

# Arctic biodiversity of stream macroinvertebrates declines in response to latitudinal change in the abiotic template

Joseph M. Culp<sup>1,2,5</sup>, Jennifer Lento<sup>2,6</sup>, R. Allen Curry<sup>2,7</sup>, Eric Luiker<sup>3,8</sup>, and Daryl Halliwell<sup>4,9</sup>

<sup>1</sup>Environment and Climate Change Canada and Wilfrid Laurier University, Department Biology and Department Geography and Environmental Studies, 75 University Avenue West, Waterloo, Ontario N2L3C5 Canada

<sup>2</sup>Canadian Rivers Institute, Department Biology, University of New Brunswick, 10 Bailey Drive, PO Box 4400, Fredericton, New Brunswick E3B 6E1 Canada

<sup>3</sup>Environment and Climate Change Canada, Fredericton, New Brunswick E3B 6E1 Canada

<sup>4</sup>National Hydrology Research Centre, Environment and Climate Change Canada, 11 Innovation Boulevard, Saskatoon, Saskatchewan S7N 3H5 Canada

**Abstract:** We aimed to determine which processes drive patterns of  $\alpha$  and  $\beta$  diversity in Arctic river benthic macrofauna across a broad latitudinal gradient spanning the low to high Arctic of eastern Canada (58 to 81°N). Further, we examined whether latitudinal differences in taxonomic composition resulted from species replacement with organisms better adapted to northerly conditions or from the loss of taxa unable to tolerate the harsh environments of higher latitudes. We used the bioclimatic envelope concept to provide a first approximation forecast of how climate warming may modify  $\alpha$  and  $\beta$  diversity of Arctic rivers and to identify potential changes in environmental variables that will drive future assemblage structure. Benthic macroinvertebrates, environmental supporting variables, and geospatial catchment data were collected to assess drivers of ecological pattern. We compared  $\alpha$  diversity (i.e., taxonomic richness) across latitudes and partitioned  $\beta$  diversity into components of nestedness and species turnover to assess their relative contributions to compositional differences. We found sharp declines in taxonomic richness along a latitudinal gradient. This  $\alpha$  diversity pattern was not associated with a change in numerical abundance.  $\beta$  diversity was highest when the most distant latitudes were compared, and pairwise latitudinal comparisons indicated that nestedness (loss of species) was the dominant contributor to compositional differences. Biotic–abiotic associations reflected both large-scale climatic drivers, including air temperature and prevalence of vegetated tundra, and small-scale secondary abiotic drivers of assemblage composition (e.g., substrate composition, water chemistry). The importance of nestedness to  $\beta$  diversity across latitudes supports the physiological tolerance hypothesis that a change in environmental tolerance is a key driver of species richness declines with increasing latitude. Distinct taxonomic assemblages among low and high Arctic latitude sites were associated with large-scale, climate-related drivers (e.g., temperature trends, terrestrial vegetation), reflecting the primary structuring of assemblages by bioclimatic envelopes. The abiotic environment was the strongest driver of assemblage structure at high latitudes because of the extreme conditions. With continued warming, biodiversity differences along latitudinal gradients are expected to become less pronounced as temperatures and vegetation become more similar from south to north, with local-scale variables becoming dominant biotic drivers.

**Key words:** Arctic, freshwater, river, alpha diversity, beta diversity, latitude, gradient, benthic macroinvertebrates

Arctic ecosystems are experiencing significant warming as a result of climate change (Olsen et al. 2011), and substantial temperature increases have occurred from 2005 to 2010 (Walsh et al. 2011). Climate has been proposed as the primary driver of large-scale patterns in biodiversity, such as latitudinal diversity gradients (Whittaker et al. 2001). As

mean temperature isotherms and degree-day boundaries move northward, the biodiversity of Arctic freshwaters is expected to respond through range expansion of southern eurythermic species and potential losses of stenothermic species (Oswood et al. 1992, Vincent et al. 2011, Culp et al. 2012b). These changes may lead to shifts in  $\alpha$  and  $\beta$  diversity.

E-mail addresses: <sup>5</sup>joseph.culp@canada.ca; <sup>6</sup>jleno@gmail.com; <sup>7</sup>racurry@unb.ca; <sup>8</sup>eric.luiker@canada.ca; <sup>9</sup>daryl.halliwell@canada.ca

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A first approximation for forecasting how climate warming could modify  $\alpha$  and  $\beta$  diversity in Arctic rivers is to examine the present differences in riverine benthic assemblage structure across latitudinal gradients. This approach uses the concept of bioclimate envelopes (Pearson and Dawson 2003), wherein regional taxonomic richness and composition are determined by physiological tolerances of individual species to climate conditions (Danks 1992, Danks et al. 1994, Currie et al. 2004). The idea of bioclimatic envelopes is dependent on the premise that climate exerts a dominant role in the biogeographical distribution of species. If this idea is correct, then the variation in diversity at a macrogeographic scale across latitudinal temperature gradients can be used to predict the shifts that might occur with gradual Arctic warming. Thus, species responses to macro-scale latitudinal gradients can inform predictions of how climate change will alter species distributions (Pearson and Dawson 2003).

To date, studies have shown that the  $\alpha$  diversity of riverine biota decreases with increasing latitude (particularly above 40°N), although the strength of this relationship is study-specific (e.g., Oswood 1997, Castella et al. 2001, Vinson and Hawkins 2003, Hillebrand 2004, Scott et al. 2011). Lower  $\alpha$  diversity at higher latitudes may result from lower energy availability or physiological tolerance thresholds being exceeded as latitude increases (Currie et al. 2004). These effects may be exacerbated by recent glaciation events and the extreme cold temperatures that limit survival of species that are not cold-adapted (Jacobsen et al. 1997, Wrona et al. 2006). Differences in species composition among latitudes (i.e.,  $\beta$  diversity) may be driven by either the replacement of species by organisms better adapted to northerly conditions or the loss of species that are unable to tolerate conditions at higher latitudes (see Baselga 2010).

The observed declines in richness of cold-sensitive Ephemeroptera, Plecoptera, and Trichoptera (ETP) species (Vinson and Hawkins 2003, Scott et al. 2011) and increased dominance of more tolerant Diptera species at high latitudes (Oswood 1989, 1997) suggest that  $\beta$  diversity among latitudes in freshwater systems may be driven more by species loss (nestedness of assemblage composition) than replacement. As climate change promotes the northward range expansion of eurythermic species (Culp et al. 2012b), these patterns may shift, with increased richness and more evidence of species replacement (turnover component of  $\beta$  diversity) at higher latitudes.

Our aims here were to evaluate patterns of  $\alpha$  and  $\beta$  diversity of benthic macroinvertebrate assemblages in streams and rivers across a broad latitudinal gradient and assess the environmental drivers related to latitudinal differences in assemblage structure. We conducted this evaluation along the latitudinal gradient from the sub- to high Arctic of eastern Canada (58 to 81°N). We expected that taxonomic richness would decrease at high latitudes because cold-intolerant

EPT taxa would be eliminated and more tolerant Diptera would predominate. Further, we expected this negative relationship to be stronger than observed in previous research on Arctic streams (e.g., Castella et al. 2001, Vinson and Hawkins 2003, Pearson and Boyero 2009, Scott et al. 2011) because our study extended far into the high Arctic. We also predicted that  $\beta$  diversity would be driven by species loss with increasing latitude (i.e., the nestedness component of  $\beta$  diversity) because we expected increased environmental harshness and large-scale climate-related environmental drivers to play the largest roles in differentiating assemblages among latitudes.

The eastern Canadian Arctic is an appropriate gradient for establishing baseline information on ecological conditions because, while it has been relatively stable over the last several thousand years, it is expected to experience significant warming in the future (Prowse et al. 2006). This study is a component of the Arctic BioNet program of the International Polar Year and represents the first attempt to sample benthic macroinvertebrate assemblage structure in the Canadian Arctic across such an extensive spatial scale.

## METHODS

### Study area

The Canadian Arctic encompasses northern regions of mainland Canada (sub- and low Arctic) and the Arctic archipelago (low and high Arctic; Culp et al. 2012a). The most northerly landmass in the Canadian Arctic is Ellesmere Island, which extends to 82°N, whereas the sub-Arctic extends as far south as 50°N in central areas of mainland Canada. The eastern Canadian Arctic is primarily comprised of 2 ecozones: the Arctic Cordillera and the Northern Arctic (Fig. 1). The Arctic Cordillera ecozone is dominated by mountain ranges, deep valleys, and fjords, whereas the Northern Arctic ecozone landscape is dominated by hills and plains (Wiken et al. 1996). Low-latitude and coastal regions of these ecozones include areas of tundra meadow with small shrubs or hummocks with mosses and lichens, but northern regions have limited vegetation (Wiken et al. 1996). Both ecozones have Arctic climates with cold temperatures, a short growing season, and substantial spring freshets. Streams and rivers are generally ice-covered September to July in the eastern high Arctic (discharge data from sites on Ellesmere Island and northern Baffin Island, results not shown; HyDAT database, [www.ec.gc.ca/rhc-wsc](http://www.ec.gc.ca/rhc-wsc)), October to June (or November–May in warmer years) in the low Arctic archipelago (discharge data from sites on southern Baffin Island, results not shown; HyDAT database, [www.ec.gc.ca/rhc-wsc](http://www.ec.gc.ca/rhc-wsc)), and November to May on the northern mainland, which includes both the sub-Arctic and low Arctic (temperature logger data from northern Labrador and Québec; results not shown). In addition, Arctic streams often freeze solid during the winter, which creates a more extreme environment than an ice-covered stream.

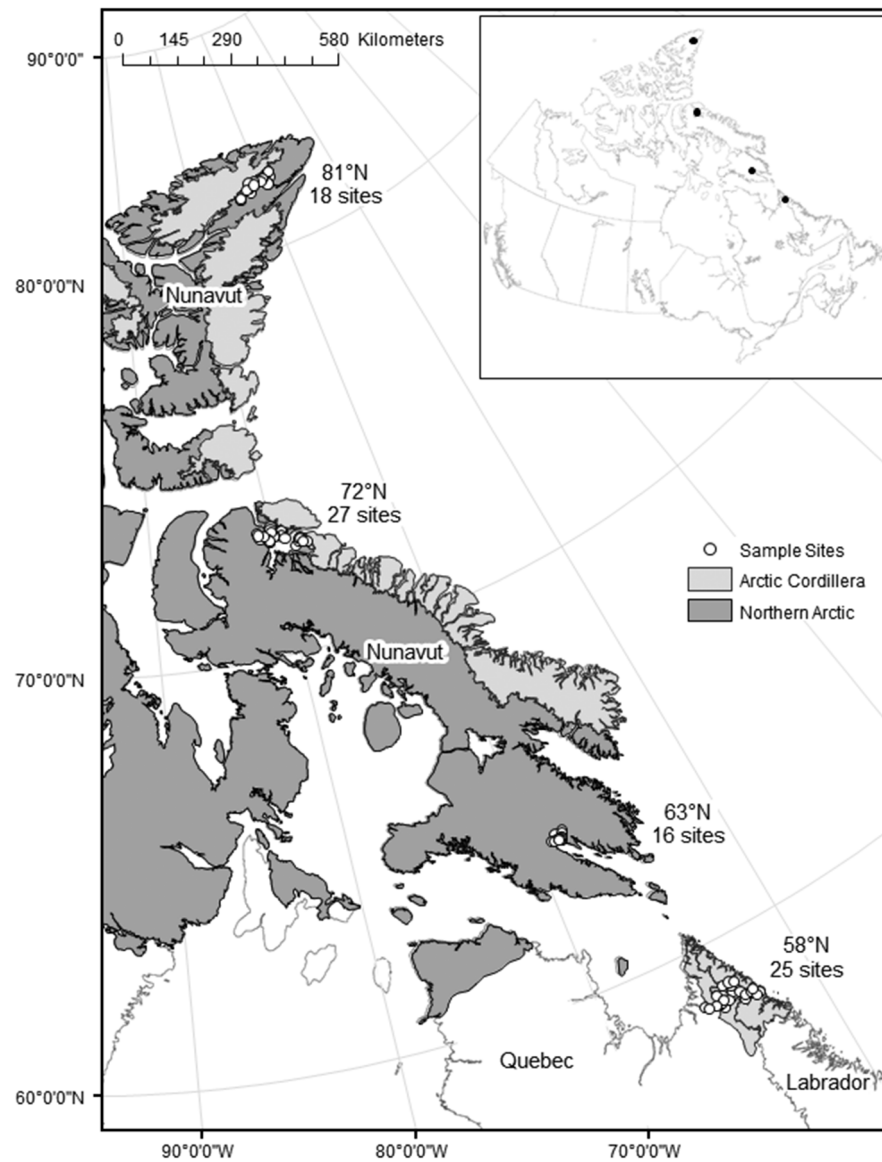


Figure 1. Map of the riverine sample sites in the eastern Canadian Arctic. Sites are at the approximate latitudes of 58°N (Torngats/Koroc), 63°N (Iqaluit), 72°N (Sirmilik), and 81°N (Lake Hazen). The extent of the Arctic Cordillera and Northern Arctic ecozones in the sampling area is indicated.

The climate in the western and central Canadian Arctic has warmed, but long-term temperature data in the eastern Canadian Arctic have shown stable temperatures or even cooling trends (Prowse et al. 2006, 2009). This temperature stability has been attributed to the strong marine influence of the Hudson Strait and Labrador Current outflows from the Arctic that have prevented northward movement in vegetation and treeline shifts in southern portions of northern Labrador and Québec relative to the west (Prowse et al. 2006). However, recent data indicate that temperatures in the east have begun to increase (Environment Canada 2012b), and predictive models suggest that a warming trend will continue in this region (Prowse et al. 2009).

### Sampling design

We sampled 86 sites along a latitudinal gradient from 58°N to 81°N in the eastern Canadian Arctic, with each site consisting of an approximately 100 m stream reach. Groups of sites were sampled around each of 4 latitudes along this gradient: 58°N (sub- and low Arctic), 63°N (low Arctic), 72°N (high Arctic), and 81°N (high Arctic; Fig. 1). Sites were spread across a wide geographic area within each latitudinal grouping (covering approximately 3,800 km<sup>2</sup> to 14,000 km<sup>2</sup> per latitude) and were generally located on different stream systems. Most sites were chosen based on helicopter access because of the highly remote nature of the sampling areas. We sampled 25 sites at 58°N within the Ko-

roc River Watershed in northeastern Québec (sub-Arctic) and in the vicinity of Torngat Mountains National Park in northern Labrador (low Arctic). We sampled 16 sites at 63°N near the city of Iqaluit (population size <7000) in southern Baffin Island, Nunavut. We sampled 27 sites at 72°N in 3 areas of northern Baffin Island near the town of Pond Inlet (population size <2000) and on Borden Peninsula and Bylot Island, which are both part of Sirmilik National Park. We sampled 18 sites at 81°N on Ellesmere Island, Nunavut, near Lake Hazen in Quttinirpaaq National Park. The eastern Canadian Arctic is sparsely populated, and human impacts were minimal at all sampling sites, as shown by the low values of N and P at all of our sampling sites (total nitrogen [TN] = 26–823 µg/L, total phosphorus [TP] = 0.9–8.5 µg/L). The mean (±SE) elevation of the sample sites was 123 (±13) m asl. Catchment area varied across sites at each latitude. Mean (±SE) catchment areas were similar at 63°N (285.8 ± 179.9 km<sup>2</sup>) and 72°N (197.1 ± 89.7 km<sup>2</sup>), and at 58°N (540.5 ± 178.4 km<sup>2</sup>) and 81°N (569.9 ± 408.2 km<sup>2</sup>), though catchment area was much more variable at 81°N. Sample sites were variably influenced by glacial, snowmelt, lake, and groundwater sources. Sites at 58 and 63°N had minimal contemporary glacial influence.

### Sampling methods

We sampled in August 2007 (58°N), August 2008 (63 and 81°N), and July 2009 (72°N). To estimate the numerical abundance of benthic macroinvertebrates, we collected kick samples following the standard CABIN (Canadian Aquatic Biomonitoring Network) approach (<http://cabin.cciw.ca>). A 400-µm, triangle-framed kick net was used to collect samples along the stream bottoms using a 3-minute traveling kick method. The sample operator moved in a zig-zag fashion upstream through the sample reach, disturbing (i.e., kicking) the substrate at a depth of ~5 to 10 cm and holding the net downstream of the disturbed area to collect any dislodged organisms and material carried by the current (Environment Canada 2012a). The 400-µm-mesh matches global standards for benthic macroinvertebrate monitoring (Buss et al. 2015). Invertebrate samples were preserved in 95% ethanol and transported to the laboratory for sorting and enumerating macroinvertebrates, which were identified to the lowest practical taxonomic level (genus when possible, though many early instar insects could only be identified to family or subfamily). We used subsampling procedures to identify and estimate the total numerical abundance of each chironomid taxon because Chironomidae were very abundant.

Water sample bottles were filled upstream of the kick net collections at each site and sent to the National Laboratory for Environmental Testing (Burlington, Ontario, Canada), run by Environment Canada, for analysis of nutrients, major anions and cations, and trace metals following standardized methods (Environment Canada 2008; Table 1).

We estimated substrate particle size at each site by measuring the *b*-axis (to the nearest 0.5 cm or nearest 0.1 cm for particles less than 1 cm) of 200 cobble particles along the 100-m stream reach. Particles were chosen haphazardly throughout each study site via a modified Wolman Pebble count (Wolman 1954) by walking in a zigzag pattern through the reach and measuring a substrate particle at the tip of every 2<sup>nd</sup> boot step. Substrate composition was summarized as the proportion of particles in the size range of sand (<0.2 cm), gravel (0.2 to <6.4 cm), cobble (6.4 to <25.6 cm), and boulder (≥25.6 cm). We used a scalpel to scrape periphyton from within a 10 cm<sup>2</sup> template on 10 haphazardly selected cobble stones (~12–20 cm) at each site (total area sampled 100 cm<sup>2</sup> per site) and preserved the composite sample in 95% ethanol for transport to the laboratory. Chl *a* concentrations (g/m<sup>2</sup>) were estimated in the laboratory by extracting the entire sample (algal mass and ethanol preservative) in hot ethanol and subsequently measuring fluorescence (Sartory 1982) to obtain a composite site value.

We estimated geospatial data for each sample site with ArcMap (Version 10, ESRI, St Paul, Minnesota), a Geographical Information System (GIS). A continuous ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer; available from: <http://asterweb.jpl.nasa.gov/gdem.asp>) 30-m resolution Digital Elevation Model (DEM) was used to delineate the upstream catchment area for each site and generate estimates of catchment morphology. These morphological estimates included metrics such as mean slope, mean elevation, and eastness. Eastness is calculated as  $\sin(\text{aspect})$ , which removes problems associated with the analysis of circular data. Eastness will take values close to 1 if the aspect is generally eastward, close to -1 if the aspect is westward, and close to 0 if the aspect is either north or south.

We extracted landcover variables from a national land cover dataset we accessed through Geogratis (<https://www.nrcan.gc.ca/earth-sciences/geography/topographic-information>). These variables summarized the relative areas of vegetation, tundra, or other forms of ground cover within each catchment and were grouped into broad categories for analysis. Finally, we used a geospatial layer with long-term (1971–2000) average air temperatures to calculate average maximum August temperatures for each delineated catchment. The long-term temperature data we used were interpolated for all of Canada through the use of thin plate, spline-smoothing algorithms (McKenney et al. 2006).

### Statistical analyses

Data pre-treatment was conducted prior to analysis to adjust taxonomic resolution, remove redundant variables, and transform data as needed. To avoid taxonomic redundancy because of mixed-level identification, we analyzed the invertebrate numerical abundance data at the level of

Table 1. Environmental variables considered for analysis of latitudinal trends, including variable descriptions, units, and source. Variables included in the final Redundancy Analysis (RDA) are indicated with \*.

Data type	Variable	Description	Units	Dataset source	Used in RDA
Water Quality	Alkalinity	Alkalinity	mg/L	Field data	*
	Cl	Chloride	mg/L		*
	SO <sub>4</sub>	Sulphate	mg/L		
	Ca	Calcium	mg/L		
	Mg	Magnesium	mg/L		
	Na	Sodium	mg/L		
	K	Potassium	mg/L		*
	TN	Total nitrogen (unfiltered)	mg/L		*
	TDP	Total dissolved phosphorus	mg/L		*
	TP	Total phosphorus (unfiltered)	mg/L		
	Chlorophyll <i>a</i>	Chlorophyll <i>a</i>	g/m <sup>2</sup>		
	AFDM	Ash-free dry mass	g/m <sup>2</sup>		*
Substrate Composition	%Sand	% sand in pebble count	%	Field data	*
	%Gravel	% gravel in pebble count	%		
	%Cobble	% cobble in pebble count	%		
	%Boulder	% boulder in pebble count	%		*
Water Source	Glacial	Presence/absence of glacial water source to stream	N/A	Field data, maps	*
Landscape Measurements	Perimeter	Catchment perimeter	km	ASTER DEM	
	Area	Catchment area	km <sup>2</sup>		*
	ElevationMean	Mean catchment elevation	m		*
	ElevationMin	Minimum catchment elevation	m		
	ElevationMax	Maximum catchment elevation	m		
	Eastness	Mean catchment aspect presented as eastness	N/A		
Bedrock Geology	SlopeMean	Mean catchment slope	degrees		*
	Sedimentary	Relative area of sedimentary bedrock	N/A	Geological Survey of Canada, Natural Resources Canada	*
	Intrusive	Relative area of intrusive bedrock	N/A		*
	Metamorphic	Relative area of metamorphic bedrock	N/A		*
Volcanic	Relative area of volcanic bedrock	N/A			
Land cover	Bare/Sparse	Relative area of barren, exposed, non-vegetated, or sparsely vegetated rock/soil/land	N/A	National Land Cover Dataset accessed through Geobase	*
	Shrubs	Relative area of bryoids or shrubs (tall, short, or dwarf)	N/A		
	Wetland	Relative area of wetlands	N/A		
	VegetatedTundra	Relative area of tundra vegetated with graminoids	N/A		*
	Coniferous	Relative area of coniferous vegetation (sparse to dense)	N/A		*
Climate	MaxAug-MeanTemp	Long-term average maximum August temperature	°C	Canadian Forestry Service	*

subfamily for Chironomidae larvae and the level of family or higher for all other taxa. Comparison of the spatial arrangement of sample sites in ordination space indicated that there were no significant differences ( $\alpha = 0.05$ ) when

subfamily or family-level taxonomy was used instead of genus-level taxonomy (Procrustes analysis; results not shown). Similarly, Bowman and Bailey (1997) have shown that family-level identification does not provide different

assemblage patterns than that of lower levels in studies when broad spatial pattern is of primary interest. Rare taxa that had a total numerical abundance of <5 individuals across all 86 sites (i.e., generally a single individual found at a single site) were removed prior to analysis to avoid putting undue weight on extremely rare taxa. In total, we removed 10 taxa from our analyses, each with total abundance of 1 to 3 individuals at 86 sites. The numerical abundances for the remaining 36 invertebrate taxa (Table 2)

were  $\log_{10}(x + 1)$  transformed to down-weight the influence of dominant taxa. Environmental variables were  $\log_{10}(x)$  or  $\arcsin(\sqrt{x})$  transformed as appropriate (Table 1). Pearson correlations between environmental variables were used to select a subset of 25 explanatory variables with minimal redundancy ( $|r| < 0.7$ ).

We estimated  $\alpha$  and  $\beta$  diversity to assess latitudinal differences in taxonomic richness and assemblage composition. First, we compared family richness across latitudes

Table 2. Benthic macroinvertebrate taxa found along the eastern Canadian Arctic latitudinal gradient from 58 to 81°N, indicating the number of sites (out of 86) at which each taxon was found, and the highest latitude at which it was collected.

Group/Order	Family	Subfamily	Abbreviation	Number of Sites	Highest Latitude (°N)
Diptera	Ceratopogonidae		D_Cerat	20	81
	Chironomidae	Chironominae	D_Chin	39	81
		Diamesinae	D_Dia	75	81
		Orthoclaadiinae	D_Orth	85	81
		Prodonominae	D_Pro	11	81
		Tanypodinae	D_Tany	33	81
	Diptera Pupa		D_Pupa	83	81
	Empididae		D_Emp	22	63
	Muscidae		D_Mus	14	81
	Simuliidae		D_Simu	51	72
	Tipulidae		D_Tipu	54	81
Ephemeroptera	Ameletidae		E_Amel	24	63
	Baetidae		E_Bae	37	72
	Ephemerellidae		E_Eph	21	58
	Heptageniidae		E_Hept	23	58
Hydracarina	Feltriidae		H_Felt	9	63
	Hydrozetidae		H_Hyd	39	81
	Hygrobatidae		H_Hyg	18	63
	Lebertiidae		H_Leb	29	81
	Sperchontidae		H_Sper	66	81
Plecoptera	Capniidae		P_Cap	38	72
	Chloroperlidae		P_Chlor	18	58
	Leuctridae		P_Leu	2	58
	Nemouridae		P_Nem	3	58
	Perlodidae		P_Perlo	20	63
Trichoptera	Apataniidae		T_Apa	3	63
	Glossosomatidae		T_Glos	11	58
	Hydropsychidae		T_Hpsy	4	58
	Hydroptilidae		T_Hpti	1	58
	Lepidostomatidae		T_Lepi	1	58
	Limnephilidae		T_Limn	8	63
	Philopotamidae		T_Phil	1	58
	Rhyacophilidae		T_Rhya	15	58
	Trichoptera Pupa		T_Pupa	3	58
Other	Acarina		Acar	18	81

to test whether  $\alpha$  diversity declined with increasing latitude. We tested for differences in mean family richness among the 4 latitude groups with a non-parametric Kruskal–Wallis 1-way analysis of variance by ranks, followed by Dunn’s test for multiple comparisons with a correction for tied data (at  $\alpha = 0.05$ ) because there were different numbers of samples and unequal variance among latitudes. Beta diversity and its component parts were described following Baselga (2010). Presence/absence data were used to calculate dissimilarity indices representing  $\beta$  diversity, turnover, and nestedness. To assess  $\beta$  diversity across latitudes, we summarized the abundance data at each latitude as presence or absence of taxa across all sites at that latitude (i.e., by summing numerical abundances across all sites sampled in a latitude group and converting data to presence/absence). We then calculated and partitioned  $\beta$  diversity with a single set of presence/absence data for each of the 4 latitudes (i.e., one set of presence/absence data each for 58°N, 63°N, 72°N, and 81°N, rather than site-specific data). Following Baselga (2010), presence/absence data were used to calculate the Sørensen dissimilarity index ( $\beta_{\text{SOR}}$ ) as a measure of  $\beta$  diversity and to partition  $\beta$  diversity into species turnover and nestedness components through pairwise comparisons of each latitude. The  $\beta$  diversity from species turnover or replacement across regions was calculated with the Simpson dissimilarity index ( $\beta_{\text{SIM}}$ ; Baselga 2010, Baselga et al. 2012). We calculated the portion of  $\beta$  diversity that is attributable to a loss of species across regions (i.e., where an assemblage is comprised of a subset of the species found in another location without the introduction of new species to replace those that are lost) as nestedness-resultant dissimilarity ( $\beta_{\text{NES}}$ ; Baselga 2010, Baselga et al. 2012). Pairwise calculation of  $\beta_{\text{SOR}}$ ,  $\beta_{\text{SIM}}$ , and  $\beta_{\text{NES}}$  was used to assess whether compositional differences between low and high latitudes were primarily the result of species turnover or nestedness.  $\beta$  diversity calculations were done in R version 3.4.2 (R Development Core Team 2015) with the *betapart* package (Baselga and Orme 2012).

We used indirect gradient analysis and analysis of similarities to examine latitudinal differences in taxonomic composition and direct gradient analysis to assess latitudinal associations of biota with environmental variables. Direct and indirect gradient approaches were chosen over distance-based methods to allow simultaneous ordination and description of patterns in sites and biota. Initially, we assessed whether the biotic data were best described by a linear or unimodal response model, which is tested with detrended correspondence analysis (DCA) to determine the degree of spatial turnover or total  $\beta$  diversity underlying the assemblage data (estimated by the gradient length in standard deviations of the first axis in the analysis; ter Braak and Šmilauer 2002). The gradient length of the first DCA axis (representing the degree of turnover in our study sites) was <3.5 standard deviations (gradient length = 2.81), which

suggested that linear response models (principal components analysis for indirect analysis and redundancy analysis for direct analysis) would be most appropriate (Legendre and Legendre 1998). Because the DCA indicated that a linear model was most appropriate for our data, we used principal components analysis (PCA) to examine changes in assemblage structure along the latitudinal gradient of stream sites. PCA was conducted on the covariance matrix of transformed abundances with post-standardization of species scores to represent correlations on the biplot (ter Braak and Šmilauer 2002). To determine whether assemblage structure differed significantly among latitudes, we conducted analysis of similarity (ANOSIM) on the Euclidean distance matrix (which underlies the PCA) for all samples. Redundancy analysis (RDA) was used to examine the association between environmental variables and assemblage structure. The number of explanatory variables (25) was  $> \frac{1}{2}$  the number of taxa (36), and to avoid overfitting the data, we further reduced the number of selected variables to 18 by removing variables that had low axis scores, appeared highly redundant with other environmental variables in ordination space, and whose removal did not appear to have a large effect on analysis results (see Table 1 for final list of environmental variables included in RDA). We expressed the RDA axis eigenvalues as a percentage of the PCA eigenvalues to determine the proportion of unconstrained assemblage variance explained by each RDA axis. Ordinations were tested in Canoco for Windows version 4.55 (ter Braak and Šmilauer 2002), and ANOSIM was conducted in PRIMER 6 (Clarke and Warwick 2001).

## RESULTS

Taxonomic richness decreased markedly with increasing latitude, and ranged from an average of 14 families at 58°N (range: 2–23 taxa per site) to an average of 4 families at 81°N (range: 1–6 taxa per site; Fig. 2, Table 3). Average richness was significantly different among latitudes (Kruskal–Wallis rank-sum test,  $H_c = 57.916$ ,  $p < 0.001$ ). Post-hoc comparisons showed that the 2 high-Arctic regions had significantly lower family richness than the 2 low-Arctic regions ( $\alpha = 0.05$ , Fig. 2). Average richness decreased across all latitudes (Fig. 2), but variability among sites did not allow for the detection of significant differences between 58 and 63°N or between 72 and 81°N (Fig. 2).

Beta diversity was highest between the most distant latitudes, a result consistent with trends in  $\alpha$  diversity (Fig. 3). Across all latitudinal comparisons, the portion of  $\beta$  diversity associated with nestedness was  $\sim 2\times$  higher than the portion associated with species turnover (Fig. 3). This difference indicates that compositional differences across the latitudinal gradient are dominated by a loss of species rather than replacement with different species.

Stream sites were clearly grouped by latitude for 58, 63, and 81°N in the PCA ordination of invertebrate assemblage

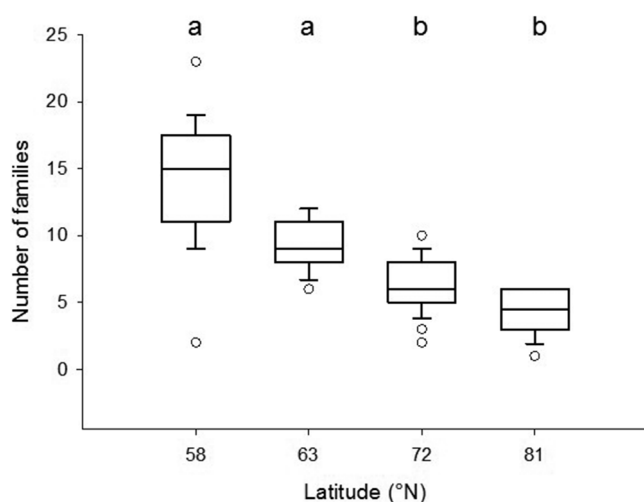


Figure 2. Boxplot estimates of  $\alpha$  diversity at riverine sites sampled at 58°N (Torngats/Koroc), 63°N (Iqaluit), 72°N (Sirmilik), and 81°N (Lake Hazen). The horizontal line indicates the sample median, box ends mark the interquartile range, whiskers indicate data range, and points denote statistical outliers. Differences in letters above latitudes indicate significant differences in their mean family richness values (Kruskal–Wallace rank-sum test and Dunn’s multiple comparison test,  $\alpha = 0.05$ ).

composition, reflecting stronger similarity in assemblage structure within than among latitudes. In contrast, sites at 72°N overlapped both the high Arctic sites at 81°N and low Arctic sites at 63°N, and therefore appeared to be tran-

sitional between them (Fig. 4). The 1<sup>st</sup> axis of the PCA ordination separated sites at 58°N from higher latitude sites and explained 26.4% of the variance in assemblage structure. The 2<sup>nd</sup> axis explained 20.5% of the variance and separated stream sites at the higher latitudes. There were distinct groupings of sites at 63 and 81°N along the 2<sup>nd</sup> axis, and the sites at 72°N were spread across the gradient. The results of the ANOSIM indicated that assemblage structure differed significantly among all latitude groups (global  $R = 0.557$ ,  $p < 0.001$ ;  $p < 0.001$  for all pairwise comparisons). However, the pairwise  $R$  for the comparison of 72 and 81°N was low (pairwise  $R = 0.298$ ), indicating a moderate similarity among sites at these latitudes (for all other latitude comparisons, pairwise  $R = 0.609$ – $0.733$ ).

Low- and high-latitude sites primarily separated along the 1<sup>st</sup> PCA axis because of differences in assemblage richness across the latitudinal gradient. Sites at 58°N were positively associated with a large number of taxa, particularly EPT families, whereas sites at higher latitudes were associated with high abundances of Oligochaeta and a number of dipteran families, particularly the chironomid subfamilies Orthoclaadiinae and Diamesinae (Fig. 4). Separation of the higher latitudes along the 2<sup>nd</sup> PCA axis was primarily associated with variation among sites in dipteran taxa and mites. The chironomid subfamilies Tanypodinae, Chironominae, and Orthoclaadiinae and 3 families of mites were associated with sites at 63°N, whereas the dipterans Muscidae and Ceratopogonidae and the chironomid subfamily Prodominae were associated with sites at 81°N (Fig. 4).

Table 3. Mean ( $\pm$ SE) values of invertebrate abundance, richness, and diversity, and a selection of abiotic variables that had high axis scores in the RDA for each latitude. For glacial source, the presented value is the proportion of sites at each latitude with a glacial water source.

Variable	Latitude			
	58°N Québec & Torngat Mountains NP	63°N Iqaluit	72°N Pond Inlet & Sirmilik NP	81°N Quttinirpaq NP
Invertebrate abundance	1077 $\pm$ 299	1827 $\pm$ 323	1740 $\pm$ 237	1492 $\pm$ 522
Family richness	14.0 $\pm$ 0.9	9.3 $\pm$ 0.5	6.2 $\pm$ 0.4	4.3 $\pm$ 0.3
Shannon–Weiner Diversity	1.82 $\pm$ 0.11	1.47 $\pm$ 0.06	1.31 $\pm$ 0.06	1.05 $\pm$ 0.08
LTA max August Temperature	9.16 $\pm$ 0.27	9.10 $\pm$ 0.17	5.05 $\pm$ 0.24	−0.37 $\pm$ 0.36
Glacial source (proportion of sites)	0%	0%	22.20%	44.40%
Relative area intrusive bedrock	14.54 $\pm$ 3.60	98.75 $\pm$ 0.72	0.75 $\pm$ 0.0.75	0
Mean catchment slope	14.20 $\pm$ 1.33	4.74 $\pm$ 0.12	12.02 $\pm$ 0.61	11.27 $\pm$ 1.24
Relative area coniferous vegetation	1.45 $\pm$ 0.34	0	0	0
Relative area vegetated tundra	0	3.56 $\pm$ 1.42	18.06 $\pm$ 2.64	7.46 $\pm$ 1.49
Relative area bare/sparse land	53.39 $\pm$ 1.93	62.23 $\pm$ 5.69	38.20 $\pm$ 4.92	29.19 $\pm$ 5.29
% boulder	4.21 $\pm$ 0.65	15.91 $\pm$ 4.00	4.13 $\pm$ 1.25	1.72 $\pm$ 0.45
Total phosphorus unfiltered (mg/L)	0.002 $\pm$ 0.0002	0.002 $\pm$ 0.0003	0.003 $\pm$ 0.0004	0.003 $\pm$ 0.0002
Alkalinity (mg/L)	0.003 $\pm$ 0.001	0.002 $\pm$ 0.000	0.045 $\pm$ 0.018	0.077 $\pm$ 0.028
Ash-free dry mass (g/m <sup>2</sup> )	1.99 $\pm$ 0.62	16.20 $\pm$ 5.80	8.82 $\pm$ 2.68	10.44 $\pm$ 6.30



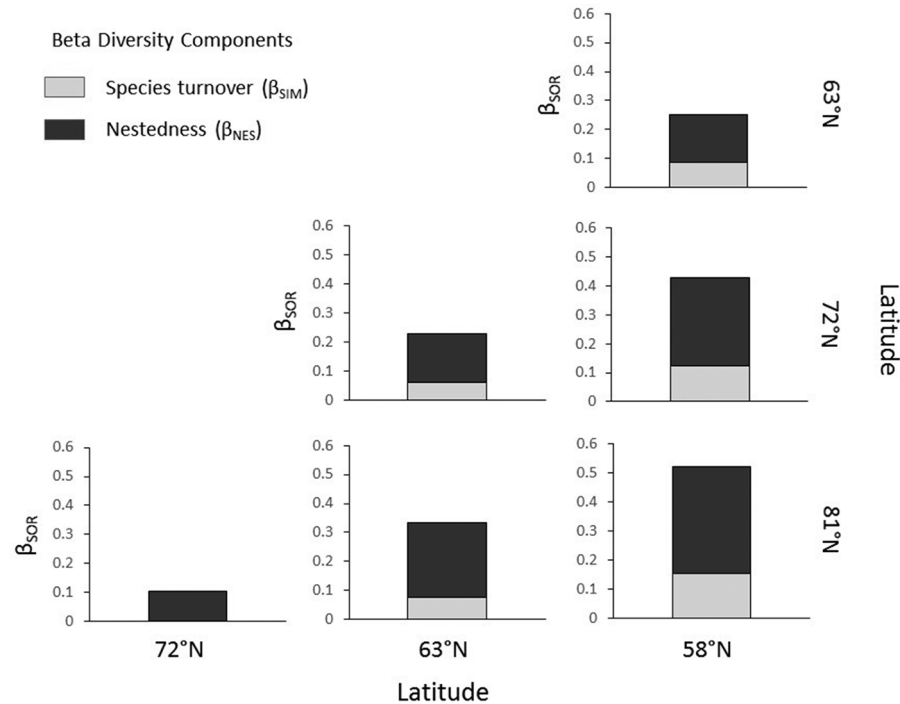


Figure 3. Beta-diversity partitioning results between pairs of latitudes. The height of each bar indicates the total  $\beta$  diversity ( $\beta_{SOR}$ ) for pairwise comparisons of latitudes, and the shading of bars indicates the amount of  $\beta$  diversity attributable to species turnover ( $\beta_{SIM}$ ; gray) and nestedness ( $\beta_{NES}$ ; black). Larger values of  $\beta_{SOR}$  indicate a greater dissimilarity between latitudes. All plots are on the same scale ( $\beta_{SOR}$  range = 0.0–0.6) to facilitate comparisons of the magnitude of dissimilarity across latitudes.

Few taxa were present at the highest latitude (81°N), and Chironomidae represented an average of >80% of the benthic macroinvertebrate population (with relative abundance of Chironomidae as high as 98.6%; Fig. 5). This contrasted sharply with sites at 58°N, where average relative abundances of Chironomidae and Ephemeroptera were similar at ~35 to 40% each (Fig. 5). Sites at 58°N had as many as 4 families of Ephemeroptera, 4 families of Plecoptera, and 6 families of Trichoptera. In contrast, sites at 63 and 72°N had at most 1 to 2 families of Plecoptera and Ephemeroptera and there were no Trichoptera at 72°N. At 81°N, these orders of insects were not found, and assemblages included Diptera (primarily Chironomidae), Hydracarina, and Oligochaeta. However, total organism abundance was higher at the more northern latitudes despite the lower taxonomic richness (Table 3), and average abundance of Chironomidae alone was 1322 individuals at 81°N, higher than the average abundance of all taxa combined at 58°N (1077 individuals; Table 3).

Invertebrate assemblage composition across latitudes was highly correlated with environmental variables. The 1<sup>st</sup> axis of the RDA explained 20.6% of the unconstrained variance in the assemblages, whereas the 2<sup>nd</sup> axis explained another 12.8% of the unconstrained variance. Together, these 2 axes explained 64.6% of the constrained variance in assemblage structure (Fig. 6). The 1<sup>st</sup> axis was primarily

associated with vegetation and temperature, and the low Arctic sites at 58°N were associated with coniferous vegetation and greater long-term average maximum August temperatures. In contrast, the sites at the highest latitudes (high Arctic sites at 72 and 81°N) were associated with vegetated tundra and lower temperatures (Fig. 6, Table 3). Ephemeroptera families were primarily associated with the presence of coniferous vegetation, whereas Oligochaetes and the chironomid subfamily Orthoclaudiinae were negatively correlated with coniferous vegetation. The chironomid subfamily Diamesinae was negatively correlated with both coniferous vegetation and long-term average maximum August temperature. Water chemistry also played a role in the primary separation of sites, and the high Arctic sites were associated with higher measurements of alkalinity, TP, and TN (Fig. 6; Table 3). TP was generally low across all latitudes (average TP across all sites was 0.002 mg/L), but several sites at 58°N had particularly low TP concentrations (as low as 0.0009 mg/L).

The 2<sup>nd</sup> RDA axis provided a more clear separation of assemblages at low and high Arctic sites than did the PCA, with most sites at 72°N grouping more clearly with sites at 81°N. This axis described a gradient in temperature, catchment, and in-stream physical and chemical conditions (Fig. 6). Assemblages at 63°N were positively associated with high relative abundance of intrusive bedrock,

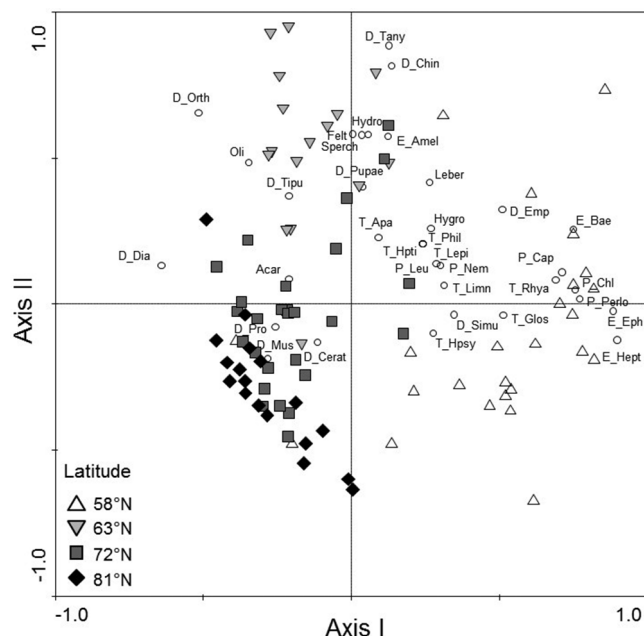


Figure 4. PCA ordination of benthic macroinvertebrate assemblage structure at Arctic riverine sample sites at 58°N (Torngats/Koroc), 63°N (Iqaluit), 72°N (Sirmilik), and 81°N (Lake Hazen). Shape and shading of sample points indicates latitude at which sample was collected. Open circles are taxon points (see Table 2 for taxonomic abbreviations).

high ash-free dry mass, and a high proportion of boulders (as high as 50% of the substrate composition), but negatively associated with mean slope and mean elevation. At 81°N, assemblages were associated with smaller particle sizes and high levels of potassium, but the high Arctic sites (72 and 81°N) appeared to be more clearly separated from 63°N along the 2<sup>nd</sup> RDA axis by temperature-related variables. For example, assemblages in the high Arctic sites displayed a strong negative association with long-term average maximum August temperature and a positive association with glacial water sources, although not all sites at these latitudes were glacially-fed (Fig. 6, Table 3).

## DISCUSSION

Analysis of benthic macroinvertebrate assemblages from rivers across a broad latitudinal gradient in the eastern Canadian Arctic showed that  $\alpha$  diversity declined with increasing latitude and that  $\beta$  diversity was highest between the most distant latitudes. The large spatial-scale differences in composition among latitudes were largely associated with the nestedness component of  $\beta$  diversity, which indicates a loss of taxa with increasing latitude. This result supports the hypothesis that physiological tolerance is an important driver of species richness. Furthermore, the differences in composition between low- and high-Arctic sites were associated with large-scale, climate-related factors such as tem-

perature trends and the presence of trees or tundra. This result implies that climatic conditions are primarily responsible for structuring Arctic stream benthic assemblages, especially at high latitudes, which is consistent with the concept of bioclimatic envelopes (e.g., Brown et al. 1996, Pearson and Dawson 2003, Shah et al. 2014). The biotic gradient in our data resulted from species loss with increasing latitude, rather than a change in total abundance, which reflects the importance of species-specific tolerances to the harsh environment of the high Arctic. The sharp declines in taxonomic richness with increasing latitude that we observed here are consistent with previous observations that freshwater invertebrate richness declines towards the poles. However, by including high latitude sites we were able to produce stronger evidence of this trend than has been reported in previous studies of non-glacial streams (Vinson and Hawkins 2003, Hillebrand 2004, Scott et al. 2011, Jacobsen and Dangles 2012).

## Latitudinal shifts in taxonomic diversity

Declines in  $\alpha$  diversity with increasing latitude in the eastern Canadian Arctic were not associated with declines in total numerical abundance of organisms. Thus, the harsh northern conditions do not necessarily limit the number of individuals that can inhabit a stream, but they instead limit only the number of taxa. Trends of decreasing  $\alpha$  diversity with increasing latitude have been previously explained

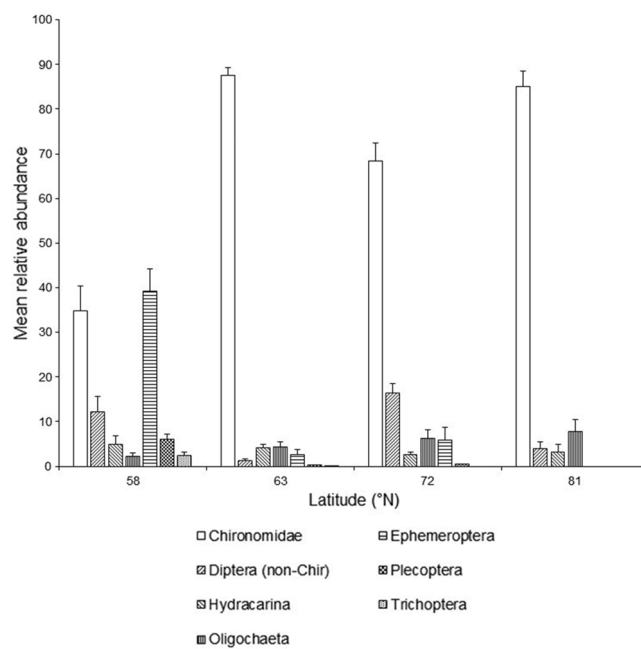


Figure 5. Mean relative abundance ( $\pm$ SE) of invertebrate taxonomic groups at each latitude of the eastern Canadian Arctic: 58°N (Torngats/Koroc), 63°N (Iqaluit), 72°N (Sirmilik), and 81°N (Lake Hazen).

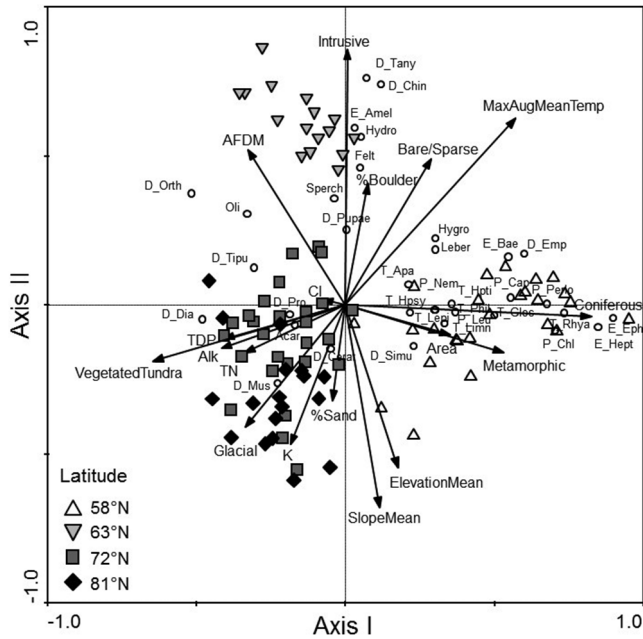


Figure 6. RDA ordination of benthic macroinvertebrate assemblages in Arctic riverine sample sites at 58°N (Torngats/Koroc), 63°N (Iqaluit), 72°N (Sirmilik), 81°N (Lake Hazen), and environmental variables. Shape and shading of sample points indicates latitude at which sample was collected. Open circles are taxon points (see Table 2 for taxonomic abbreviations). Labeled vectors indicate direction of change of environmental variables (see Table 1 for description of environmental variables).

mechanistically by a number of hypotheses, including those that describe richness as a function of energy availability or physiological tolerance levels (Currie et al. 2004). In particular, the energy-richness hypothesis (see Currie et al. 2004) predicts that numerical abundance, biomass, and richness should all decline as resource availability decreases. Our finding that  $\alpha$  diversity declined with increasing latitude follows this hypothesis, but our finding that there is no commensurate change in numerical abundance is counter to this hypothesis. However, biomass may have been lower at the most northerly sites because there was a dominance of small-bodied organisms. The high numerical abundances at these sites occurred despite low primary productivity (evident as a significant decline in Chl *a* at 81°N; results not shown) that was probably a result of the low nutrient levels and short growing season (albeit with continuous daylight).

The latitudinal richness gradient we observed is most consistent with hypotheses related to physiological tolerance levels. Specifically, the loss of species with increasing latitude, as evidenced by the dominance of the nestedness component of  $\beta$  diversity, suggests that temperature tolerance shapes assemblage composition by filtering out species that cannot survive the environmental conditions at

the highest latitudes (sensu Poff 1997). The taxa that proliferated in our northernmost sites, including Oligochaeta and the Chironomidae subfamilies Diamesinae and Orthocladiinae, are similar to the taxa found at northern glacial sites in Svalbard (Castella et al. 2001). Moreover, models of glacially-fed systems describe bioclimatic envelopes for the most cold-tolerant taxa and provide important information about temperature tolerances of organisms that may be found throughout the Arctic, even in non-glacial systems (e.g., Milner and Petts 1994, Brittain and Milner 2001, Milner et al. 2001). In these glacial models, Orthocladiinae, Oligochaeta, and Diamesinae are all described as the most cold-tolerant taxa, with Diamesinae in particular found to be tolerant of temperatures below 2°C (Milner et al. 2001). Thus, assemblages at the highest latitudes in the eastern Canadian Arctic provided support for the bioclimatic envelope concept and were dominated by cold-tolerant taxa (e.g., Diamesinae, Orthocladiinae, and Oligochaeta; Milner et al. 2001).

The shift in taxonomic composition from 58 to 81°N was most evident as a loss of EPT taxa, resulting in a high nestedness component of  $\beta$  diversity. This pattern is consistent with other studies that sampled as far north as 70°N (e.g., Vinson and Hawkins 2003, Scott et al. 2011, Shah et al. 2014), but in our study, which extended the latitudinal gradient to 81°N, declines in EPT taxa were more severe. In particular, Vinson and Hawkins (2003) and Scott et al. (2011) found weaker declines in Trichoptera than in Ephemeroptera or Plecoptera up to 70°N. In contrast, we found only 2 families of Trichoptera at 63°N, and all other trichopterans were absent above 58°N. The stronger declines in richness that we observed at similar latitudes relative to other studies probably occurred because the eastern Canadian Arctic has experienced greater long-term stability of air temperatures (i.e., less warming) than other areas of the Arctic (Prowse et al. 2006). In particular, the majority of sites at 58°N in the eastern Arctic (i.e., northern Labrador) are above the treeline, whereas the western Canadian Arctic treeline has moved above 68°N in some areas (Scott et al. 2011). As a result, sites sampled at 58°N in the eastern Canadian Arctic more closely resemble sites at 70°N in other areas of the Arctic with respect to climate and surrounding vegetation, which appears to be reflected in their biodiversity.

The latitudinal patterns within our study are similar to those described by Castella et al. (2001), who found sharp declines in richness with increasing latitude in glacially-fed stream systems. These changes may have resulted from increasing environmental harshness that was driven by glacial inputs (Jacobsen and Dangles 2012). In this study, there was a higher predominance of glacially-fed systems in the high Arctic latitudes we sampled, indicated by the importance of glacial source as a driver of the benthic macroinvertebrate assemblage. However, not all of our high Arctic

sites were glacially-fed (only 22% of sites at 72°N and 44% of sites at 81°N), so the large loss of EPT taxa we found was not driven solely by glacial influence. This result contrasts with that of Blaen et al. (2014) who found that Svalbard rivers in non-glaciered basins often were more diverse and had higher macroinvertebrate abundance than assemblages in glacierized basins.

### Drivers of biotic change along the latitudinal gradient

If climate exerts a dominant role in determining assemblage composition, as suggested by the concept of bioclimate envelopes (Pearson and Dawson 2003), then large-scale environmental drivers that are influenced by climate should be closely associated with compositional changes along a latitudinal gradient. Temperature can be a particularly important driver of diversity along latitudinal gradients of stream benthic macroinvertebrates (Jacobsen et al. 1997, Castella et al. 2001). Our data support this idea, as a distinct shift in assemblage structure was associated with decreasing temperatures along the latitudinal gradient. For example, winter freezing and low temperatures are important environmental factors that affect mayfly (Ephemeroptera) distributions (Brittain 2008), which were notably absent at the highest latitudes where temperatures were coldest. Furthermore, low latitude sites were positively associated with coniferous vegetation, and higher latitude sites were positively associated with vegetated permafrost. Both of these vegetational patterns are driven by climate. This pattern reflects the shift in stream conditions along the latitudinal gradient, with increasingly cold temperatures and declining vegetation towards the north resulting in a habitat characterized by a short growing season and low primary productivity in streams and the surrounding riparian zone (Vinson and Hawkins 2003). This type of latitudinal change in abiotic conditions may lead to limited taxonomic richness through exceedance of stress thresholds (e.g., related to temperature, food availability, and habitat quality) for a number of taxa (Brown et al. 1996, Currie et al. 2004). In addition, oceanic barriers between continents and islands may also contribute to these biodiversity gradients (Brittain 1990).

Large-scale drivers were associated with the dominant patterns along our latitudinal gradient, but smaller-scale drivers (i.e., site-scale variables such as water chemistry and substrate composition) were also important because there was a secondary gradient that drove patterns across the higher latitudes. This finding supports the suggestion of Pearson and Dawson (2003) that bioclimatic envelope models should be viewed in a hierarchical framework, similar to the landscape-filtering mechanisms proposed by Poff (1997). Climate acts at the largest scales (global to regional) to structure assemblages, topography and land cover act at intermediate scales (regional to local), and in-stream abiotic characteristics and biotic interactions act at the smallest

scales (local to micro). In our study, secondary drivers of assemblage structure were related to intermediate- and small-scale variables, including bedrock composition and in-stream differences in substrate composition and water chemistry. Drivers related to substrate structure and stability are important determinants of assemblage structure in glacial streams (Castella et al. 2001) and also play an important role in structuring assemblage composition in non-glacial streams in the low Arctic (Lento et al. 2013).

### Predicting the impacts of climate change on Arctic freshwater communities

As warming of Arctic environments continues because of climate change (e.g., see review in Prowse et al. 2009), biodiversity differences along latitudinal gradients, such as those in this study, are expected to become less pronounced. The primary drivers of temperature and vegetation will probably shift and become more similar across the latitudinal range, with high latitude conditions beginning to resemble those at low latitudes. For example, Isaak and Rieman (2013) developed stream isotherm shift rates based on stream temperature and stream slope and predicted global shifts in stream isotherms of 5 to 143 km with air temperature increases of 2°C. In addition, Wrona et al. (2016) suggested that the proliferation of shrubs (i.e., shrubification, *sensu* Myers-Smith et al. 2011) within riparian zones of Arctic rivers will provide additional allochthonous material to enhance riverine productivity. Moreover, Domisch et al. (2013) used bioclimatic envelope models to predict distributional shifts in stream macroinvertebrates across Europe with climate warming and projected shifts in suitable habitats of 4.7 to 6.6°N on average.

As conditions in the high Arctic change to more closely resemble those currently found in the low Arctic, we predict that macroinvertebrate assemblage composition will also begin to resemble that currently found in the low Arctic. In particular, we expect strong compositional shifts in high Arctic systems characterized by marked increases in macroinvertebrate richness. Mustonen et al. (2018) noted that the strongest shifts in the invertebrate assemblages of Finland streams in response to climate change are predicted to occur at the highest latitudes and that they will be most evident as species replacement. Such findings have strong implications for the eastern Canadian Arctic, where nestedness is currently the dominant component of  $\beta$  diversity across latitudes. Barriers to dispersal may play a role in slowing assemblage shifts in the Canadian Arctic archipelago, but northward distributional shifts may mean that the strong distinction that is currently evident among assemblages at 58, 63, and 81°N will become less clear. Alpha diversity may become more similar across these latitudes as more species ranges expand northward, and  $\beta$  diversity across latitudes may become more driven by species turnover than nestedness as thermal tolerances play less of

a role in structuring assemblages (Mustonen et al. 2018). If obligate cold-water species of macroinvertebrates exist within the most cold-tolerant taxonomic groups (e.g., within the Diamesinae, Orthocladiinae, and Oligochaeta), loss of these species at the highest latitudes would be expected with warming. In addition, a northward expansion of EPT taxa may be expected in response to warming conditions, causing a reduced dominance of dipteran taxa at the highest latitudes. This northward expansion will probably proceed faster in western than eastern Arctic rivers of North America as warming has been disproportional among these areas to date (Prowse et al. 2006).

As differences in climate-driven environmental drivers across latitudes become less extreme, small-scale environmental drivers, such as substrate composition and water chemistry, may assume greater importance. In our study, nutrients were not strongly associated with benthic assemblage structure at any latitude because all sites along the latitudinal gradient had extremely low nutrient levels. With climate change, however, nutrients could begin to play a larger role in determining assemblage composition in streams (Wrona et al. 2016) because these ecosystems are sensitive to nutrient enrichment. Nutrient enrichment may arise as a result of human expansion into the north or erosion by wind or water associated with dryer soils. In the western Canadian Arctic, permafrost thawing has led to significant inputs of nutrients, solutes, and suspended sediments into stream systems (Kokelj et al. 2013), and these inputs have been shown to negatively affect macroinvertebrate abundance (Chin et al. 2016). Permafrost degradation will be a growing concern in the east with continued warming (Bring et al. 2016, Wrona et al. 2016), and the changes to the physical and chemical environments caused by permafrost-related slumping (e.g., Chin et al. 2016) may become a dominant driver of benthic assemblage composition.

Our analysis of stream macroinvertebrates is the 1<sup>st</sup> assessment of this scale in the Canadian Arctic, and provides important information regarding baseline conditions in these systems—information that is vital to allow detection of trends in response to a changing climate. With continued warming, differences in benthic macroinvertebrate assemblages along the latitudinal gradient are expected to become less pronounced as temperatures and vegetation become more similar from south to north and as small-scale drivers increase in importance. Instead, variables such as substrate composition and water chemistry will probably become the dominant drivers of biotic composition.

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