



*Researchers collect aquatic invertebrates from small ponds on the Arctic Coastal Plain, Alaska.
Photo: Christian Zimmerman, USGS*

5. Freshwater Biodiversity Synthesis

5.1. Circumpolar Comparisons Among FECs

General patterns of diversity were compared across FECs to identify areas of the Arctic with consistently high or low diversity. Such patterns can help identify diversity hotspots, where diversity is high among multiple FECs, as well as areas where diversity is low and might be expected to change if warming temperatures lead to the northward movement of eurythermal species. Furthermore, patterns in diversity across FECs can help identify relevant drivers of diversity, e.g., where regional conditions in an area of low diversity differ from those in areas of high diversity. Comparisons were made among ecoregions that had moderate to high sample coverage (e.g., those ecoregions that had sufficient numbers of stations to examine alpha diversity rarefied to 25 or more stations). There were no ecoregions with moderate to high numbers of stations for all FECs for lakes, and only three ecoregions for rivers, and therefore comparisons were made among ecoregions with sufficient coverage of at least two FECs.

Fennoscandia (in particular, the Scandinavian and Russian Taiga, which is the inland ecoregion) represented a diversity hotspot for lake macrophytes, zooplankton, benthic macroinvertebrates, and fish (there was insufficient sampling of diatoms and phytoplankton to assess the regional patterns in these FECs; Table 5-1). The Northwest Russian-Novaya Zemlya Tundra in Russia was a hotspot for zooplankton and fish, ranking first and second, respectively, for diversity of these FECs. The Arctic Coastal Tundra in Alaska (northern coastal ecoregion) ranked as the most diverse ecoregion for lake diatoms and phytoplankton, and was among the most diverse ecoregions for fish, zooplankton, and BMI (Table 5-1). The low Arctic in Greenland had diverse plankton assemblages (both phytoplankton and zooplankton), but ranked the lowest in diversity for diatoms (Table 5-1). Ecoregions in Canada and Iceland were found to be less diverse for many of the FECs, indicating lower diversity than was found overall in inland Fennoscandia, eastern Russia,

and along the northern Alaskan coast. The warmer climate in Fennoscandia (particularly in the less mountainous taiga ecoregion) and strong connectivity to the mainland may play a role in the overall high diversity of the area. Similarly, connectivity of the Alaskan coastal region and lack of recent glaciation in that area may have contributed to high diversity of diatoms, phytoplankton, and fish.

Similar results were obtained when the diversity of river FECs was compared across ecoregions. The Scandinavian and Russian Taiga was overall the most diverse ecoregion across all three FECs, though the Arctic Coastal Tundra in Alaska ranked highest in diversity for diatoms and fish (Table 5-2). The Brooks-British Range Tundra in Alaska ranked low in diversity for both rivers and lakes, suggesting an effect of the presence of mountains which was also supported by the slightly lower diversity rankings for the Scandinavian Montane Birch Forest and Grasslands Table 5-1, Table 5-2). Interestingly, the Alaskan ecoregions south of the Brooks-British Range ranked low for fish diversity, which may have reflected barriers for dispersal of anadromous species south from the diverse Arctic Coastal Tundra. Diversity was lowest for diatoms and benthic macroinvertebrates in eastern and northern Canada, though patterns across these two FECs appeared to differ (i.e., ecoregions that ranked the lowest for benthic macroinvertebrates were not the lowest diversity ecoregions for diatoms; Table 5-2). Greenland ranked near the least diverse for both BMI and fish (Table 5-2).



Table 5-1 Ranking of rarefied alpha diversity of lake diatoms, phytoplankton (Phyto), macrophytes, zooplankton (Zoo), benthic macroinvertebrates (BMI), and fish in ecoregions with a sufficient number of samples to rarefy to 25-40 stations. Ecoregion rankings are colored from green (highest diversity) through red (lowest diversity). Numbers in colored cells refer to ecoregion ranking, but are a different scale depending on how many ecoregions were compared for each FEC. Ecoregions are grouped by geographic region of the Arctic, and listed from west to east, as relevant.

Region	Lake Ecoregions	FECs					
		Diatoms	Phyto	Macrophytes	Zoo	BMI	Fish
Alaska	Arctic coastal region	1	1		3	3	3
	Brooks british Range Tundra				7		5
Canada	Low Arctic Tundra	5	3		5		
Greenland	Kalaallit Nunaat low arctic tundra	6	2		4		
Iceland	Iceland boreal birch forests and alpine tundra	2		3	6	4	6
Fennoscandia	Scandinavian Montane Bircg forest and grasslands	4		1		2	4
	Scandinavian and Russian taiga			2	2	1	1
Russia	Northwest Russian Novaya Zemlya Tundra				1		2
	Taimyr-Central Siberian Tundra	3	4				

Table 5-2 Ranking of rarefied alpha diversity of river diatoms, benthic macroinvertebrates (BMI), and fish in ecoregions with a sufficient number of samples to rarefy to 25-40 stations. Ecoregion rankings are colored from green (highest diversity) through red (lowest diversity). Numbers in colored cells refer to ecoregion ranking, but are a different scale depending on how many ecoregions were compared for each FEC. Ecoregions are grouped by geographic region of the Arctic, and listed from west to east, as relevant.

Region	River Ecoregions	FECs		
		Diatoms	BMI	Fish
Alaska	Arctic coastal tundra	1	6	1
	Brooks british Range Tundra		8	6
	Interior Alaska-Yukon lowland taiga		5	5
Canada	Northwest Territories taiga		2	4
	Low Arctic tundra	6	7	
	Middle Arctic tundra	4	10	
	High Arctic tundra	5	12	
	Eastern Canadian Shield taiga	7	3	
	Tongat Mountain tundra	8	9	
Greenland	Kalaallit Nunaat low arctic tundra		11	7
Fennoscandia	Scandinavian Montane Birch forest and grasslands	3	4	3
	Scandinavian and Russian taiga	2	1	2

Turnover was the dominant component of beta diversity for the majority of FECs, and only fish and zooplankton had a large number of ecoregions in which turnover and nestedness were approximately equal or nestedness dominated. Soininen et al. (2018) noted that turnover generally dominates across a number of ecosystems, but suggested that the relative importance of turnover and nestedness might differ as a function of latitude, with increased nestedness at higher latitudes. There was little support for a latitudinal shift in the importance of nestedness within ecoregions in this circumpolar analysis (when tested for some FECs, there was no evidence of a relationship between % nestedness and latitude). However, Culp et al. (In Press) found strong evidence for increased importance of nestedness in river BMI when more distant latitudes were compared, indicating that assemblage composition in high Arctic streams was a subset of (nested within) what was found at lower latitudes. Across the suite of FECs in our analysis, nestedness often played a larger role in spatially-isolated areas (e.g., islands such as Iceland and Svalbard). This result may be indicative of the smaller taxonomic pool on isolated islands (following from theories of island biogeography). However, nestedness was also low in ecoregions with few samples or with spatially-restricted sampling (e.g., ecoregions in Canada where many stations were grouped in a small geographic area), which indicated

that beta diversity estimates and partitioning were affected by sample frequency and sample distribution. With greater spatial coverage of stations, it may be possible to conduct a more accurate assessment of the relative importance of turnover and nestedness across Arctic freshwaters.

5.2. Regional Comparisons Among FECs

5.2.1. North America

River data for North America showed high spatial coverage for diatoms, benthic macroinvertebrates, and fish allowing for assessment across multiple FECs. All FECs were sampled in northern coastal Alaska and the lower Arctic Archipelago, and other areas of North America had data for either benthic macroinvertebrates and fish or benthic macroinvertebrates and diatoms. Alpha diversity patterns were compared across ecoregions to evaluate whether trends across Canada and USA were similar for each of the FECs. We also examined whether there were latitudinal trends in alpha diversity by calculating family richness within hydrobasins. Finally, FEC patterns were compared with spatial patterns in abiotic variables to explore potential drivers of biodiversity for each of the FECs.

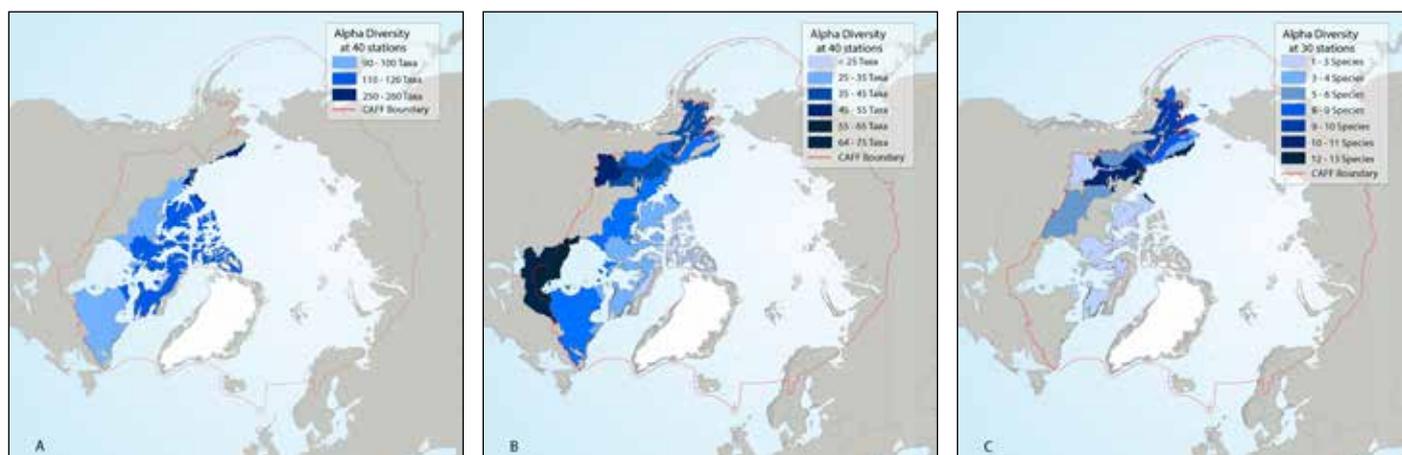


Figure 5-1 Rarefied alpha diversity of river (a) diatoms from benthic samples, (b) benthic macroinvertebrates, and (c) fish in ecoregions across North America.

Different spatial patterns of biodiversity were evident for river diatoms, benthic macroinvertebrates, and fish across North America (Figure 5-1). The lowest biodiversity of diatoms was in the more southern ecoregions of Canada, whereas biodiversity was higher towards the north, in the Arctic Archipelago (Figure 5-1a). In contrast, benthic macroinvertebrates showed a clear decline in alpha diversity towards the north in Canada, with the highest biodiversity south of Hudson Bay, and gradual declines in the number of families with increasing latitude (Figure 5-1b). Fish did not appear to display strong latitudinal trends in Canada in our limited data (Figure 5-1c), although it is known that the High Arctic ecoregion includes only one fish species (Arctic charr) and that there is a latitudinal decline in diversity of this FEC (see Scott and Crossman 1973). The highest biodiversity of both diatoms and fish was found in northern Alaska, in the Arctic Coastal Tundra ecoregion (Figure 5-1a, c), whereas there was only moderate diversity of benthic macroinvertebrates in that ecoregion (Figure 5-1b). However, benthic macroinvertebrates and fish displayed a similar latitudinal gradient in alpha diversity across the two southern Alaska ecoregions, with fish diversity further declining into the mountainous Brooks-British Range tundra (Figure 5-1b, c).

Latitudinal assessment of diversity across hydrobasins indicated no evidence of a latitudinal decline in either benthic diatoms or fish, though both showed a peak in diversity at around 70°N (stronger in diatoms), corresponding to hydrobasins in the Arctic Coastal Tundra ecoregion (Figure 5-2a, c). At other latitudes, diversity of diatoms remained similar for both eastern and western North America, whereas fish diversity (only tested in western hydrobasins) varied widely across remaining latitudes. Conversely, there was a clear decline in alpha diversity with increasing latitude for benthic macroinvertebrates (Figure 5-2b). Furthermore, western Arctic hydrobasins had consistently higher alpha diversity than eastern Arctic hydrobasins from similar latitudes (Figure 5-2b).

The contrasting spatial patterns of diversity among diatoms, benthic macroinvertebrates, and fish relate to differences in the response of each FEC to environmental drivers. For example, the latitudinal and longitudinal patterns in river benthic macroinvertebrates reflect temperature gradients across the North American Arctic. In addition to a strong latitudinal decline in temperatures, there is also a west-east temperature gradient in the North American Arctic, with higher temperatures in western North America than what is found in eastern North America at similar latitudes (Figure 5-3a). Benthic macroinvertebrates have thermal preferences and vary in their tolerance levels for extreme cold (Danks 1992, Danks et al. 1994, Wrona et al. 2013). As a result, several studies have noted declines in benthic macroinvertebrate diversity with increasing latitude that follow from a lower number of invertebrate taxa with the physiological tolerance levels for extreme cold conditions (Scott et al. 2011, Culp et al. In Press). Our results confirm these trends for the North American Arctic region and further indicate that benthic macroinvertebrate diversity also reflects the west-east temperature gradient, as diversity was consistently higher in the warmer western ecoregions than in the cooler eastern ecoregions at similar latitudes.

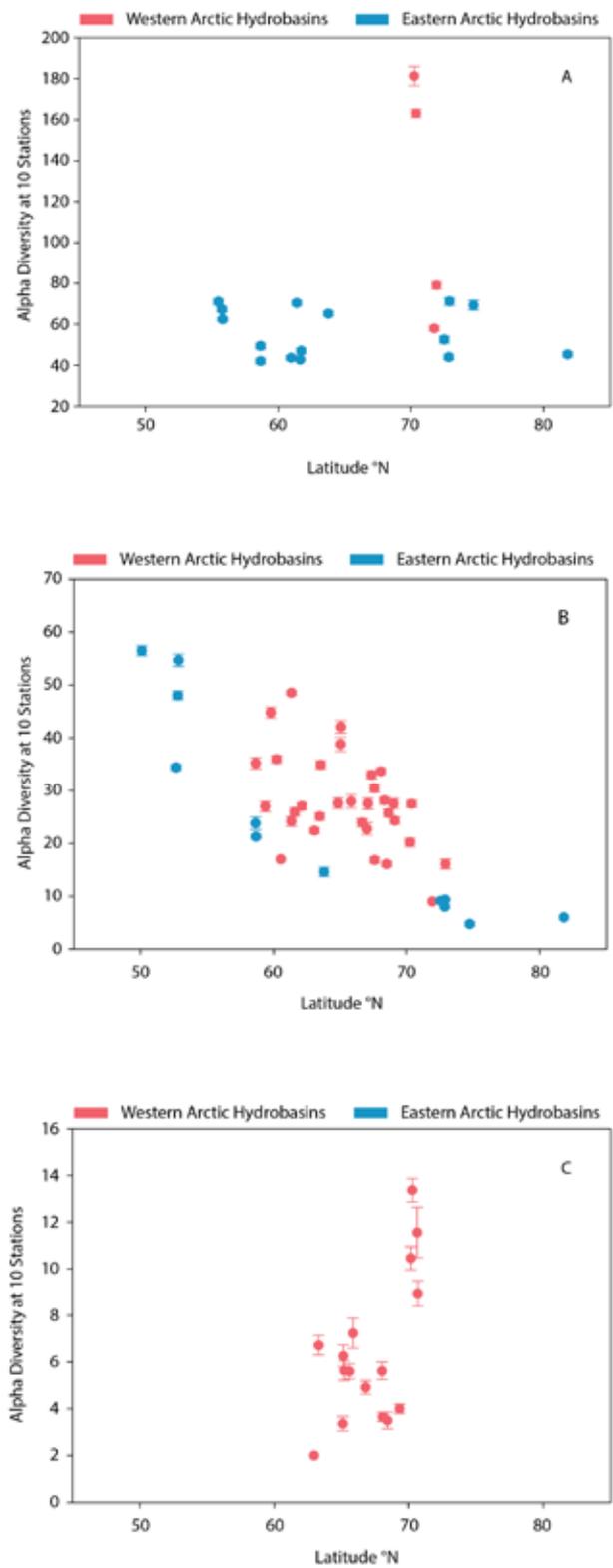


Figure 5-2 Alpha diversity (\pm standard error) of river (a) diatoms from benthic samples, (b) benthic macroinvertebrates, and (c) fish within hydrobasins in western and eastern North America plotted as a function of the average latitude in each hydrobasin. Alpha diversity is rarefied to 10 stations per hydrobasin, using size level 5 hydrobasins for all panels.

Although fish species have thermal preferences and tolerance levels, factors related to dispersal and glaciation may also play a predominant role in driving fish diversity patterns. For example, fish assemblages in the most northern latitudes of North America are limited to anadromous species that are able to access the productive marine environment for foraging (Wrona et al. 2013). Dispersal barriers in mountainous regions (e.g., Brooks-British Range Tundra) further limit species diversity of fish (Matthews 1998, Hugueny et al. 2010). In contrast, the areas of highest fish diversity, including northern and southern Alaska and the Northwest Territories Taiga, may reflect the lack of recent glaciation in these areas (Figure 5-3b), which would have eliminated the need for recolonization and maintained species diversity.

Similar to fish, the high diversity of river diatoms in coastal Alaska may have reflected patterns of glaciation in this area (Figure 5-3b). However, diatoms patterns did not appear to reflect temperature trends across North America, as higher diversity was noted in more northern ecoregions. Diatom assemblages are known to differ in response to underlying geology, due to its influence on water chemistry and nutrient availability (Grenier et al. 2006). Sampled areas of the southern ecoregions in Canada are underlain primarily by intrusive bedrock, whereas the northern ecoregions included sampling in areas of metamorphic, sedimentary, and volcanic bedrock (Figure 5-3c). This diversity in geological composition and the associated differences in water chemistry across the northern sampled areas may have contributed to the diversity of diatoms, as samples would have reflected different habitat conditions.

5.2.2 Fennoscandia

We analyzed a data set covering 13 Fennoscandian subarctic lakes that were situated between 62.1°N and 69.3°N, and had data for five FECs (phytoplankton, macrophytes, zooplankton, benthic macroinvertebrates and fish), covering both pelagic and benthic food webs and three trophic levels. These data were compared with a full set of abiotic and geospatial variables to study relationships between biodiversity and environmental drivers. The percentage taxa share (i.e., taxa richness in a lake relative to the total taxa richness in all Fennoscandian lakes) of individual FECs was calculated based on presence-absence data. This approach combines the summed information among all five organism groups (FECs) and not the traditional splitting of analyses for different organism groups. All FEC, abiotic and geospatial variables were averaged in the order: samples -> stations -> months -> years, to obtain inter-annual averages for each lake. Redundancy analysis (RDA) based on correlations was used to investigate the environmental drivers of the FEC patterns. Explanatory abiotic and geospatial variables were tested with permutational ANOVA, and only significant explanatory variables ($p < 0.05$) were included in the RDA.

The results showed that the FECs were strongly influenced by climatic drivers (e.g., latitude, temperature, precipitation) and vegetation cover (percent grasslands and woody savannas in hydrobasins) (Figure 5-4a and Figure 5-4b). Fish seemed to be more correlated with primary producers than with zooplankton and benthic macroinvertebrates. This correlation likely reflects the top-down trophic cascades in food chains and partly corresponds to a gradient between nutrient-poor

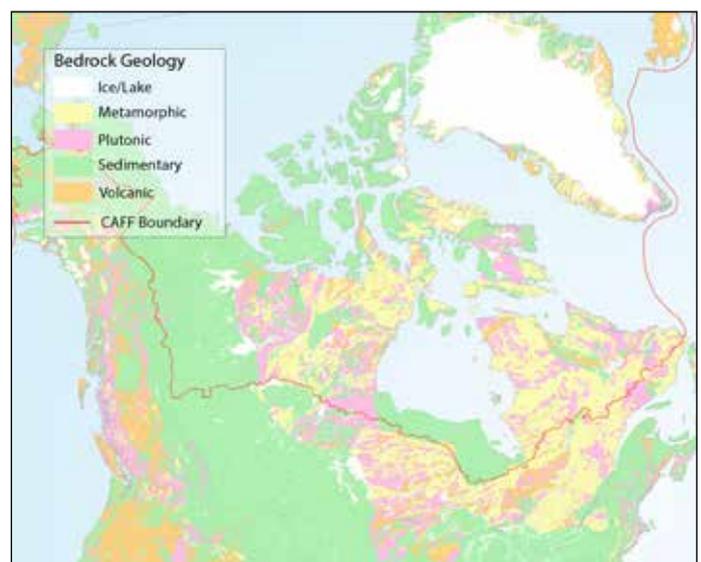
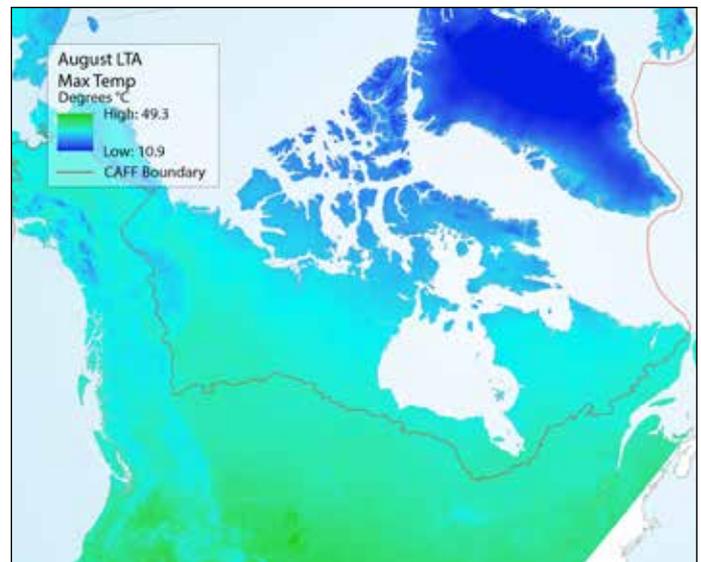


Figure 5-3 Abiotic drivers in North America, including (a) long-term average maximum August air temperature, (b) spatial distribution of ice sheets in the last glaciation of the North American Arctic region, and (c) geological setting of bedrock geology underlying North America. Panel (a) source Fick and Hijmans (2017). Panel (b) adapted from: *Physical Geography* by Steve Earle, freely available at <http://open.bccampus.ca>. Panel (c) source: Geogratia.

and more nutrient-rich lakes. As the fish taxa could occupy various trophic positions in the Fennoscandian lakes, the correlation may also reflect that the diversity within and between trophic levels (i.e., horizontal and vertical diversity; Duffy et al. 2007) of the lake food webs were tightly coupled. A similar positive correlation in biodiversity index between fish and phytoplankton had been reported for Swedish boreal lakes that were either relatively pristine or subjected to long-term acidification with or without management interventions (Lau et al. 2017). Zooplankton and benthic macroinvertebrates taxa share increased with increasing altitude and decreasing relative cover of evergreen needle-leaf forests in hydrobasins. This result likely indicates climate effects on the intermediate trophic levels along the elevation gradient. Overall, the average species taxa share among FECs increased with increasing latitudes and altitudes. This analysis, however included relatively few lakes, largely due to a lack of data for primary producers for many of the lakes in our data set.

A second RDA analysis was run using 39 lakes situated between 62.1°N and 71.0°N with three FECs (zooplankton, benthic macroinvertebrates, and fish) and corresponding abiotic and geospatial variables. This analysis corroborated

the weak correlation between fish, zooplankton, and benthic macroinvertebrates (Figure 5-4c and Figure 5-4d). In this analysis, fish and the average taxa share correlated strongly with lake total nitrogen concentrations, i.e., productivity, and the relative coverage of Scandinavian and Russian taiga vegetation, and negatively with open shrublands. The latter reflects the transition from evergreen pine forests to the tundra shrub vegetation along a latitudinal gradient and at higher altitudes in Fennoscandia. Results from our first (13 lakes) and second (39 lakes) RDAs together suggest that fish biodiversity is functionally important for supporting the overall biodiversity (i.e., average taxa share), and that fish can be an indicator FEC group to represent average taxa share in subarctic Fennoscandian lakes. Our second analysis also shows that the climate effects (e.g., latitude, annual mean precipitation) on fish and average taxa share could be strongly mediated by nutrients, and that zooplankton and benthic macroinvertebrates (%ShareBMI) were negatively correlated to latitude. The latitudinal trend in benthic macroinvertebrate diversity in Fennoscandian lakes is particularly consistent with that observed in North American hydrobasins (see section 5.2.1). Overall, these analyses reflect the biodiversity changes in the Fennoscandian lakes along latitudinal and nutrient gradients. Unfortunately, due to

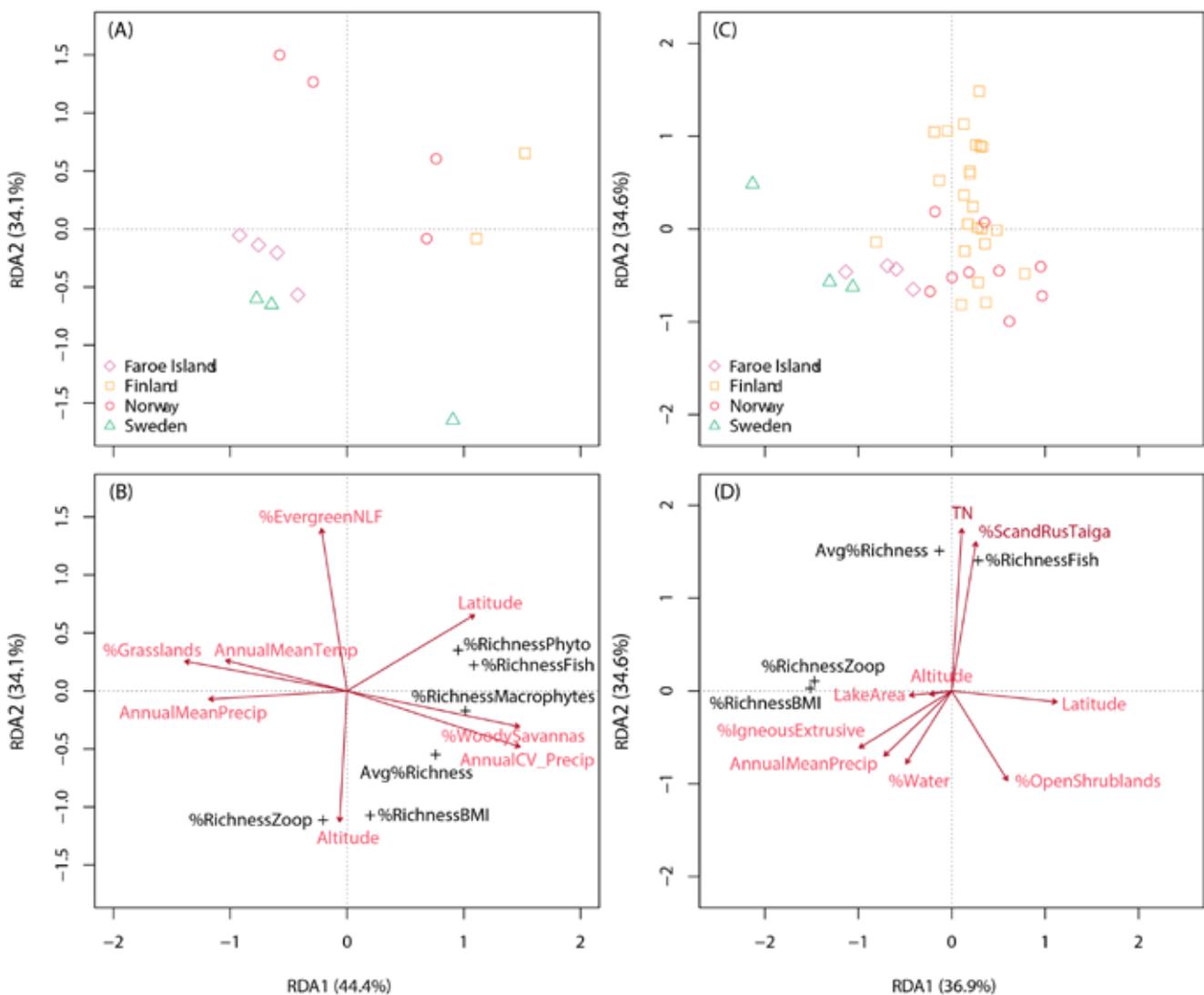


Figure 5-4 Redundancy analysis of percentage species taxa share among 5 FECs (phytoplankton, macrophytes, zooplankton, benthic macroinvertebrates and fish) in 13 Fennoscandian lakes (panels A and B) and among 3 FECs in 39 Fennoscandian lakes (panels C and D). The upper panels show lake ordinations, while the bottom panels show explanatory environmental variables (red arrows), as indicated by permutation tests ($p < 0.05$). Avg%Share: average percentage species taxa share calculated from all FECs (i.e., including benthic algae if present); %Share BMI: relative taxa share in benthic macroinvertebrates; %EvergreenNLF: percentage cover of evergreen needle-leaf forests.

data deficiency our analysis did not include local habitat variables (e.g., substratum type, vegetation), which are important descriptors for macroinvertebrate assemblages (Johnson and Goedkoop 2002). Although taxonomic composition is constrained by the size of the regional species pool, habitat heterogeneity and the outcome of biotic interactions are, along with climate, important descriptors of assemblage composition and diversity, both for benthic macroinvertebrates, zooplankton and fish.

5.3. Relation of Biodiversity to the Abiotic Template

Differences in biodiversity among ecoregions were hypothesized to be driven by temperature differences in many cases, and comparison of North American BMI diversity patterns with long-term average air temperature supported this idea (see section 5.2.1). To investigate this on a circumpolar scale, maximum long-term average August air temperatures were overlain on the ecoregions used in the SAFBR analysis (Figure 5-5). Clear patterns emerged with respect to temperature differences among ecoregions. For example, high latitude ecoregions such as the Kalaallit Nunaat High Arctic Tundra in Greenland, the Arctic Desert in Svalbard, the Wrangel Island Arctic Desert in Russia, and the eastern regions of the High Arctic Tundra and Middle Arctic Tundra in Canada were among the coldest areas. Unsurprisingly, several lower-latitude, high-altitude ecoregions were also colder than surrounding ecoregions, including the Scandinavian Montane Birch Forests and Grasslands, the Ogilvie-Mackenzie Alpine Tundra in western Canada, and the Brooks-British Range Tundra in Alaska. The biotic association with these climate patterns was most evident in the BMI, which generally showed lower diversity in these colder ecoregions than in neighbouring ecoregions (Figure 4-29 and Figure 4-30). However, fish diversity did also appear to be lower in many of these colder ecoregions (Figure 4-36), which indicated that both fish and BMI diversity relate to temperature. Biodiversity hotspots, such as the Scandinavian and Russian Taiga (lakes and rivers) and the Northwest Russia-Novaya Zemlya Tundra (lakes), have historically warmer temperatures (Figure 5-5) and are primarily not underlain by permafrost (Figure 5-6), which may have contributed to the higher diversity noted in these ecoregions for several FECs.

Warming water temperatures in Arctic rivers and lakes may lead to an increase in biodiversity, as southern benthic macroinvertebrate and fish species expand their range (Heino et al. 2009), but cold stenotherms may face extirpation from waters that are above their thermal tolerance (Wrona et al. 2006a). Changing temperatures in combination with increased human development have the potential to increase the risk of invasive species, which may significantly affect biodiversity of Arctic lakes and rivers through loss of native species. For example, *Bythotrephes longimanus*, also called the spiny water flea, is a native species in Eurasia, that has affected diversity in North America since its introduction to the Great Lakes in 1982, after which it rapidly dispersed (Yan et al. 1992, Strecker et al. 2006). Its distribution in the Arctic is restricted to Eurasia according to our dataset, but a northward dispersal on the North American continent could be possible in the future, particularly if climate change improves suitability of northern lake habitats and if human population growth in the north provides additional means for transport and introduction to these systems. In addition, a warmer and wetter climate will increase rates of mineral weathering, decomposition of soil organic matter, erosion and sedimentation as permafrost thaws and the permafrost extent shifts (Figure 5-6) that likely will lead to higher concentrations of dissolved organic matter (humic compounds), minerals (e.g. Ca, Mg), and nutrients (N and P) (Nadelhoffer et al. 1997). Such change in key drivers of the freshwater environment can affect large-scale processes (e.g., brownification, nutrient enrichment, sedimentation) and biodiversity in lake and river ecosystems as outlined in the impact hypotheses developed in the Freshwater Plan (Culp et al. 2012a).

Brownification of lakes was detected in the early 1990s by Forsberg (1992) and can be partly attributed to climate change (Graneli 2012), but is also a consequence of declines in acid precipitation that affect soil processes and lead to higher pH of run-off (Evans et al. 2006, de Wit et al. 2007, Monteith et al. 2007, de Wit et al. 2016). Brownification is a large-scale process in many areas of northern Europe (e.g., Erlandsson et al. 2008) and North America (e.g., Keller et al. 2008) that is related to permafrost thaw and the release of old carbon. This process reduces light penetration through the water column, thereby affecting primary production (Karlsson et al. 2009) and the distribution of submersed water plants (Mormul et al. 2012), with knock-on effects for consumers (i.e., reduced food resources for grazers with repercussions for fish production). Although brownification mostly has been described for temperate and boreal freshwater ecosystems, increased export of dissolved carbon from thawing soil layers has been observed in the Arctic (Wauthy et al. 2017). Increased nutrient transport from catchment soils to rivers and lakes contributes to increased algal production. This could affect biodiversity in rivers and lakes by changing the benthic habitat (e.g., through increased bryophyte growth) or through changes in the food web (Welch et al. 1989, Jorgenson et al. 1992, Slavik et al. 2004). In the pelagic zone of lakes, nutrient enrichment can result in the shading of benthic algae and water plants. While these effects are currently uncommon in Arctic lakes, they may become particularly severe in the future if, for example, cyanobacterial blooms are induced in N-limited lakes that receive increasing loads of nutrients. This is because cyanobacteria tend to accumulate in high densities at the water surface leading to shading primary producers in



Sheenjek River, Alaska
Photo: Alexis Bonogofsky, USWFS

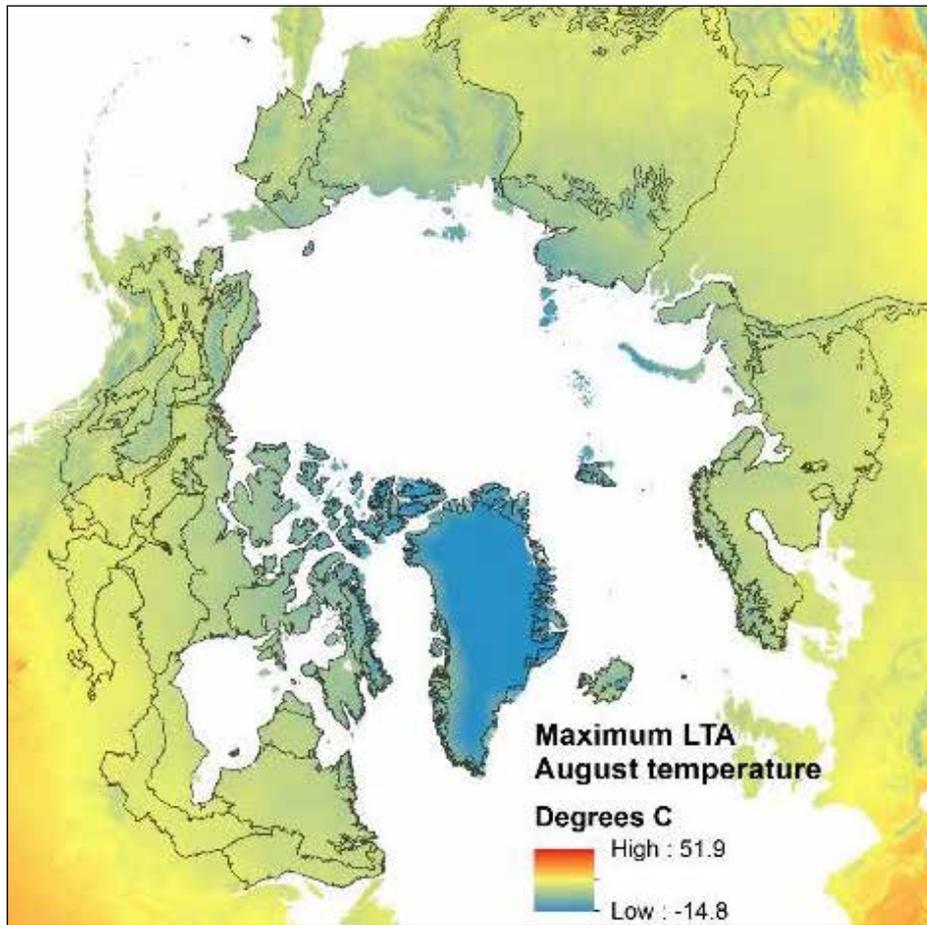


Figure 5-5 Maximum LTA (long-term average) August air temperatures for the circumpolar region, with ecoregions used in the analysis of the SAFBR outlined in black. Source for temperature layer: Fick and Hijmans (2017).

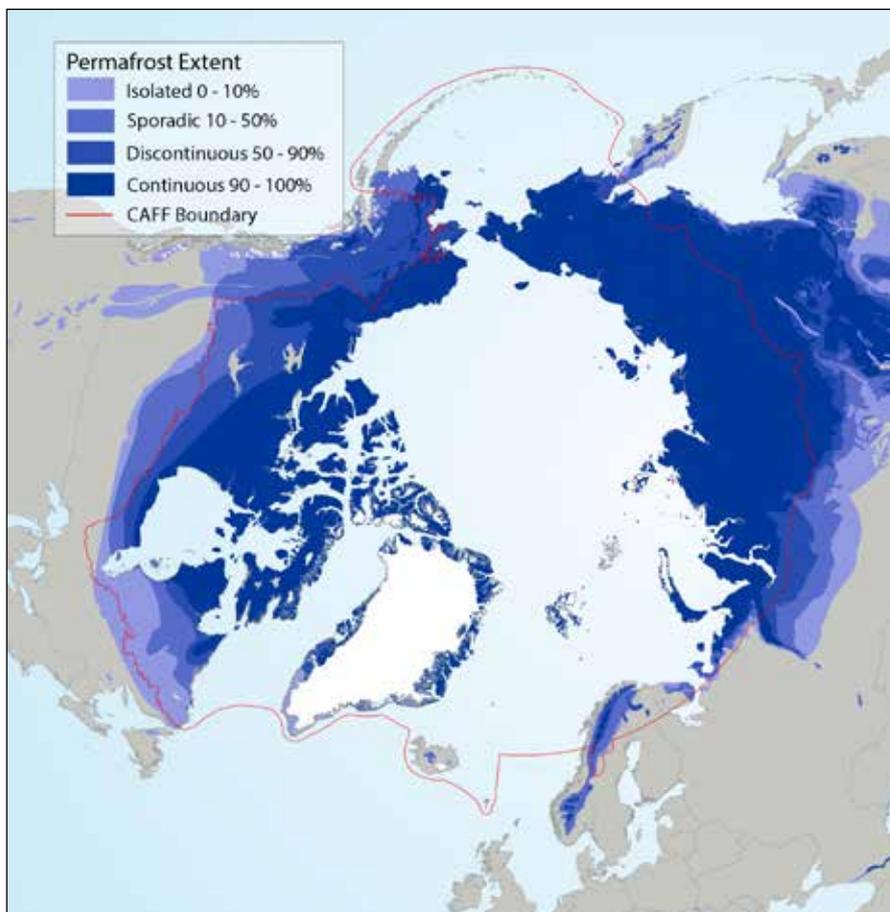


Figure 5-6 Circumpolar permafrost extent overlain on ecoregions used in SAFBR analysis, indicating continuous (90-100%), discontinuous (50-90%), sporadic (10-50%), and isolated (0-10%) permafrost extent. Source for permafrost layer: Brown et al. (2002).

deeper water strata and benthic habitats (cf. Scheffer 1989). Cyanobacteria further affect food webs as they are a poor food source (e.g., Ravet et al. 2003) and many taxa produce toxins (Christoffersen 1996).



In contrast to the effect of increased transport of nutrients from catchments to rivers and lakes, large-scale climate- and human-induced changes in landscapes can contribute to the documented oligotrophication of many northern lakes (Yan et al. 2008, Arvola et al. 2011, Huser et al. 2018)

and potentially to rivers. For example, Huser et al. (2018) reported dramatic declines in total-P concentrations of many Swedish lakes since the mid-1990s. Large-scale catchment processes that contribute to reductions in nutrient runoff are (i) the observed changes in tundra vegetation cover, a.k.a. the “Greening of the Arctic” (Pouliot et al. 2009, Elmendorf et al. 2012) mediated by elevated N-mineralization and increased nutrient uptake by rooted plants (Aerts et al. 2006), (ii) the more efficient trapping of P that originates from soil pH increases (Gérard 2016), and (iii) low and declining trends in N-deposition (Karlsson et al. 2018). The concerted action of these large-scale changes contributes to the gradual transformation of northern freshwaters toward more nutrient-poor conditions and in lakes is expected to increase in the predominance of N₂-fixing cyanobacteria. Furthermore, hydropower development and damming of large northern rivers can cause declines in nutrients downstream of dams and can affect species richness by providing barriers to dispersal.

Sediment load in freshwater systems is predicted to intensify with further permafrost degradation as temperatures and precipitation increase in many Arctic regions (Syvitski 2002, Kokelj et al. 2013, Kokelj et al. 2015). Hillslope thermokarst is common throughout northern Russia, northern Alaska (the Arctic Coastal Tundra and Arctic Foothills Tundra ecoregions), and in the northwestern Canadian Arctic (Figure 5-7). Among the most dramatic thermokarst features are retrogressive thaw slumps – large depressions of exposed permafrost

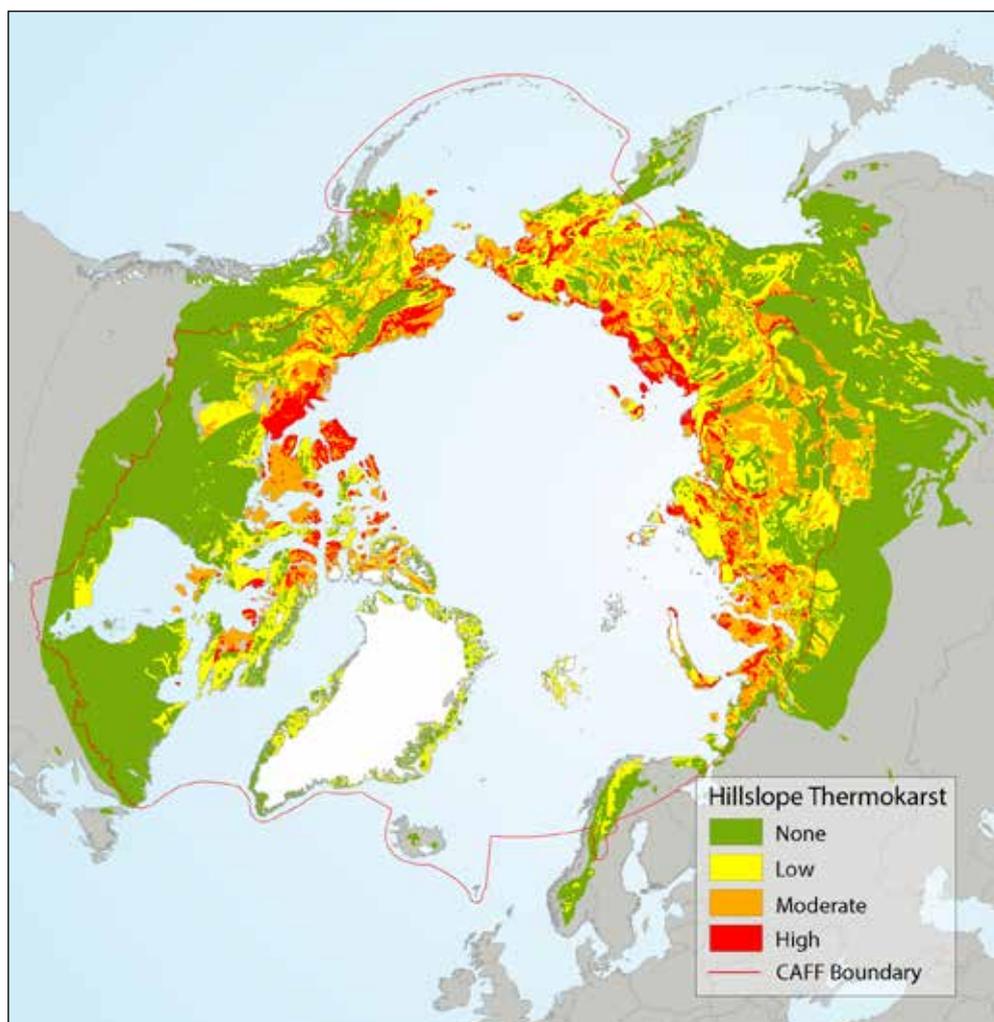


Figure 5-7 Spatial distribution of hillslope thermokarst across the circumpolar area, overlain with ecoregions used in the SAFBR analysis, showing no, low, moderate, and high thermokarst. Source for thermokarst layer: Olefeldt et al. (2016)

(see Figure 3-4a) that have increased in size and frequency on landscapes underlain by ice-rich permafrost (Lantz and Kokelj 2008). Retrogressive thaw slumps form in areas where permafrost is embedded with large masses of buried ice, such as the Peel Plateau,

Canada (Kokelj et al. 2013), the Brooks Range and foothills in Alaska (Jorgenson et al. 2006, Balser et al. 2014) and the northern Taymyr Peninsula in Siberia (Ulrich et al. 2010), with formation and growth driven primarily by precipitation events (Kokelj et al. 2015) and by warm air temperatures (Lacelle et al. 2010). Found along the shores of lakes and coastlines, river valleys, they can exceed 5 ha in area (Kokelj et al. 2013) and significantly impact aquatic ecosystems. As slump headwalls collapse, the resultant debris forms a mud slurry that can flow into nearby lakes and rivers (Figure 3-4). In lakes, this slurry settles to the bottom, increases pH and conductivity, and ultimately leads to higher water transparency (Mesquita et al. 2010). Biological effects observed in lakes include increased biomass of diatoms (Thienpont et al. 2013) and macrophytes (Mesquita et al. 2010), greater benthic invertebrate abundance and shifts in community composition (Moquin et al. 2014). In rivers, thaw slumps increase total nutrient and solute concentrations as well as sediment loads (Kokelj et al. 2013). Less intensive thermokarst disturbances may initially increase algal and invertebrate abundance in rivers if positive nutrient effects offset the negative impacts of sediments (Bowden et al. 2008, Levenstein 2016). However, large thaw slumps negatively impact riverine biodiversity by decreasing benthic algal biomass (Levenstein et al. 2018) and invertebrate abundance (Chin et al. 2016), and by increasing invertebrate drift (Levenstein 2016).

5.4. Conclusions

This chapter identifies and provides examples of how higher temperatures, as the overriding driver, and other environmental variables of ecological change affect the water quality and biodiversity of Arctic freshwaters. These examples show both large-scale, slowly progressing landscape-level processes that will have long-lasting effects, as well as rapid modifications that have more local and short-term effects. The concerted action of these environmental drivers and their subsequent and cumulative effects on biological assemblages will depend on regional conditions. Slow response times will make some of these processes progress for decades to come, while others may induce sudden biological shifts with strong repercussions on aquatic ecosystems when critical threshold levels are exceeded and functional redundancy is low. Examples of this are shifts to strong N-limitation, which will induce cyanobacterial blooms that will cause substantial shading for other primary

producers, or permafrost degradation that may drain entire lakes. Furthermore, increases in the rate of glacier retreat cause changes to hydrologic, thermal, and sediment regimes that can lead to significant changes in taxonomic and functional diversity of freshwater systems receiving glacial inflows (Brown and Milner 2012, Milner et al. 2017). In addition, the loss of species with low physiological tolerances for higher temperatures and the northward movement of species tolerant of a broader range of temperature will affect alpha and beta biodiversity.

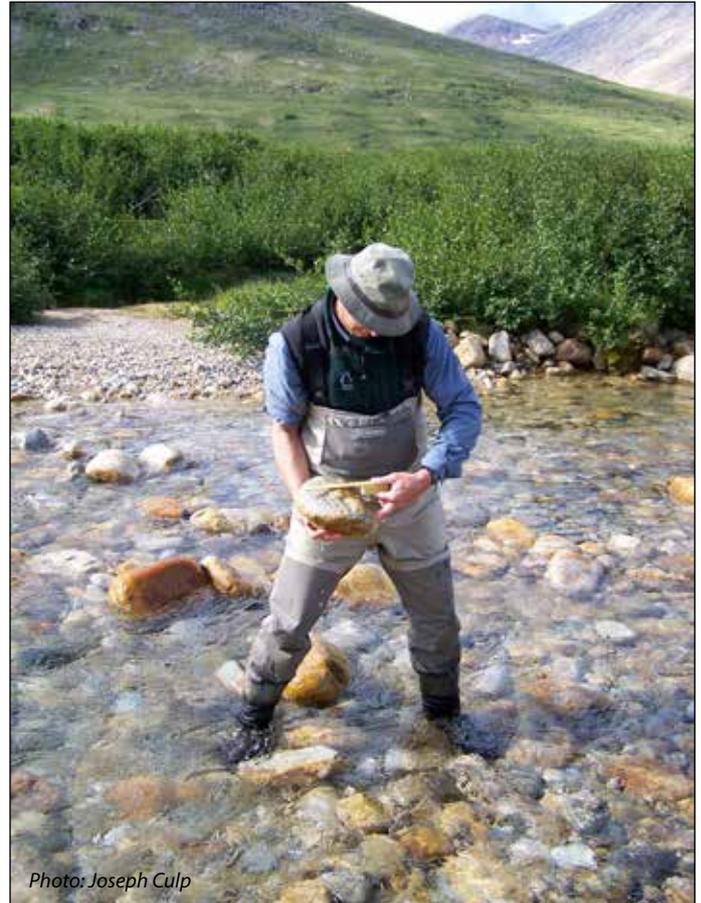


Photo: Joseph Culp

In our analysis, we did not directly identify distinct environmental gradients. However, some gradients, such as climatic and/or latitudinal and vegetation gradients, were inherent in our large dataset. Multivariate statistical approaches are useful tools to unravel relationships between biological assemblages and environmental gradients. Our analysis showed marked regional differences in biodiversity of several FECs and apparent changes in alpha diversity along latitudinal gradients. These analyses form the baseline to which future assessment can be compared and partly address some of the impact hypotheses in the freshwater biodiversity monitoring plan (Culp et al. 2012a).