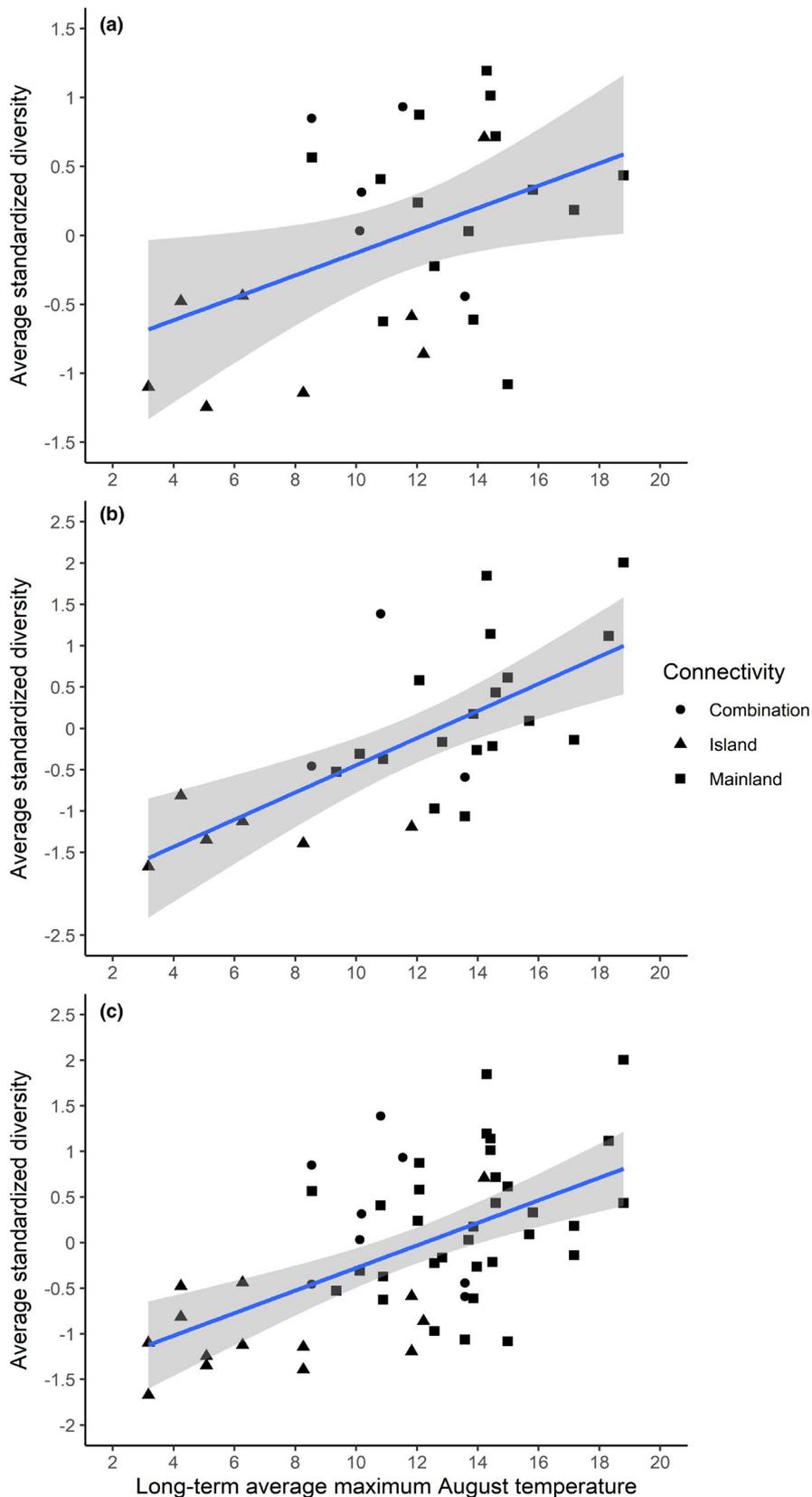
Beta diversity measures the level of dissimilarity in community structure among sites within a defined region (Whittaker, 1972). High β diversity indicates large differences in the taxonomic composition of assemblages among sites, whereas low β diversity indicates a high level of taxonomic similarity. Beta diversity thus provides an estimate of the degree of assemblage differentiation among sites in a region. Beta diversity can also be partitioned into its component parts: turnover, which indicates the replacement of species between sites, and nestedness, which describes the loss of species between sites (Baselga, 2010, 2012).

Patterns in β diversity were a focus of several regional or organism-specific assessments in this special issue (e.g., see Brittain et al., 2022; Laske et al., 2022; Schartau et al., 2022), but these did not compare large-scale patterns across all organism groups. Here, we provide a broader circumpolar comparison across all organism groups by calculating β diversity and the contributions of its components within ecoregions for phytoplankton, benthic diatoms, macrophytes, zooplankton, benthic macroinvertebrates, and fish in lakes, and for benthic diatoms, benthic macroinvertebrates, and fish in rivers. We used Sørensen's dissimilarity coefficient, β_{Sor} to estimate β diversity (Baselga, 2010). The value of β_{Sor} ranges from 0 to 1, where 0 indicates identical taxonomic composition at all sites and 1 denotes that sites have completely different sets of taxa. The metrics β_{SIM} and β_{NES} were used to estimate the portion of β diversity that was attributed to turnover and nestedness, respectively (see Baselga, 2010, 2012; Baselga & Orme, 2012 for details). Beta diversity and its components were estimated in R Version 4.0.2 (R Development Core Team, 2015) using the package β part (Baselga & Orme, 2012).

3.1 | Synthesis of beta diversity for all organism groups

The circumpolar analysis of beta diversity showed strong spatial variability among ecoregions for most organism groups in lakes (Figure 4) and rivers (Figure 5). Although β diversity was low for some ecoregions on high-latitude islands (i.e., strong similarity among sites), the pattern was not consistent for lakes or rivers and did not represent a trend of lower β diversity at higher latitudes (correlation between β diversity and latitude: $r = -0.01$ for lakes and $r = 0$ for rivers). Moderate to high

FIGURE 3 Least-squares simple linear regression of average standardized α diversity (rarefied within ecoregions) as a function of the long-term average maximum August air temperature (as a proxy for maximum summer water temperature) within an ecoregion for (a) lakes, (b) rivers, and (c) lakes and rivers combined, with points for each ecoregion indicating whether the ecoregion is on the continental mainland (squares), is on an island (triangles), or is composed of mainland and islands (circles). A regression line is shown (blue) with 95% confidence intervals (grey shading) on each plot



β diversity was common for ecoregions in Alaska and Fennoscandia, with β_{Sor} exceeding 0.5 for most organism groups in lakes and rivers (Figure 4 and Figure 5), consistent with the higher β diversity for these regions reported in the special issue papers (Laske et al., 2022; Schartau et al., 2022). At the circumpolar scale, the high degree of

assemblage dissimilarity within many ecoregions and the overall high variability in β diversity among ecoregions is not surprising considering that our data set covered large parts of the Arctic region and a wide range of environmental conditions (e.g., different climatic and habitat conditions, system size, nutrient concentrations, etc.).

TABLE 1 Results of linear regressions of average standardised α diversity (rarefied for ecoregions) as a function of long-term average maximum August air temperature, with separate regression completed for lakes, rivers, and lakes and rivers combined

Response variable	Intercept	Slope	<i>t</i>	<i>p</i>	RMS	<i>r</i> ²
Lake diversity	-0.941	0.081	2.366	0.026	0.461	0.177
River diversity	-2.089	0.164	4.553	<0.001	0.561	0.453
Lake and river diversity	-1.515	0.124	4.898	<0.001	0.525	0.312

Note: Regression slopes and intercepts represent the change in α diversity with increasing temperature. The table presents intercepts, slopes, and *t* and *p*-values for slopes, residual mean squares (RMS), and *r*² for the regressions

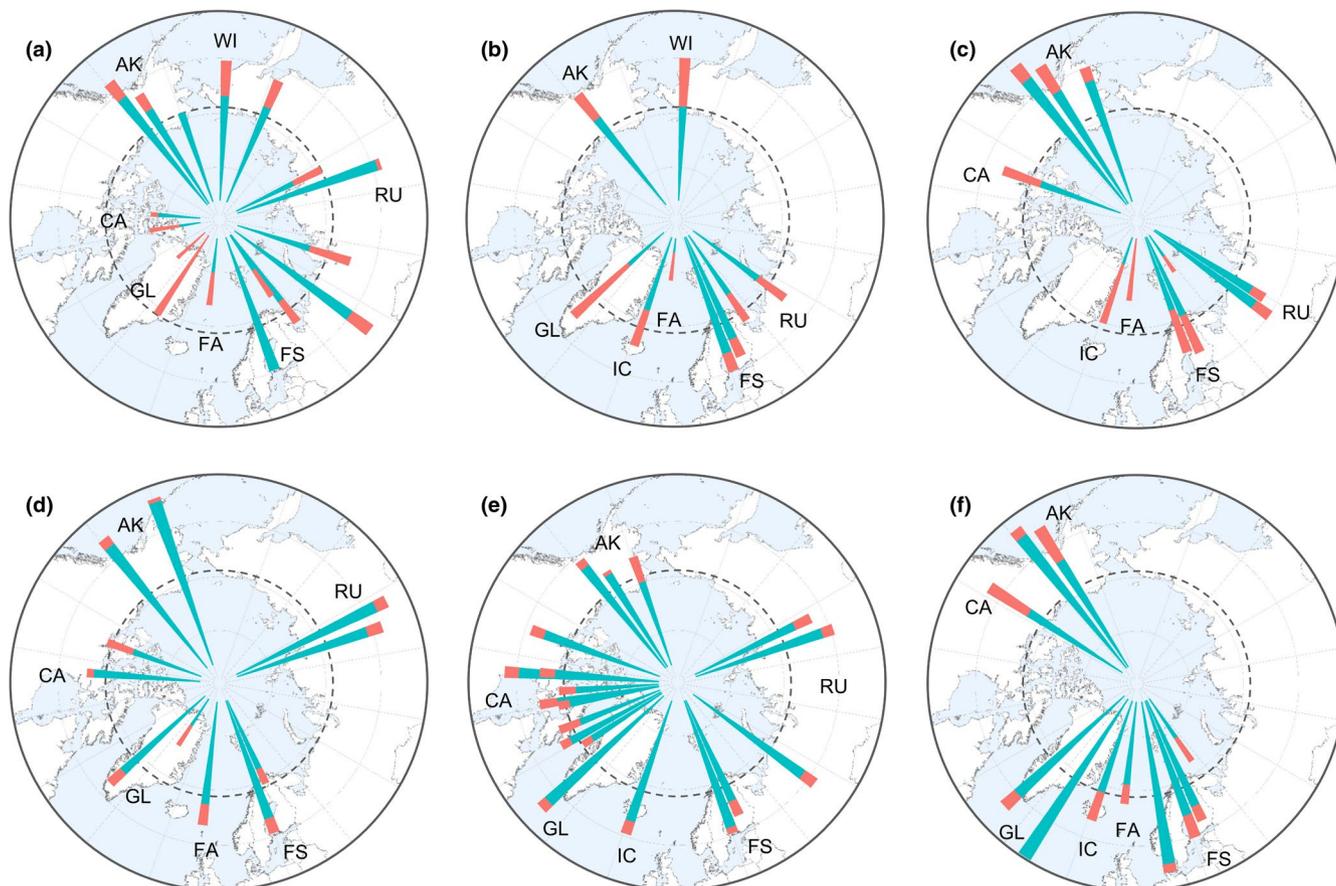


FIGURE 4 Average lake β diversity within ecoregions of consumers (a) zooplankton, (b) benthic macroinvertebrates, and (c) fish, and producers (d) phytoplankton, (e) benthic diatoms, and (f) macrophytes, with total β diversity (bars) partitioned into (turquoise) turnover and (coral) nestedness. The solid circle indicates β diversity = 1, and the dashed circle indicates β diversity = 0.5. Beta diversity was calculated within hydrobasins and averaged across hydrobasins for each ecoregion. Bars represent the total β diversity in an ecoregion, divided into the diversity that is due to turnover and due to nestedness and are arranged longitudinally by the centre of each ecoregion. Geographic regions of the Arctic are indicated by codes (AK = Alaska, CA = Canada, GL = Greenland, IC = Iceland, FA = Faroe Islands, FS = Fennoscandia, RU = Russia mainland, WI = Wrangel Island). Bars are absent in areas where data were lacking or insufficient to calculate β diversity. Country layer (white) and ocean layer (light blue) from www.naturelearthdata.com

Beta diversity partitioning showed that turnover (i.e., the replacement of species across sites) generally contributed more to β diversity than nestedness. Turnover accounted on average for 66% (benthic macroinvertebrates) to 89% (diatoms) across groups for lakes and 61% (fish) to 76% (diatoms) for rivers (Figures 4 and 5). We interpret the high contributions of turnover in lakes and rivers as a consequence of several ecological and/or logistical factors, including: (1) natural taxonomic differences among sites due to differences in environmental conditions within ecoregions (Johnson

& Goedkoop, 2002); (2) non-synchronous range expansion of taxa into ecoregions (Pecl et al., 2017); and (3) sampling effort within ecoregions that was not sufficient to capture the full range of taxonomic richness among sites, leading to a lower ability to detect rare taxa. Nestedness had a moderate to high contribution to total β diversity in some ecoregions, although this varied among organism groups. For example, zooplankton, macroinvertebrates, and fish in lakes displayed a greater contribution of nestedness to β diversity than did primary producers (benthic diatoms, phytoplankton, and

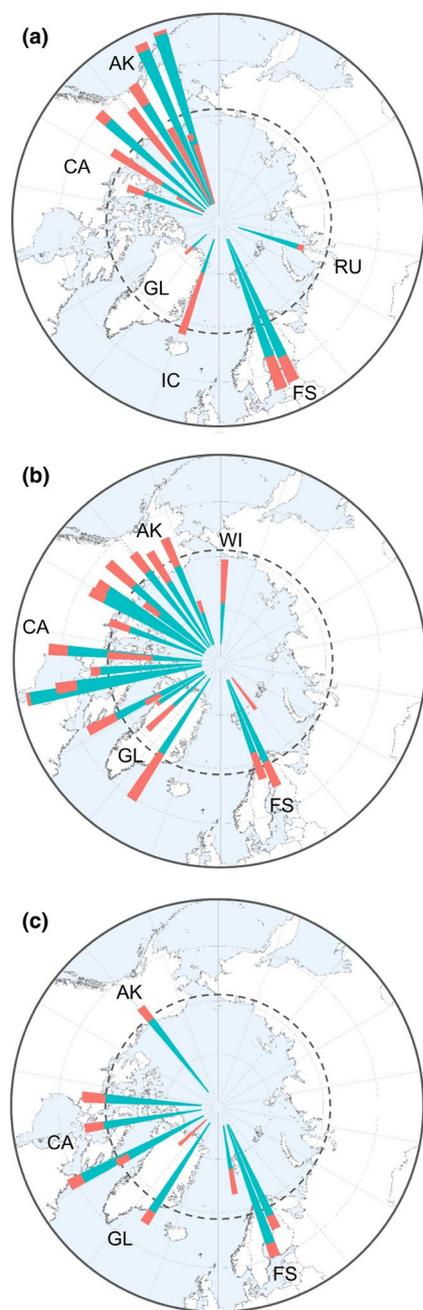


FIGURE 5 Average river β diversity within ecoregions of consumers (a) benthic macroinvertebrates and (b) fish, and primary producers (c) benthic diatoms, with total β diversity (bars) partitioned into (turquoise) turnover and (coral) nestedness. The solid circle indicates β diversity = 1, and the dashed circle indicates β diversity = 0.5. Beta diversity was calculated within hydrobasins and averaged across hydrobasins for each ecoregion. Bars represent the total β diversity in an ecoregion, divided into the diversity that is due to turnover and due to nestedness and are arranged longitudinally by the centre of each ecoregion. Geographic regions of the Arctic are indicated by codes (AK = Alaska, CA = Canada, GL = Greenland, IC = Iceland, FA = Faroe Islands, FS = Fennoscandia, RU = Russia mainland, WI = Wrangel Island). Bars are absent in areas where data were absent or insufficient to calculate β diversity. Country layer (white) and ocean layer (light blue) from www.naturalearthdata.com

macrophytes; Figure 4). A similar pattern was observed for rivers, with a higher contribution of nestedness in higher trophic levels (Figure 5). This pattern, which indicated that there was a greater proportion of community dissimilarity that was due to taxa turnover in lower trophic levels, is probably related to the high taxonomic richness (large regional species pool, and therefore high probability of encountering different species when sampling across the region) and good dispersal capabilities of groups such as phytoplankton and benthic diatoms.

Our assessment indicates that β diversity and its components are a powerful and integral part of Arctic biodiversity analyses, as these metrics capture both the northward migration of sub-Arctic species (e.g., Pecl et al., 2017) and the concurrent extinctions of cold-adapted Arctic species (Heino et al., 2020) through assessment of community dissimilarity. Thus, it provides critical information about changes in biodiversity that is complementary to summary metrics such as species richness. Hillebrand et al. (2018) argued that trends in richness are insufficient to detect important compositional shifts in biodiversity, as richness can increase even in deteriorating or changing environments if species immigration rates exceed extinction rates. This is also true at the larger spatial scales of Arctic regions where unique species, which often have high conservation value, may go extinct and be irreversibly replaced by less cold-tolerant species or invasives as a result of warming, resulting in no net change or a net gain of taxa with warming (Heino et al., 2020). Biodiversity assessments therefore need to go beyond the simple analysis of richness and use more meaningful estimates of biodiversity such as turnover species exchange ratios (Korhonen et al., 2010) to detect true changes in biodiversity.

4 | CURRENT STATE OF MONITORING

Our ability to detect impacts on Arctic freshwater biodiversity under continued climate change and human development is highly dependent on having an established set of baseline conditions and monitoring changes from those baselines. The papers in this special issue and the CBMP-Freshwater State of Arctic Freshwater Biodiversity Report (Lento et al., 2019) have made considerable advancements in establishing such baselines. Future monitoring should aim at detecting temporal changes in diversity and community composition, range shifts of species, and re-definition of the boundaries of the Arctic biome based on altered climatic conditions. Our data compilation and assessments highlight the many gaps in the spatial and temporal coverage of monitoring efforts (Figure 1) and, consequently, our limited knowledge of Arctic freshwater biodiversity (Figures 4 and 5). Relatively densely populated, smaller countries generally had better spatial data coverage than larger countries with more remote, sparsely populated areas of the Arctic. However, time series data were largely non-existent throughout the circumpolar Arctic, which makes it difficult to detect temporal biodiversity change. Despite a tremendous effort by staff from all Arctic countries, we undoubtedly

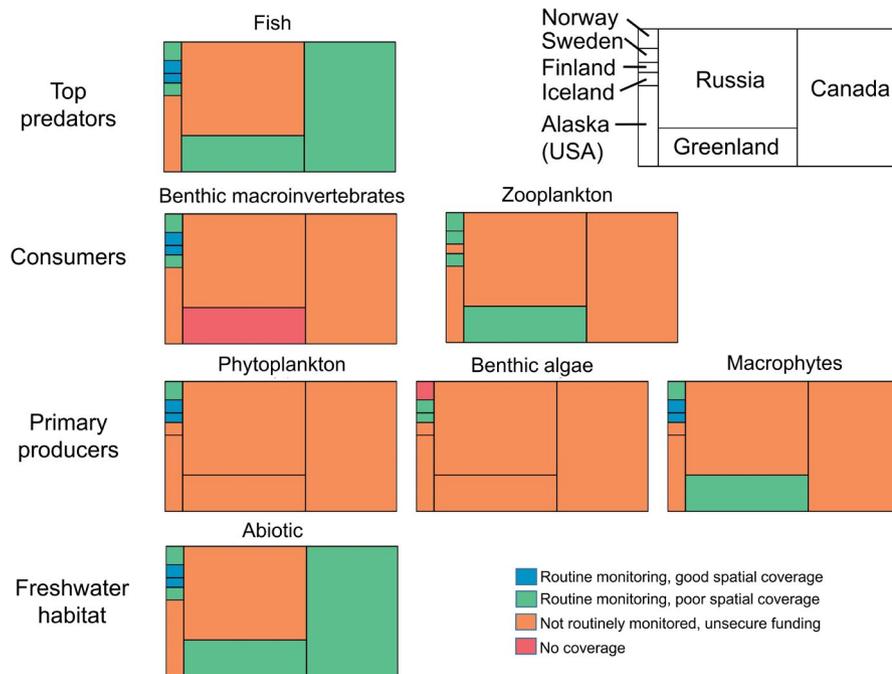


FIGURE 6 Treemaps summarizing monitoring status in lakes for each organism group (fish, benthic macroinvertebrates, zooplankton, phytoplankton, benthic algae, macrophytes) and abiotic variables, with each rectangle in the treemap corresponding to a region of the Arctic as indicated by the key in the upper right-hand corner of the figure, and with the size of each rectangle proportional to the land area in the Arctic within the region and the colour of each rectangle indicating the level of monitoring (routine monitoring with secure funding and good spatial coverage; routine monitoring with secure funding and poor spatial coverage; not routinely monitored with insecure or sporadic funding; and no coverage)

missed data from less available data sources, such as those in less accessible government and research archives. This underscores the importance of data preservation and availability from research projects, which currently is a high priority of research funders in many countries. Therefore, additional investments in appropriate database infrastructure is a critical priority, as this is a prerequisite for future data availability and science-based assessments of freshwater biodiversity status and trends.

Beyond the existing data gaps, there is also a great need to improve the design and coverage of ongoing and future monitoring, as this will further improve our ability to detect changes in biodiversity. To assess the current state of monitoring activities in Arctic freshwaters, we classified existing monitoring efforts for each organism group in each Arctic country based on whether: (1) there was routine monitoring with consistent funding and good spatial coverage; (2) routine monitoring with consistent funding and poor spatial coverage; (3) sporadic or limited monitoring with insecure funding (no routine monitoring, but generally only academic research programmes or other such limited efforts); or (4) no coverage. We visualised these classifications by plotting findings for each country as a subset area proportional to its total land area in the Arctic. The most apparent finding is that most of the routine monitoring with secure funding takes place in countries with relatively small land areas in the Arctic (Norway, Sweden, Finland, Iceland), particularly for lakes (Figures 6 and 7). Canadian routine monitoring shows a strong focus on rivers (although with poor spatial coverage), while that of lakes is extremely limited. Similarly, Alaska and the Russian Arctic lack routine monitoring with consistent funding for biota in lakes and rivers, and generally only have sporadic/limited sampling with insecure funding. Greenland also lacks routine monitoring for several organism groups, with the exception of a few long time-series for lakes. Without secure funding for routine monitoring, collection of time series data

will be impossible, and our ability to detect changes in response to climate warming will be extremely limited. Of course, the remoteness and geographical expanse of the Arctic leads to extremely high costs and difficult logistics for monitoring (Mallory et al., 2018) and contributes to its poor status.

5 | AN IMPROVED FRAMEWORK FOR ASSESSMENT OF FRESHWATER ECOLOGICAL CHANGE IN THE ARCTIC

Recent publications have addressed key research themes (Harper et al., 2021) and the need for societal responses and action plans (Tickner et al., 2020) to halt the global loss of freshwater biodiversity, without specifically addressing biodiversity change in the Arctic. Societal responses to predicted impacts in freshwaters globally and in the Arctic generally fall into: (1) actions to improve detection of changes; and (2) actions to reduce the impact of unwanted changes. Actions to reduce the impact of unwanted changes and to prevent such changes include global reductions of CO₂ emissions, international agreements on measures to limit impacts of climate change and development on freshwater ecosystems, and increased conservation action for these ecosystems. An important response would be ensuring that global freshwater biodiversity, and the conservation of the unique biodiversity in Arctic freshwaters, is included in the Secretariat of the United Nations' Convention on Biological Diversity's post-2020 Global Biodiversity Framework, which guides biodiversity conservation and monitoring actions up to 2030 (Convention on Biological Diversity, 2021) and relevant chapters in Keith et al. (2020) that address Arctic freshwater typology. Lower-latitude species are predicted to move northward into Arctic freshwaters as warming continues, which implies that overall species

richness will increase, but that this increase will be at the cost of unique species and the low-diversity assemblages that characterise Arctic freshwaters (Heino et al., 2020). This is a challenging message to communicate to decision makers and the public, as high biodiversity is commonly more valued than low biodiversity. Indeed, the first draft of the post-2020 Global Biodiversity Framework targets increased biodiversity globally, despite the fact that this is an unwanted change predicted to occur in Arctic systems with continued warming (Taylor et al., 2020). If Arctic countries have the ambition to halt the loss of unique biodiversity in Arctic regions, then they need to account for these species' vulnerability through environmental management (c.f. Williams et al., 2008). Such management decisions to specifically protect vulnerable species can, however, only be successful if we also manage to reduce global CO₂-emissions in line with international agreements and put a halt to continued warming.

Detection of the gradual or abrupt changes in the state of freshwater ecosystems requires intensified monitoring at larger spatial scales through a combination of globally harmonised monitoring activities, long-term ecological studies, remote sensing, and engagement with Arctic residents and Indigenous Peoples to develop community-based monitoring and to better weave western science with Indigenous Knowledge. Arctic countries could tackle the sampling of remote Arctic lakes and rivers by launching a monitoring programme that combines remote sensing (e.g. snow cover, chlorophyll water concentrations, landscape greening) with a sampling design that allows more intensive monitoring (i.e., time series of biological variables and supporting water chemistry variables) on a regional scale. The latter could, for example, cover a population of lakes and rivers near settlements and/or research stations and engage local community members. The lack of species-level information for

speciose organism groups such as chironomids and diatoms can be overcome by applying DNA-metabarcoding techniques that have developed rapidly during the last decade; this would deliver better insight into the biodiversity of organism groups with a complex taxonomy (e.g. Brodin et al., 2013). Also, environmental DNA techniques, which test for DNA sequences in water samples, may be useful for the early detection of new and potentially invasive species.

One of the primary goals of CBMP-Freshwater is to offset the current lack of spatial monitoring coverage through the promotion of coordinated, harmonised circum-Arctic monitoring of freshwaters (see Lento et al., 2019 for full discussion of recommended approaches). Arctic countries would benefit from a reporting system that obliges them to report on changes in the biodiversity and water quality (i.e., both baseline and pollution monitoring) of their Arctic lakes and rivers. In the European Union, monitoring and assessment initiatives build upon science-based methods and target specific stressors such as eutrophication, acidification, and ecological integrity while assessing baseline water quality conditions. Such requirements are part of legislative frameworks such as the European Water Framework Directive (EC, 2000). An important first step towards coordinated circumpolar monitoring would be better harmonisation of sampling approaches (including equipment type, sampled habitats within a system), which would increase the inter-comparability of data from different sources and improve the capacity for large, circumpolar assessments. Harmonisation of sampling methods has been identified as a priority for both regional and global assessment of freshwater biodiversity (Turak et al., 2017), and coordination among Arctic countries could contribute to such global efforts. Similarly, European Arctic countries apply common monitoring methods

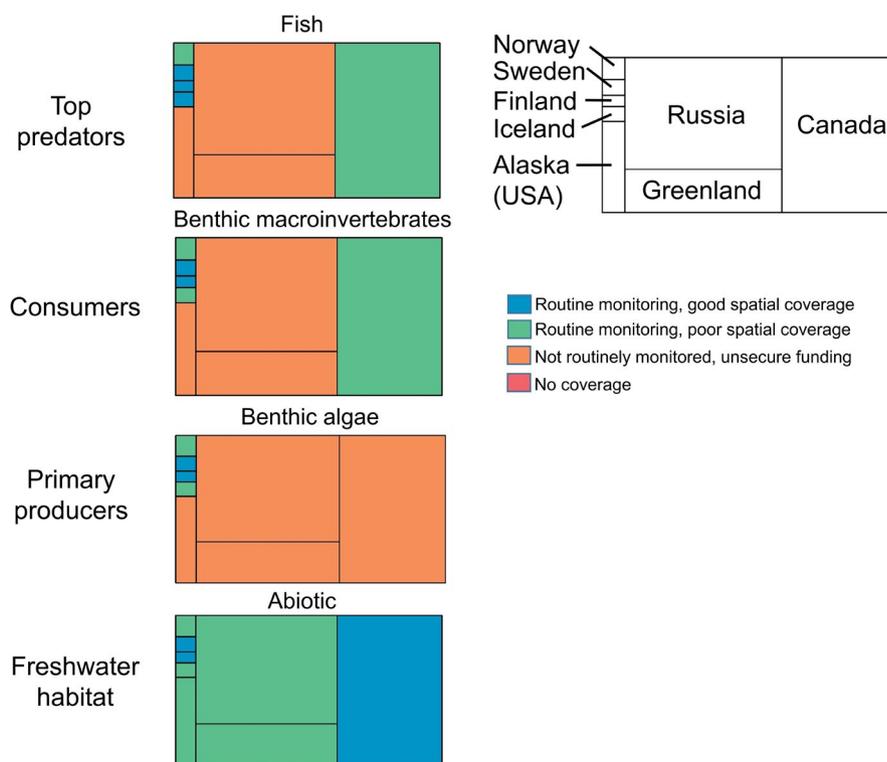


FIGURE 7 Treemaps summarising monitoring status in rivers for each organism group (fish, benthic macroinvertebrates, benthic algae) and abiotic variables, with each rectangle in the treemap corresponding to a region of the Arctic as indicated by the key in the upper right-hand corner of the figure, and with the size of each rectangle proportional to the land area in the Arctic within the region and the colour of each rectangle indicating the level of monitoring (routine monitoring with secure funding and good spatial coverage; routine monitoring with secure funding and poor spatial coverage; not routinely monitored with insecure or sporadic funding; and no coverage)

(e.g. sampling effort, size fraction) that quantify the richness and composition of assemblages, provide a good measure of biodiversity, and allow for an analysis of systematic changes in time and space. These frameworks offer a model for other Arctic and non-Arctic countries and could easily be extended to include assessment of biodiversity and ecological change of Arctic freshwaters.

One other area of Arctic freshwater monitoring and assessment that is currently lacking in most countries is engagement with Indigenous communities and consideration of Indigenous Knowledge and methodologies (Sidorova, 2020; Wong et al., 2020). Indigenous Peoples of the Arctic perceive strong bonds with the natural environment in which they live, a world view that integrates their way of life with the ecosystem and the benefits that they derive from it (Inuit Circumpolar Council Alaska, 2020). In this special issue, Knopp et al. (2022) found that documented Indigenous Knowledge on Arctic freshwater biodiversity included greater spatial coverage of fish observations with additional species that were absent in the CBMP-Freshwater database. Documented Indigenous Knowledge included widespread observations of a number of freshwater habitat shifts, such as permafrost thaw and changes to ice on/ice off regimes, consistent with predicted impacts of climate change. Recognising the importance of Indigenous observations and methodologies to monitor landscape change, it is important to develop ways of engagement that are founded on mutual sharing of knowledge (Wong et al., 2020; Woo et al., 2007). Weaving western science and Indigenous Knowledge rather than attempting to integrate Indigenous Knowledge into western science frameworks recognises both ways of knowing as independent and unique, and mobilises the knowledge from both systems while retaining that independence (Henri et al., 2021; Tengö et al., 2017). However, the engagement of Indigenous communities in the design and implementation of monitoring must include adequate financial compensation for participants to support their contribution of knowledge, time, and land management. Such an approach focuses on increasing the capacity for participation and building relationships that ensure a respectful collaboration with Indigenous communities and that are founded on strong communication, as well as the sharing and co-production of knowledge.

6 | CONCLUSION

The most recent IPCC report (IPCC, 2021) indicates that climate change is causing warming at unprecedented rates, particularly in the Arctic. Our synthesis of Arctic freshwater biodiversity shows that diversity is lowest in high latitudes, high elevations, and cold, spatially-disconnected regions. Continued warming will therefore put constraints on the cold-stenotherm species that form the unique fauna and flora of Arctic freshwaters. The gradual movement of cold-stenotherms to higher latitudes is a conveyor-belt analogue to the *escalator to extinction* described for species that migrate to higher elevations in the tropics (Urban, 2018) and is an irreversible process. These changes ultimately affect the ecosystem services by freshwaters that are key to Indigenous Peoples and other residents of the

Arctic. This process is already occurring at large spatial scales, as evidenced by the long-term changes in community composition identified in this special issue, and will accelerate with continued warming. To detect species migrations/replacements/extinctions in the remote regions of the north, the Arctic Council countries should consider launching an intensified monitoring programme that combines circumpolar remote sensing with on-site monitoring on a regional scale. Such an approach would benefit from international agreements that include repeated reporting of the changes in biodiversity and water quality of Arctic freshwaters. This monitoring would ideally be co-developed with Indigenous Peoples to ensure interweaving of western science and Indigenous methods, and it must be built on a funding model that provides adequate compensation for Indigenous contributors. The Arctic Council (e.g. working groups CAFF, Arctic Monitoring and Assessment Programme) is the key organisation and forum for dialogue and implementation of such an Arctic observational network in which freshwater ecosystems should play a key role as they integrate catchment change across landscapes.

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CONFLICT OF INTEREST

The authors assert that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The metadata and (where allowed by data contributors) raw data used in this paper will be made available on the CAFF Arctic Biodiversity Data Service (ABDS; abds.is). The ABDS is the Arctic GBIF (Global Biodiversity Information Facility).

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