

Ecological correlates of riverine diatom and macroinvertebrate alpha and beta diversity across Arctic Fennoscandia

John E. Brittain^{1,2}  | Jani Heino³  | Nikolai Friberg^{4,5,6}  | Jukka Aroviita³ | Maria Kahlert⁷  | Satu-Maaria Karjalainen³ | François Keck⁷  | Jennifer Lento⁸  | Petri Liljaniemi⁹ | Heikki Mykrä³ | Susanne C. Schneider⁴  | Jukka Ylikörkkö⁹

¹Norwegian Water Resources & Energy Directorate, Oslo, Norway

²Natural History Museum, University of Oslo, Oslo, Norway

³Finnish Environment Institute, Freshwater Centre, Oulu, Finland

⁴Norwegian Institute for Water Research, Oslo, Norway

⁵Freshwater Biological Section, University of Copenhagen, Copenhagen, Denmark

⁶water@leeds:ecology, School of Geography, University of Leeds, Leeds, UK

⁷Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden

⁸Canadian Rivers Institute and Department of Biology, University of New Brunswick, Fredericton, NB, Canada

⁹Ministry of the Environment, Helsinki, Finland

Correspondence

John E. Brittain, Natural History Museum, University of Oslo, PO Box 1172 Blindern, 0318 Oslo, Norway.
Email: j.e.brittain@nhm.uio.no

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Abstract

1. Arctic freshwaters support biota adapted to the harsh conditions at these latitudes, but the climate is changing rapidly and so are the underlying environmental filters. Currently, we have limited understanding of broad-scale patterns of Arctic riverine biodiversity and the correlates of α - and β -diversity.
2. Using information from a database set up within the scope of the Arctic Council's Conservation of Arctic Flora and Fauna Circumpolar Biodiversity Monitoring Plan, we analysed patterns and correlates of α - and β -diversity in benthic diatom and macroinvertebrate communities across northern Norway, Sweden, and Finland. We analysed variation in total β -diversity and its replacement and richness difference components in relation to location of the river reach and its drainage basin (Baltic Sea in the south, the Barents Sea in the east and the north, and the Norwegian Sea in the west), in addition to climate and environmental variables.
3. In both macroinvertebrates and diatoms, the replacement and richness difference components showed wide variation. For macroinvertebrates, the richness difference component was the more important, whereas for diatoms, the replacement component was the more important in contributing to variation in β -diversity. There was no significant difference in β -diversity between the three main drainage basins, but species composition differed among the drainage basins.
4. Based on the richness difference component of β -diversity, climate variables were most strongly associated with community variation in macroinvertebrates. In diatoms, both environmental and climate variables were strongly correlated with community compositional variation. In both groups, there were also significant differences in α -diversity among the three main drainage basins, and several taxa were significant indicators of one of these drainage basins. Alpha diversity was greater in areas with a continental climate, while the oceanic areas in the west harboured greatly reduced flora and fauna.

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5. The correlates of biodiversity were relatively similar in macroinvertebrates and diatoms. Climate variables, in particular temperature, were the most strongly associated with biodiversity patterns in the Arctic rivers of Fennoscandia. Sedimentary geology may be associated with increased productivity and, to a lesser extent, with sensitivity to acidification. There was considerable variation in community composition across Arctic Fennoscandia, indicating the necessity of protecting several stream reaches or even whole catchments within each region to conserve total riverine biodiversity. Furthermore, it is likely that the predicted changes in temperature in Arctic areas will influence riverine diversity patterns across Fennoscandia.

KEYWORDS

biodiversity, biogeographical patterns, climate, community composition, temperature

1 | INTRODUCTION

Arctic biodiversity is strongly jeopardised by global change (Meltofte, 2013) and this is particularly true for freshwater ecosystems (Wrona et al., 2013). Freshwater ecosystems are well represented at high latitudes (Wrona et al., 2013), although they usually do not harbour as high biodiversity as more southerly locations (Strayer & Dudgeon, 2010). Nevertheless, Arctic freshwaters, especially those in mainland areas of the subarctic and low Arctic, contain a diverse fauna and flora adapted to the harsh conditions at these latitudes (Meltofte, 2013). In addition, the relative importance of freshwater ecosystems to overall biodiversity increases with latitude, as they are proportionally more diverse than terrestrial ecosystems in the Arctic (Culp et al., 2012; Danks, 1992). Exploring patterns of biodiversity in Arctic freshwater ecosystems is of increasing importance in a period of significant global climate change that has adverse effects at high latitudes (AMAP, 2017; Moss et al., 2009). The Arctic regions of Fennoscandia, covering the northern parts of Norway, Sweden, and Finland, have a large number of rivers that differ with regard to natural setting (Brittain et al., 2009; Tockner, Uehlinger, & Robinson, 2009), which is likely to influence their biodiversity (Heino, Muotka, Mykrä, et al., 2003; Tolonen et al., 2016). These regions are also subject to the impacts of climate warming and hydrological alterations, with repercussions for riverine biodiversity (Heino, Virkkala, & Toivonen, 2009; Mustonen et al., 2018).

Biodiversity can be decomposed into α , β , and γ components (Whittaker, 1960), where measures of β -diversity are particularly interesting because they comprise variation in community composition among sites (Anderson et al., 2011). Moreover, β -diversity can be partitioned into its replacement and richness difference components (Carvalho, Cardoso, & Gomes, 2012; Podani & Schmera, 2011), providing further insights into spatial variation in community composition (Legendre, 2014). For example, a large contribution of the replacement component to total β -diversity suggests that most of the variation in community composition is due to different species inhabiting different localities. By contrast, a high richness difference component suggests that variation in community composition is due to gain or loss of species owing to differences in species richness

among sites. The variation in the replacement and richness difference components of β -diversity has been rarely studied (see review by Legendre, 2014) in freshwater ecosystems (Heino, Alahuhta, Fattorini, & Schmera, 2019; Rocha et al., 2018), although it provides important information on the spatial variation of community composition and offers a suitable background for biodiversity assessment studies (Alahuhta et al., 2017; Cardoso, Rigal, & Carvalho, 2015; Legendre, 2014). Consequently, we analysed β -diversity and explored biodiversity patterns in rivers across Arctic Fennoscandia.

Currently, our knowledge of Arctic riverine biodiversity in terms of α -, β -, and γ -diversity in freshwater algae and benthic macroinvertebrates is lacking, with the exception of recent studies of such communities from northernmost Fennoscandia (Lindholm et al., 2018; de Mendoza et al., 2018; Tolonen, Leinonen, Erkinaro, & Heino, 2018; Tolonen, Leinonen, Marttila, Erkinaro, & Heino, 2017; Tolonen et al., 2016). However, all of the studies mentioned above were conducted within a single drainage basin, so broad-scale patterns and determinants of riverine biodiversity are not well understood across entire Arctic Fennoscandia. The existing studies on algae and benthic macroinvertebrates from northern regions, as well as many other regions of the world, suggest that: (1) different drainage basins support different taxon richness (Heino, Muotka, Mykrä, et al., 2003) and community composition (Heino, Soininen, Alahuhta, Lappalainen, & Virtanen, 2017); (2) climatic (e.g. mean annual temperature), catchment (e.g. catchment size, geology) and local environmental (e.g. pH, nutrients) factors all affect community structure (Pajunen, Luoto, & Soininen, 2016; Sandin, 2003); and (3) these patterns are mainly determined by species-specific responses to environmental variation (Alahuhta et al., 2017; Heino, Muotka, & Paavola, 2003; de Mendoza et al., 2018). Many of these studies spanned beyond Arctic Fennoscandia to more southerly boreal regions. Therefore, geographically targeted studies are required to guide biodiversity assessment, conservation planning, and bioassessment programmes in this large region of the Arctic (Vilmi et al., 2017).

The present study is part of the Arctic Council's Conservation of Arctic Fauna and Flora, Freshwater Group of the Circumpolar Biodiversity Monitoring Plan (CBMP-Freshwater) (Culp et al.,

2012). The CBMP is a step forward in increasing our knowledge of Arctic biodiversity as well as gathering existing data and analysing it in new contexts. However, at present, we have limited knowledge regarding which environmental conditions may be associated with variation of α - and β -diversity in Arctic rivers and, in particular, how global climate change might influence these patterns. Recent papers from the subarctic imply that temperature increases will be a major driver of fundamental ecosystem properties that could completely change biodiversity in high-latitude rivers in the future (Friberg, Bergfur, Rasmussen, & Sandin, 2013; O'Gorman et al., 2014).

In this study, we focused on benthic macroinvertebrates and diatoms because these are key groups in understanding structure and function of riverine ecosystems, covering multiple trophic levels and ecological roles (Allan & Castillo, 2007). Diatoms are regarded as the major food resource for macroinvertebrates at the base of the food web (Woodward et al., 2010; Woodward & Hildrew, 2002), which in turn link to higher trophic levels such as fish (Wallace & Webster, 1996). Furthermore, as both diatoms and macroinvertebrates are sensitive to environmental change, they are used as biological quality elements in the implementation of the European Water Framework Directive (EU, 2000), making them important in a management context (Friberg, 2014). More pragmatically, because of their use in the Water Framework Directive, existing data are available from a network of monitoring stations across Norway, Finland, and Sweden that can be used in the analysis of biodiversity patterns. We used these and other data sources to explore large-scale patterns in β -diversity, its replacement and richness difference components (Carvalho et al., 2012; Podani & Schmera, 2011), and the environmental correlates of community composition and α -diversity.

Our overall aim is to provide insights, from existing data, into biodiversity patterns in Arctic Fennoscandian rivers, in addition to supplying a basis for future spatially and temporally more extensive assessments than are feasible with the data accessible today. Specifically, we hypothesise that patterns in α - and β -biodiversity can be related both to: (1) location of the river, with the western part of the Fennoscandian peninsula being less species rich due to dispersal constraints and hence with a prominent degree of richness difference across the region; and (2) variation in environmental variables, from local to regional scales. We specifically expected that climatic conditions, especially temperature, the degree of continentality and major drainage basins would be strongly associated with spatial patterns in both taxonomic groups. We also expected that differences in species composition would be larger for macroinvertebrates than for diatoms and that diatom biodiversity would be more strongly related to local environmental filters than that of macroinvertebrates. This is because diatoms may disperse relatively freely and passively across large distance, whereas macroinvertebrates are expected to be more dispersal limited owing to differences in propagule size and dispersal modes (Heino, Melo, Siqueira, et al., 2015; Kristiansen, 1996). Furthermore, we aimed to demonstrate the scope and advantages

of using different components of β -diversity (Carvalho et al., 2012; Podani & Schmera, 2011), both in the Arctic and other regions, in the analysis of spatial freshwater community data in order to promote use of this approach among scientists and managers (Heino et al., 2020).

2 | METHODS

2.1 | Study area

The focus of this analysis was rivers in the most northerly part of the Fennoscandian region, north of the Arctic Circle. This area is bordered in the west by the Norwegian Sea, in the north by the Barents Sea and in the east by the Russian Federation (Figure 1). The Baltic Sea is located in the southeast of the region. Thus, the rivers of the region drain to these three different seas. The land area is in the low Arctic and dominated by boreal forest, an extension of the taiga forests that stretch all the way to the Pacific Ocean in the east. However, at the northern extremities and at higher altitudes, the forests give way to Arctic tundra. Much of the region, especially in the east, consists of a mosaic of rivers, lakes, and wetlands (Brittain et al., 2009).

2.2 | Data collection and site selection

Biological data and local environmental variables, collected from national monitoring databases, scientific papers, reports, and institute databases, were formatted and entered into a database established by the CBMP-Freshwater within the scope of the Arctic Freshwater Biodiversity Monitoring Plan (Culp et al., 2012). Restrictions apply to the availability of these data. For the present analysis, relevant data on Fennoscandian (Norway, Sweden, and Finland) rivers north of the Arctic Circle were extracted. The analysis was limited to medium to large rivers, with catchment areas greater than 100 km². The selection of medium to large rivers was based on their spatial importance and making data sets consistent between the three countries, whereby relatively large differences were found in the database regarding the number of monitoring stations and the stream sizes sampled. Both Sweden and Finland had more extensive monitoring data sets than Norway but consisted primarily of small streams. However, these smaller streams were excluded as their inclusion would have introduced a spatial bias in the analyses because of the uneven distribution of stream sizes sampled across the region. For sites closer than 5 km in the same river, only one of the sites was included in the dataset to ensure site independence. The site furthest from other stations in the same river was chosen, although if only two sites close together were on the same river, the one with the most environmental variables was selected. The final dataset comprised 79 sites for benthic macroinvertebrates and 36 sites for diatoms, distributed across Arctic Fennoscandia (Figure 1).

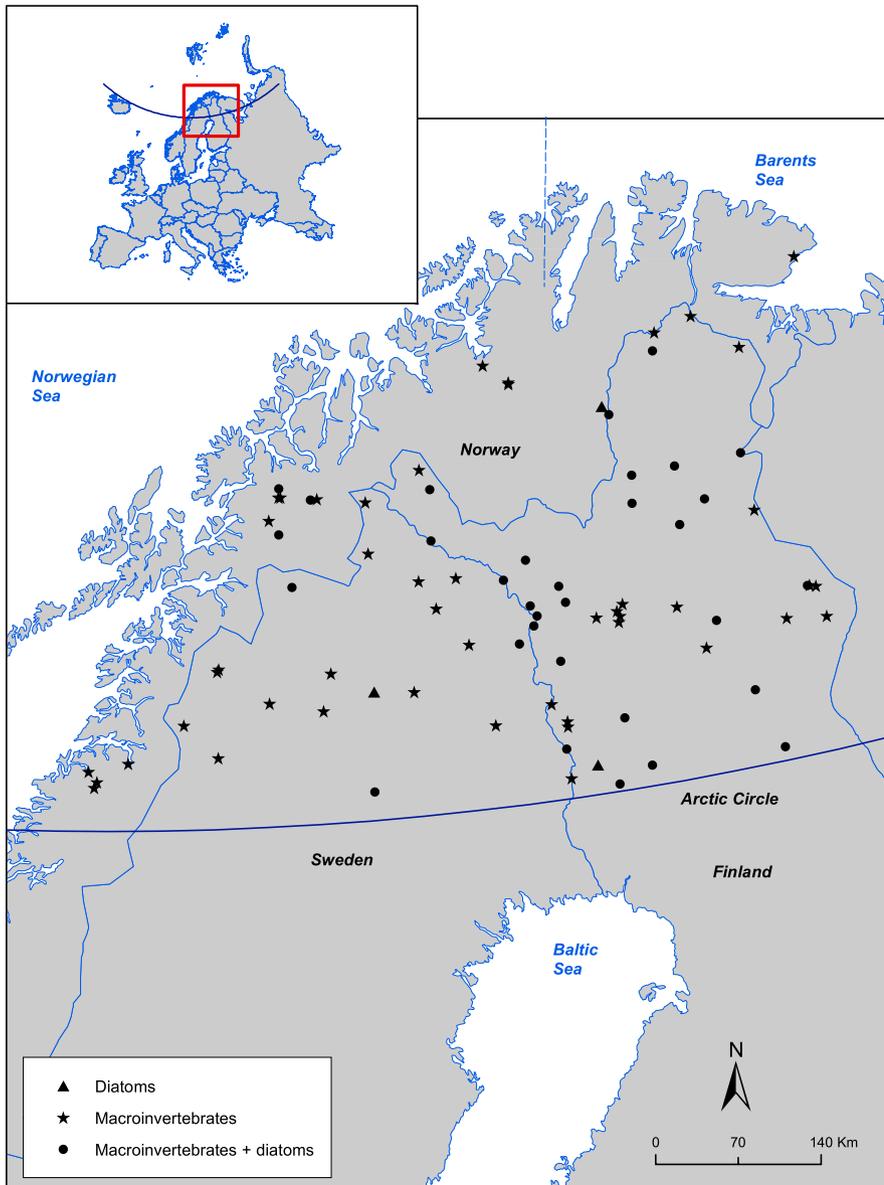


FIGURE 1 Map of the macroinvertebrate and diatom sampling sites across northern Fennoscandia

Time series data for diatoms were not available for the selected sample sites, as all sites with diatom data were only sampled once. The years in which sites were sampled for diatoms differed somewhat between countries. Diatom sites in Finland were sampled between 2006 and 2013, whereas sites in Sweden were all sampled in 2011. Diatom sites in Norway were sampled in 1980 (two sites) and 1989–1990 (two sites).

Benthic macroinvertebrate sites in the database included some re-sampling, but only three sites had data for more than 3 years (sites in Sweden sampled for 6–9 years), and there was thus insufficient data to allow analysis of temporal trends across Fennoscandia. Benthic macroinvertebrate sites in Finland were sampled only once, with most sites sampled between 2004 and 2011 and two sites sampled in 1998. The majority of sites in Sweden were sampled in both 1995 and 2000, though one site was sampled over 3 years (2013–2015) and three sites were sampled over the period from 2007 to 2012 or 2015. For each site, a single sample date was chosen for

analysis based on the availability of accompanying environmental data. Benthic macroinvertebrate sites in Norway were sampled once or twice, and the timing of sampling was more variable than for Finland or Sweden. Norwegian benthic macroinvertebrate data included data from 1974–1976 (5 sites), 1984 (5 sites), and 2004–2008 (5 sites); where re-sampling occurred, the date with the greatest amount of accompanying environmental data was chosen.

Although some samples from Norway were collected much earlier than samples from Finland or Sweden, their inclusion was necessary to maximise the spatial coverage of the data. Broad-scale river monitoring data from across the circumpolar regions typically include 2–3 decades of surveying due to the high cost and difficulties involved in accessing remote locations, and such samples have been analysed in spatial contexts to maximise the number of regions that can be considered (Izaguirre et al., 2016; Lento et al., 2022). In addition, Huttunen et al. (2012) demonstrated the temporal stability of benthic macroinvertebrate assemblages across northern

Fennoscandian streams (66–67°N) among years, indicating that data could be merged across years. In contrast, inter-annual variation in environmental conditions is much greater in high Arctic areas (e.g. Docherty et al., 2018) compared to the low Arctic of northern Fennoscandia (e.g. Huttunen et al. 2012). Although some caution should be used in the interpretation of spatial patterns, as they may reflect some temporal differences underlying the data from Norway, these data provide an important baseline for assessing patterns of diversity across the Fennoscandian Arctic.

2.3 | Field sampling and laboratory methods

Diatom sample collection and processing were generally consistent across datasets. Diatoms were brushed from the surface of five to 10 cobbles, pooled into one sample and preserved in ethanol or formalin at the sampling site. Samples were treated with hydrogen peroxide or strong acid solution ($\text{HNO}_3 + \text{H}_2\text{SO}_4$; 2:1) for cleaning the frustules. Diatoms were identified to species level with DIC-equipped light microscope at 1,000× magnification level. Older samples from Norway (1980, 1989, and 1990) were re-analysed to ensure that appropriate magnification and identification procedures were used.

Benthic macroinvertebrate sampling procedures were similar and comparable among datasets. For benthic macroinvertebrates, a total of 2- to 3-min of kick-net samples were taken at each river site, with the exact field sampling method varying slightly between the countries (see Heino, Muotka, Mykrä, et al., 2003; Sandin, 2003). However, a similar sampling effort (see above) and a net mesh size of either 250 or 450 μm were employed. Fennoscandian studies in connection with calibration for monitoring for the EU Water Framework Directive have demonstrated that there is no difference in taxa recorded by such differences in sampling methods (Friberg et al., 2006; Johnson et al., 2001). The macroinvertebrate samples were preserved in 70% ethanol in the field, sorted in the laboratory, and identified to the lowest possible taxonomic level, usually species or genus. Identification was undertaken using national lists and keys, as well as the identification keys listed in Nilsson (1996, 1997). The more recent data was sampled and processed according to the European Water Framework Directive protocols.

Earlier data for both diatoms and macroinvertebrates were harmonised to be consistent with present-day taxonomy, and taxonomic resolution was harmonised to species-level data for diatoms. The harmonised nomenclature included species complexes to account for ambiguous identification and mixed-level taxonomy (see Kahlert et al., 2022 for details). Benthic macroinvertebrate data were harmonised to species or genus level. It should be noted that many of the Fennoscandian Ephemeroptera, Plecoptera, and Trichoptera (EPT) genera have only a single species. Chironomidae and Oligochaeta were excluded from the dataset, as they were usually not identified to genus or species in bioassessment studies and were only counted in a subset of Finnish rivers. Thus, exclusion of these groups increased spatial coverage of sites in Finland with only

minor loss of information. Further, our analysis considers northern Fennoscandia, which although north of the Arctic Circle, is a region of boreal and subarctic forests. In this region, EPT taxa are both numerous and diverse at genus and family levels (Brittain et al., 2009; Huttunen et al. 2012; Kärnä et al., 2015), unlike for example glacier and snowmelt dominated systems on Svalbard and Greenland (Blaen, Brown, Hannah, & Milner, 2014; Docherty et al., 2018; Milner, Brittain, Castella, & Petts, 2001) where Chironomidae are the dominant benthic invertebrates. Thus, our analysis considers a substantial part of macroinvertebrate diversity in these northern rivers.

2.4 | Environmental and spatial data

Environmental data consisted of water chemistry and catchment variables (total P, total N, pH and conductivity, catchment area, and four geological types: % igneous, % extrusive, % sedimentary, and % supracrustal, denoted **ENV** in the following subsection), climatic variables (mean annual air temperature, *SD* of annual temperature, mean July air temperature, mean August air temperature, mean annual precipitation, and coefficient of variation of annual precipitation denoted **CLI**), and geographical variables (altitude, latitude and longitude denoted **GEO** in the following subsection). Catchment based climatic variables were derived from WorldClim (<http://www.worldclim.org/>). We also included a dummy variable denoting region identity (**REG**). We did not use more complex spatial variables, for example, those derived from using Moran eigenvector maps (Dray et al., 2012; Legendre & Legendre, 2012) because, for simplicity, we were only interested in linear geographical and altitudinal gradients. In addition, the use of such methods may not be ideal if there are large spatial gaps between groups of sampling points (see also Declerck, Coronel, Legendre, & Brendonck, 2011), as was the case in our survey data (Figure 1).

2.5 | Statistical methods

There are basically two main approaches to decompose total β -diversity into two components. The first focuses on the turnover and nestedness components (Baselga, 2010), and the second refers to the replacement and richness differences components (Carvalho et al., 2012; Podani & Schmera, 2011). In these two approaches, *richness difference* refers to the fact that one community may harbour a larger number of species than another, whereas *nestedness* is a type of richness difference pattern shown by the species at a site being a strict subset of the species at a richer site (Legendre, 2014). Legendre (2014) provided a clear example of these differences: “In a comparison of two sites, richness difference can be interpreted as nestedness *sensu stricto* only if the sites have a species in common, with $a > 0$, and they differ in other species, one site being richer than the other. When $a = 0$, the richness difference between two sampling units cannot be interpreted as nestedness, which is logically 0 in that situation

(Carvalho et al., 2012; Podani & Schmera, 2011). In that case, the difference in species composition measured by dissimilarity indices is equal to species replacement plus richness difference, without reference to ecological processes producing nestedness.” In this study, we focused on the replacement and richness difference components for two reasons: (1) we were interested in all kinds of richness differences between sites and not only nestedness; and (2) the observed nestedness component has been usually shown to be very small (Soininen, Heino, & Wang, 2018) and in freshwater datasets in particular (Heino & Tolonen, 2017; Hill, Heino, Thornhill, Ryves, & Wood, 2017), partly hindering the usefulness to model such small differences in nestedness between ecological communities. However, both approaches are useful in different situations and complementary in the analyses of ecological communities (Legendre, 2014).

First, we calculated three β -diversity indices (or components) for macroinvertebrates and diatoms based on Sørensen coefficient following the approach devised by Podani and Schmera (2011) and Carvalho et al. (2012). In this approach, total β -diversity is decomposed into replacement and richness difference components: $B_{total} = B_{repl} + B_{rich}$. B_{total} reflects both species replacement and loss-gain; B_{repl} refers to replacement of species identities alone; and B_{rich} relates to species loss-gain or richness differences alone. A recent review found this decomposition a suitable approach for addressing complex issues in β -diversity (Legendre, 2014). We calculated dissimilarities among multiple sites using the function *beta.multi*, and produced site-by-site dissimilarity matrices based on species presence-absence data using the function *beta* in the R package BAT (Cardoso et al., 2015). Each of the resulting site-by-site dissimilarity matrices was used as response data in permutational multivariate analysis of variance using distance matrices (PERMANOVA; Anderson, 2001), Multivariate homogeneity of group dispersions (PERMDISP; Anderson, 2006) and distance-based redundancy analysis (dbRDA; Legendre & Anderson, 1999). PERMANOVA was used to examine differences in community composition between rivers flowing into the three different marine drainage basins in the study area (Norwegian Sea, Baltic Sea, and Barents Sea) with available data. PERMANOVA tests were run using the function *adonis* in the R package *vegan* (Oksanen et al., 2017). We used PERMDISP to examine differences in average distances of riverine communities to group multivariate centroids (median) among the three drainage basins. This analysis thus examines differences in β -diversity among the drainage basins, and it was run using the *betadisper* function in the R package *vegan*. We used dbRDA-based forward selection to select the final local and catchment environmental (ENV), climatic variables (CLI), latitude, longitude, and altitude (GEO) and dummy variable region identity (REG), for the models of each biological dissimilarity matrix using the functions *capscale* and *ordiR2step* in the R package *vegan* (Table S1). In this case, the ENV and CLI variable selection processes were based on the two stopping rules as explained in Blanchet, Legendre, and Borcard (2008), whereas GEO and REG were forced in all analyses to detect geographical patterns. After the final sets of variables for each predictor variable group were selected, we proceeded

with partitioning variation in each dissimilarity matrix (Y) using ENV, CLI, GEO, and REG as predictor variables using the function *varpart* in the R package *vegan*. In all dbRDA-related analyses, a square root transformation of dissimilarities ($\text{sqrt.dist} = \text{TRUE}$) was added in the R script to *euclidify* biological dissimilarities (Legendre, 2014). Presence-absence data were used in all analyses to eliminate any bias that might be introduced by differences in sampling effort that could affect abundance data. We also used a similar variable selection and variation partitioning approach as described above to examine the effects of ENV, CLI, GEO, and REG on variation in α -diversity (taxonomic richness) across the sites. This analysis was based on partial linear regression and was also conducted using the function *varpart* in the R package *vegan*. For α -diversity, we also tested for significant differences in taxonomic richness between drainage basins using analysis of variance (ANOVA).

Finally, in order to examine whether there were significant differences in single macroinvertebrate and diatom indicator taxa between different marine drainage basins (Norwegian Sea, Baltic Sea, and Barents Sea), we conducted an indicator value analysis (Dufrene & Legendre, 1997). *IndVal* combines a species mean abundance and frequency of occurrence (in our case) in each group. A high indicator value exists when a species occurs in most sites (fidelity) belonging to a group. The indicator value ranges from 0 to 1, with 1 referring to a perfect indicator taxon. *IndVal* was run using the function *indval* in the R package *labdsv* (Roberts, 2016).

3 | RESULTS

A total of 278 diatom taxa and 124 macroinvertebrate taxa were present in the dataset. The occurrence of the individual taxa ranged from presence at only a single site to being recorded widely across northern Fennoscandia. The most common taxa of diatom, recorded at 83–97% of sites, respectively, were *Fragilaria tenera* complex, *Rossethidium pusillum anastasiae*, *Tabellaria flocculosa* complex, *Fragilaria capucina* complex, and *Achnantheidium minutissimum* (Table S2). The most common genera of macroinvertebrate, recorded at 73–96% of sites, respectively, were *Diura*, *Rhyacophila*, *Heptagenia*, *Ephemera*, and *Baetis* (Table S2).

3.1 | Macroinvertebrate β - and α -diversity

For total β -diversity, the multiple site dissimilarity value was 0.561, with the richness difference component (value: 0.316) being somewhat more important than the replacement (value: 0.245) component.

We did not find significant differences in β -diversity between the three main drainage basins (i.e. Norwegian Sea, Baltic Sea, and Barents Sea; PERMDISP; $p > 0.700$ Figure 2), but mean differences in community composition were significantly different between drainage basins for total β -diversity (PERMANOVA, $p = 0.001$) and the richness difference component (PERMANOVA, $p = 0.001$). The

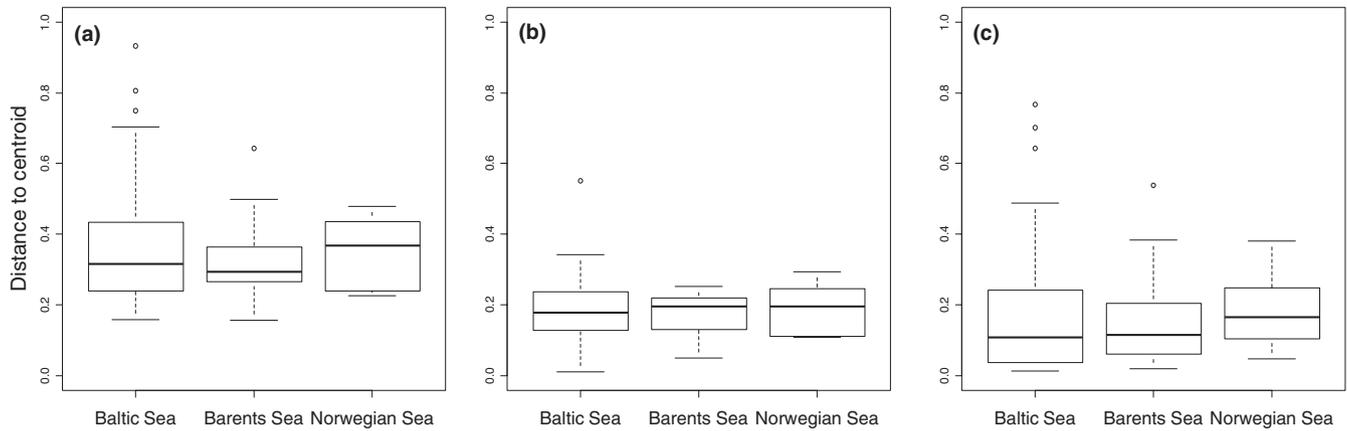


FIGURE 2 Boxplots of median distance to centroid for (a) total β -diversity (Sørensen), (b) the replacement component, and (c) richness difference component for each region in the macroinvertebrate data. The line within the box represents the median, the ends of the box show the upper and lower quartiles, the extreme line shows the highest and lowest value excluding outliers, and dots show potential outliers

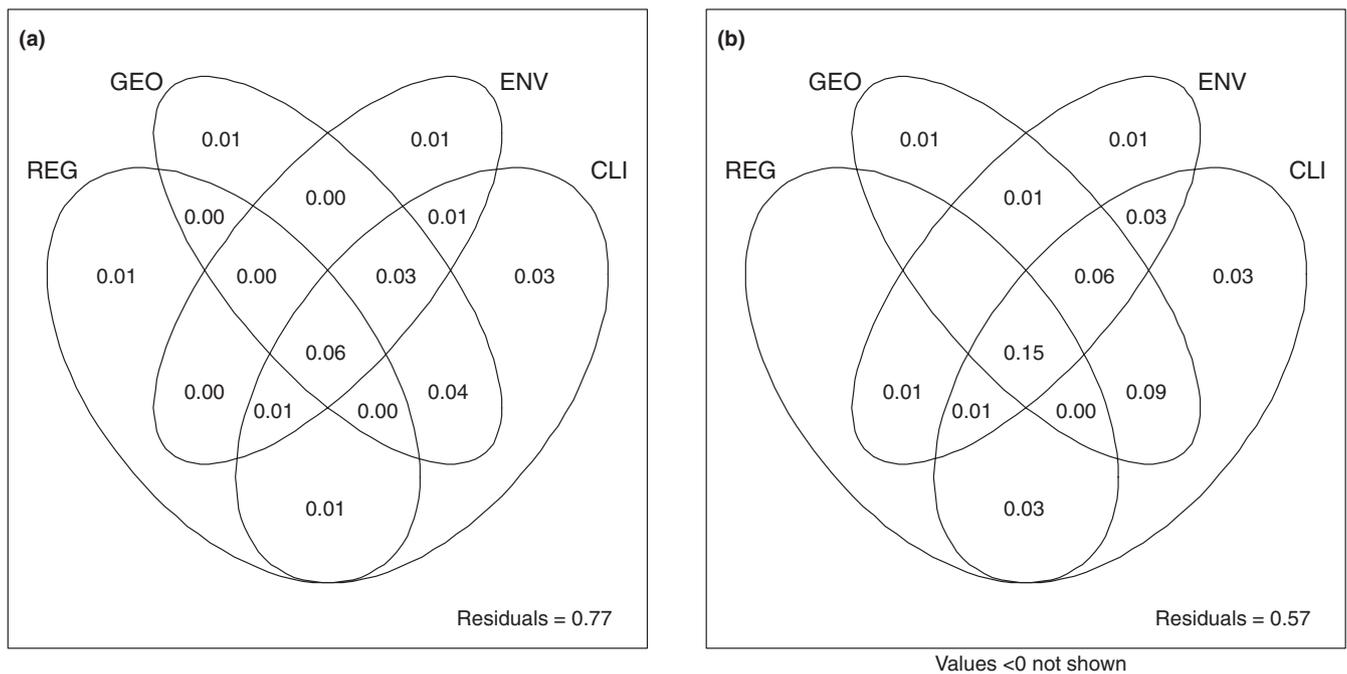


FIGURE 3 Venn diagrams of variation partitioning of macroinvertebrate community composition based on total dissimilarity as response (a) and the richness difference component as response (b). ENV = local and catchment environmental variables; CLI = climate variables; GEO = latitude, longitude, and altitude; REG = region identity. Numbers in the diagrams are adjusted r^2 values

replacement component did not vary significantly between the drainage basins (PERMANOVA, $p = 0.257$).

Constrained ordination through dbRDA showed that slightly different sets of ENV and CLI were selected in the models. For total β -diversity these included, in order of importance, sedimentary geology, total phosphorus, total nitrogen, and catchment area (ENV), as well as annual SD of temperature, annual mean temperature, annual mean precipitation, July mean temperature, and annual coefficient of variation of precipitation (CLI). For the richness difference component, these comprised total phosphorus, sedimentary geology, and total nitrogen (ENV), as well as temperature annual SD, temperature annual mean and July mean temperature (CLI). For the replacement

component, no significant ENV or CLI variables entered the dbRDA models. Variation partitioning showed that, for total β -diversity, most variation was shared between ENV, CLI, GEO, and REG, and that CLI had the most important unique effect on total β -diversity. The richness difference component was similarly mostly explained by the shared fraction between the four predictor variable groups, again with CLI having the most important unique influence on community variation based on this component of β -diversity (Figure 3).

We found significant differences in α -diversity (taxonomic richness) between the main drainage basins (ANOVA; $p < 0.001$), with Norwegian Sea region differing significantly from the Baltic Sea and Barents Sea drainage basins (Figure 4, Figure S1a). Forward

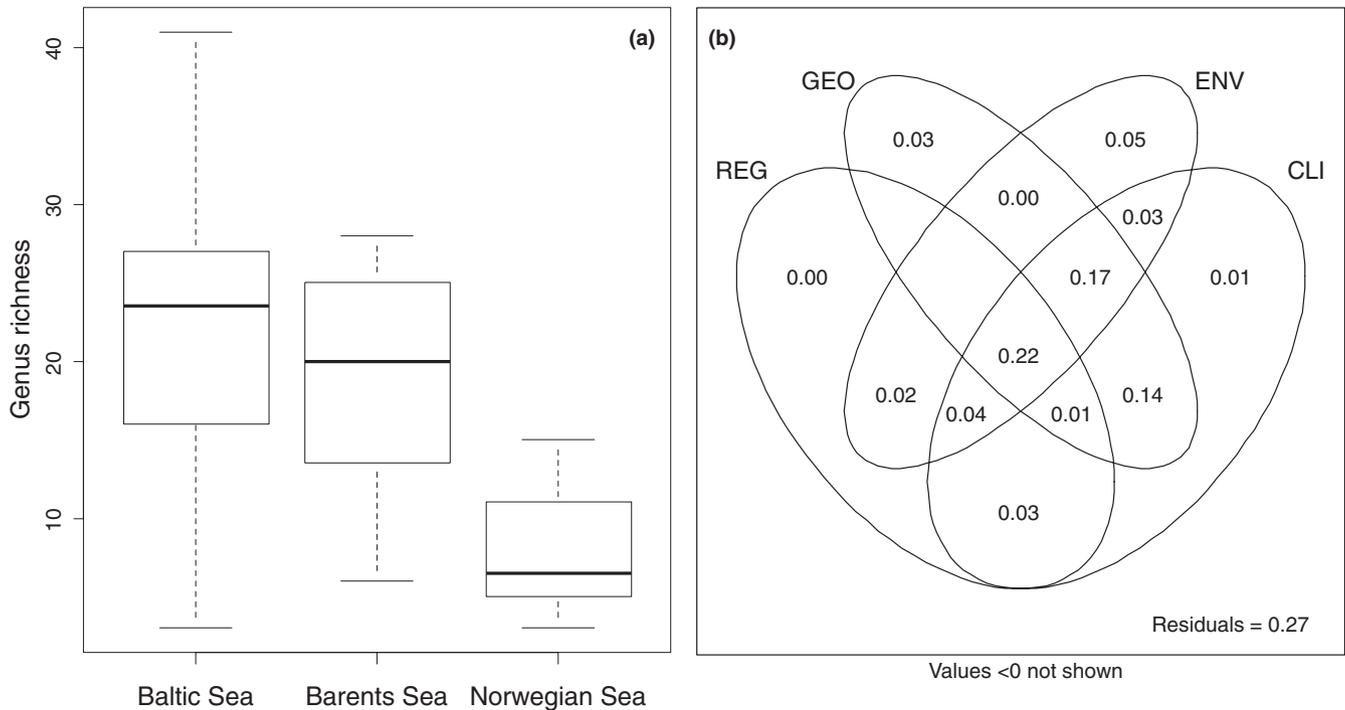


FIGURE 4 A boxplot showing differences in macroinvertebrate genus richness between the three regions (a). Also shown is a Venn diagram of variation partitioning of genus richness as response variable (b). ENV = local and catchment environmental variables; CLI = climate variables; GEO = latitude, longitude, and altitude; REG = region identity. Numbers in (b) are Adjusted r^2 values

selection of ENV and CLI explanatory variables in the regression analysis showed that the ENV variables, sedimentary geology, total phosphorus, and total nitrogen, as well as the CLI variables August mean temperature and July mean temperature were selected in the models. Partial linear regression showed that most of the variation in α -diversity was explained by the shared fractions among two or more explanatory variable groups, and only the unique GEO and ENV components were recognisable. This model explained a considerable share of variation in α -diversity (adj. $r^2 = 0.73$).

We detected 16 significant macroinvertebrate indicator taxa for the main drainage basins in this study (Table 1). Eight taxa were significant indicators for the Baltic Sea drainage basin, six taxa for the Barents Sea drainage basin and two taxa for the Norwegian Sea drainage basin.

3.2 | Diatom β - and α -diversity

Total multiple site β -diversity value was 0.617, with the replacement component (value: 0.405) being clearly more important than the richness difference component (value: 0.212).

We did not find significant differences in β -diversity between the main drainage basins (i.e. Norwegian Sea, Baltic Sea, and Barents Sea; PERMDISP; all $p > 0.20$, Figure 5), but average differences in community composition were significant between the drainage basins based on total β -diversity and the richness difference component (PERMANOVA, all $p < 0.034$).

TABLE 1 Results of Indval analysis for macroinvertebrates

	Baltic Sea	Barents Sea	Norwegian Sea	p -value
<i>Acentrella lapponica</i>	0.000	0.007	0.512	0.001
<i>Agapetus ochripes</i>	0.280	0.000	0.000	0.011
<i>Alainites muticus</i>	0.229	0.422	0.000	0.005
<i>Asellus aquaticus</i>	0.320	0.000	0.000	0.005
<i>Brachyptera risi</i>	0.000	0.000	0.143	0.023
<i>Capnopsis schilleri</i>	0.082	0.308	0.000	0.019
<i>Centroptilium luteolum</i>	0.013	0.333	0.000	0.003
<i>Elmis aenea</i>	0.409	0.269	0.000	0.009
<i>Leuctra</i> spp.	0.216	0.360	0.072	0.040
<i>Limnius volckmari</i>	0.421	0.008	0.000	0.003
<i>Micrasema</i> spp.	0.441	0.008	0.000	0.002
<i>Nemoura</i> spp.	0.228	0.348	0.004	0.030
<i>Oulimnius tuberculatus</i>	0.365	0.238	0.000	0.026
<i>Rhyacophila</i> spp.	0.408	0.283	0.043	0.009
<i>Sericostoma personatum</i>	0.323	0.010	0.000	0.006
<i>Taeniopteryx nebulosa</i>	0.340	0.399	0.024	0.013

Note: The significant ($p < 0.05$) indicator values for a drainage basin are in bold font. Indicator values range from 0 to 1.

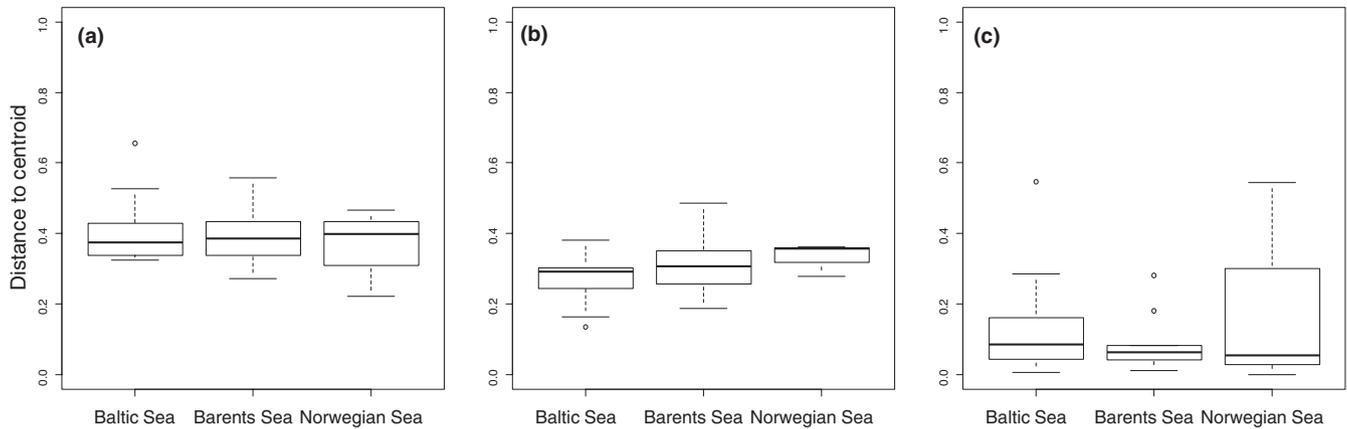


FIGURE 5 Boxplots of median distance to centroid for (a) total β -diversity (Sørensen), (b) the replacement component, and (c) richness difference component for each region in the diatom data. The line within the box represents the median, the ends of the box show the upper and lower quartiles, the extreme line shows the highest and lowest value excluding outliers, and dots show potential outliers

Constrained ordination through dbrDA showed that slightly different sets of ENV and CLI variables were selected in the diatom models. For total β -diversity, these included sedimentary geology and total phosphorus (ENV), as well as annual SD of temperature and annual mean precipitation (CLI). For the richness difference component, these comprised pH (ENV), as well as annual SD of temperature (CLI). For the replacement component, no significant ENV and CLI variables entered the dbrDA models. Variation partitioning showed that, for total β -diversity, most variation was shared among ENV, CLI, GEO, and REG. The richness difference component was similarly explained by the shared fractions between two or more predictor variable groups, although CLI had the greatest unique

influence on community variation based on this component of β -diversity (Figure 6).

There were significant differences in α -diversity (taxonomic richness) of diatoms between the main drainage basins (ANOVA; $p < 0.001$), with Norwegian Sea drainage differing significantly from Baltic Sea and Barents Sea drainage basins (Figure 7, Figure S1b). Forward selection of ENV and CLI explanatory variables in regression analysis showed that the ENV variable pH, as well as the CLI variable annual SD of temperature were selected in the models (Table 2). Partial linear regression showed that most of the variation in α -diversity was explained by the shared fractions among two or more explanatory variable

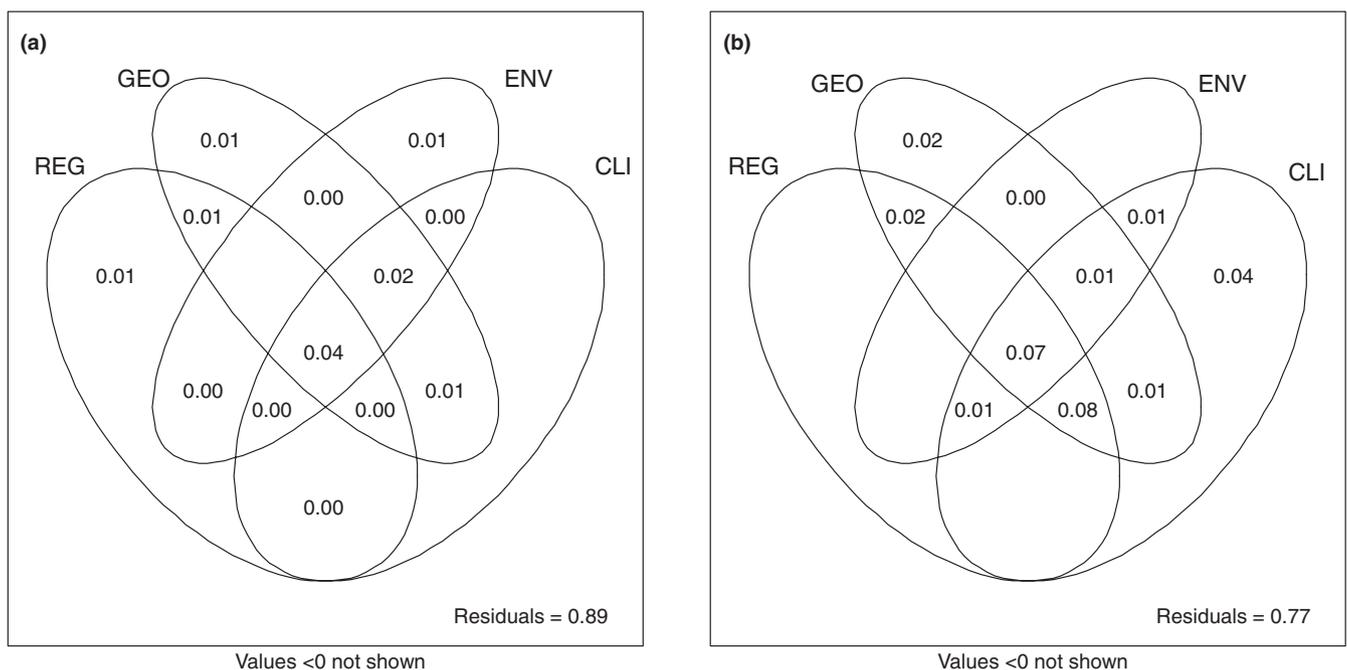


FIGURE 6 Venn diagrams of variation partitioning of diatom community composition based on total dissimilarity as response (a) and the richness difference component as response (b). ENV = local and catchment environmental variables; CLI = climate variables; GEO = latitude, longitude, and altitude; REG = region identity. Numbers in the diagrams are adjusted r^2 values

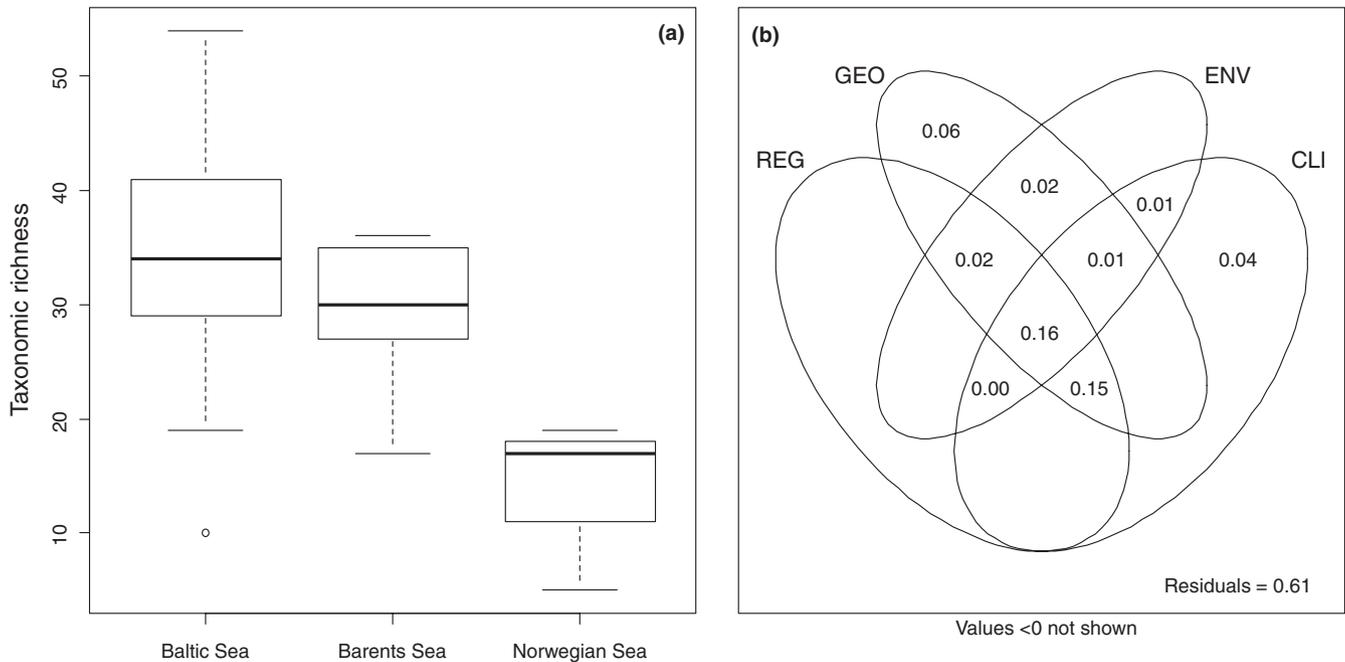


FIGURE 7 A boxplot showing differences in diatom taxonomic richness between the three regions (a). Also shown is a Venn diagram of variation partitioning of taxonomic richness as response variable (b). ENV = local and catchment environmental variables; CLI = climate variables; GEO = latitude, longitude, and altitude; REG = region identity. Numbers in (b) are Adjusted r^2 values

TABLE 2 Results of Indval analysis for diatoms

	Baltic Sea	Barents Sea	Norwegian Sea	<i>p</i> -value
<i>Didymosphenia geminata</i>	0.013	0.030	0.752	0.010
<i>Encyonopsis cesatii</i>	0.000	0.400	0.000	0.047
<i>Eunotia implicata</i> complex	0.479	0.252	0.000	0.010
<i>Fragilaria tenera</i> complex	0.460	0.447	0.000	0.017
<i>Nitzschia perminuta</i> complex	0.565	0.000	0.000	0.027
<i>Tabellaria flocculosa</i> complex	0.400	0.437	0.049	0.020
<i>Ulnaria ulna</i> var. <i>acus</i>	0.009	0.012	0.521	0.026

Note: The significant ($p < 0.05$) indicator values for a drainage basin are in bold font.

groups, and only the unique GEO and CLI effects were of particular importance.

We found seven significant diatom indicator taxa for the different drainage basins (Table 2). Three taxa were significant indicators for the Baltic Sea drainage basin, two taxa for the Barents Sea drainage basin and two for the Norwegian Sea drainage basin.

4 | DISCUSSION

Climate variables were overall the most important correlates of biodiversity patterns in Arctic rivers of Fennoscandia, both for macroinvertebrates and for diatoms. This is consistent with a number of studies showing the importance of climatic variables for high latitude rivers such as precipitation patterns, hydrology and water temperature (Blaen et al., 2014; Friberg et al., 2013; Mustonen et al., 2018; O'Gorman et al., 2014). With regard to macroinvertebrates in our study, climate variables relating to temperature, in particular mean July temperature, had the most important effect on β -diversity, whereas there was a less strong signal for α -diversity. In support of these findings, it has previously been shown that temperature is an important driver of β -diversity in high latitude rivers (Friberg et al., 2013).

For both macroinvertebrates and diatoms, the replacement and richness difference components showed much variation. The richness difference component was more important than the replacement component in macroinvertebrates, whereas the opposite was true in diatoms. However, the replacement component did not show significant relationships with the ENV and CLI variables in either organism group. Instead, the richness difference component was similarly explained by the shared fractions between two or more predictor variable groups, and that CLI had the most important influence on community variation based on this component of β -diversity. It thus appears that climate has an influence on richness differences between sites. This finding is in agreement with studies that have shown variation in boreal macroinvertebrate and diatom communities to be relatively strongly related with climatic and environmental

variables (Mustonen et al., 2018; Pajunen et al., 2016). These findings also suggest that Arctic riverine biodiversity is potentially highly sensitive to climate change (Heino et al., 2009; Moss et al., 2009).

More specifically, the community composition of macroinvertebrates varied mostly along the standard deviation of mean annual temperature, sedimentary geology, altitude, and longitude. Temperature has been shown to be a crucial factor in the ecology of freshwater insects, regulating growth, emergence, and life cycle length as well as distributional range of individual species (Brittain, 1990; Lillehammer, Brittain, Saltveit, & Nielsen, 1989; Schneider & Petrin, 2017; Vannote & Sweeney, 1980; Ward, 1992), and this is clearly also the case in the rivers of northern Fennoscandia. In particular, there is a gradient from the continental areas of northern Fennoscandia to the western coastal areas with an oceanic climate. This is expressed in the standard deviation of mean annual temperature, whereby the temperature amplitude is greater in the continental areas, with cold winters and warm summers, compared to the oceanic areas. Ward and Stanford (1982) stressed that an increase in species diversity is usually associated with a wide annual temperature range, while Vannote and Sweeney (1980) put forward the hypothesis that stream biotic biodiversity closely parallels that of the diel thermal maxima along the stream profile. This biodiversity gradient, from continental to oceanic climates, was well documented for stoneflies (Plecoptera) by Lillehammer (1985) and correlates well with longitude across northern Fennoscandia, as well as with the rivers flowing into the Norwegian Sea, the Barents Sea, and the Baltic Sea. In the oceanic areas, ubiquitous species such as *Baetis rhodani* (Ephemeroptera), *Nemoura cinerea* (Plecoptera), and *Polycentropus flavomaculatus* (Trichoptera) dominate, whereas the rarer, possibly more specialised species, are restricted to the more continental areas (Aagaard & Dolmen, 1996; Walseng & Huru, 1997). This is reinforced by the indicator species analysis for macroinvertebrates with all indicator taxa, with the exception of *Acentrella lapponica* and *Brachyptera risi*, are significant for either the Barents Sea or the Baltic Sea. It may be argued that dispersal of macroinvertebrates to northern Fennoscandia from the south and the east after the last Ice Age is still not complete and that biodiversity is thus lower in the rivers draining to the Norwegian Sea. This post-glacial dispersal westwards was hampered by the barrier formed by the mountain chain and the catchment divide along the Swedish-Norwegian border. For example, the stonefly *Brachyptera risi* and the mayfly *Acentrella lapponica* were the only two significant indicator species for rivers draining to the Norwegian Sea. Of these species, *Brachyptera risi* is widespread in Europe, but is primarily a western species and has spread to Fennoscandia from the south-west and is absent from southern Finland (Lillehammer, 1988). The mayfly *Acentrella lapponica*, an arctic-alpine species, has also spread from the south along the Scandinavian mountain chain.

Temperature also plays a major role with regard to altitude, and there are many classical studies of altitudinal gradients in the distribution of freshwater insects (Jacobsen, 2004; Ormerod et al., 1994; Ward, 1982). In addition, sedimentary geology provides higher ionic concentrations and is likely to result in increased biomass

and productivity as well as buffering against possible acidification. Certain areas of northern Fennoscandia have been affected by acidification, primarily from metal smelters in neighbouring parts of Russia (Lappalainen, Tammi, & Puro-Tahvanainen, 2007). Such negative effects of acidification may thus be partly seen in the influence of sedimentary geology on macroinvertebrate communities.

For diatoms, the species composition in terms of the richness difference component and taxon richness varied mostly with regard to sedimentary geology, pH, total phosphorus (ENV), geographical position (GEO), and standard deviation of mean annual temperature (CLI), of which geographic and climatic variables had the strongest unique influences on diatom biodiversity. As already mentioned for macroinvertebrates, the effects of sedimentary geology may be associated with increased productivity and decreased sensitivity to acidification as a result of alkalinity and minimum pH, both of which might influence diatom community composition and be related to increased taxon richness (Rantala, Luoto, Weckström, Rautio, & Nevalainen, 2017; Schneider & Petrin, 2017; Soininen, 2007). Geographical location and climatic variables are likely to portray macroclimatic effects on diatom distributions, corroborating previous findings from more southerly Fennoscandia (Pajunen et al., 2016). At this broad scale across Arctic Fennoscandia, our results suggested that the correlates of biodiversity are relatively similar between diatoms and macroinvertebrates, although there are some minor differences in the relative strength of different predictor variables.

Our constrained ordination models showed that only a relatively small part of biological variation was explained by the predictor variable groups included. Such rather low effect sizes (i.e. adjusted r^2 values) are highly typical in analyses of community composition data (Beisner, Peres-Neto, Lindström, Barnett, & Longhi, 2006; Peres-Neto, Legendre, Dray, & Borcard, 2006). For example, a number of previous studies that were based on constrained ordination and adjusted r^2 values have ended up in similar conclusions (Alahuhta et al., 2018; Heino, Melo, Bini, et al., 2015). However, such low adjusted r^2 values are still meaningful and, actually, they point out the fact that explaining variation in community composition is extremely challenging (see also Low-Décarie, Chivers, & Granados, 2014).

Arctic rivers are subject to several impacts that threaten their biodiversity (Heino et al., 2020), and that may also explain the unexplained variation or be associated with our selected predictor variables. These include long-range transboundary pollutants, exotic species, hydropower development, and increased investments in mining. Long-range transport of pollutants (AMAP, 2009) combined with the low nutrient status of many Arctic ecosystems makes them especially vulnerable to the uptake and effect of contaminants as well as the influence of increased nutrient enrichment. The introduction of exotic species and pathogens has also the potential to modify ecosystem structure and lead to species extinction. The regulation of rivers for hydropower, through changes in flow and temperature, has been documented to have wide-ranging consequences for the aquatic flora and fauna (Brittain & Saltveit, 1989; Koksvisik & Reinertsen, 2008; Saltveit, Brittain, & Lillehammer, 1987; Schneider & Petrin, 2017).

Our results provide tentative ideas for protecting and assessing biodiversity in Arctic areas. For example, we were able to distinguish the main correlates of both β - and α -diversity across northern Fennoscandia, which also suggested that different drainage basins (Baltic Sea, Barents Sea, and Norwegian Sea) harbour significantly different riverine communities and different levels of α -diversity. This regional gradient coincides with strong gradients in actual climatic conditions and potential post-glacial dispersal routes (see above), implying that conservation and protection stratified by region delineations could be a suitable starting point for more sophisticated conservation planning and bioassessment programmes (Heino, Muotka, Mykrä, et al., 2003; Sandin, 2003). However, within each region, there is considerable variation in community composition (or β -diversity based on the replacement and richness difference components), suggesting that many stream reaches or even catchments should be conserved within each region to protect wholesale riverine biodiversity, a notion supported by the study of Göthe, Friberg, Kahlert, Temnerud, and Sandin (2014) in mid-latitude headwater streams in Sweden. Thus, conservation plans must consider biodiversity variation at multiple spatial scales. This is because focussing on a single region only ignores variation in another region and because inclusion of too few sites results in an inadequate preservation of community compositional variation along environmental gradients. It was also notable that the main spatial patterns were relatively similar between macroinvertebrates and diatoms, yet the specific responses of these two organism groups to localised environmental variation should be carefully considered in conservation planning and bioassessment of Arctic rivers (Lindholm et al., 2018; Tolonen et al., 2016). For example, different sites might be needed to conserve macroinvertebrate and diatom biodiversity, although the discrepancies in the responses of the two organism groups to local environmental variables may also stem from the exact sets of sites used in our present analyses.

The negative impact of global climate change on Arctic freshwater ecosystems is circumpolar (AMAP, 2017; Moss et al., 2009) and several recent studies in other parts of the Arctic have observed trends comparable with our findings from Arctic Fennoscandia. Culp, Lento, Curry, Luiker, and Halliwell (2019) found in the high Arctic of eastern Canada that macroinvertebrate diversity was associated with large-scale, climate-related drivers such as temperature trends and terrestrial vegetation. Moreover, Lento et al. (2022) found that spatial patterns in macroinvertebrate diversity was primarily related to temperature in a circumpolar study of both lakes and rivers. Furthermore, in accordance with our findings with respect to diatoms, Kahlert et al. (2022) found less strong linkages between diatom diversity and environmental drivers, including temperature, when analysing samples taken across the circumpolar area in lakes and rivers. They found that differences in diatom assemblage composition across circum-Arctic regions were gradual rather than abrupt, which might reflect less dispersal limitation of diatoms in comparison with macroinvertebrates. In a wider perspective, climate change could, through increasing temperatures, be a serious threat to

Arctic freshwater insect diversity, with insects constituting the main part of overall macroinvertebrate diversity. Globally, biodiversity of insects declining at disturbing rates (Sánchez-Bayo & Wyckhuis, 2019) and this is also evident in Arctic regions in relation to climate change (e.g. Loboda, Savage, Buddle, Schmidt, & Høye, 2017). However, both spatial comparative studies such as ours, and time-series data, are rare in Arctic context and this calls for urgent action in terms of more sampling and harmonised monitoring (Lento et al., 2019).

5 | CONCLUSIONS

Using a large, harmonised dataset from Finland, Sweden, and Norway, we have demonstrated the importance of climate parameters as correlates of biodiversity patterns in rivers across northern Fennoscandia. Alpha diversity is greater in the areas with a continental climate, while the oceanic areas in the west harbour much reduced sets of taxa. Our study was based on existing data to elucidate baseline patterns in biodiversity in an understudied region. It has to be acknowledged that there are limitations in the available data base across the Fennoscandian region and that the conclusions must be viewed in this context. Nevertheless, the dataset will form an important baseline to assess future impacts, including climate change and other environmental stressors, in Arctic rivers.

To detect future changes, it is also imperative that sampling methods, sampling sites, analytical methods and taxonomy are standardised across the whole Arctic region (Culp et al., 2012; Heino et al., 2020). Our analysis considers a substantial part of macroinvertebrate diversity in northern streams. Nevertheless, in both ongoing and future broad-scale monitoring of Arctic freshwaters, Chironomidae should be identified, preferably to genus or species. This is particularly important in the monitoring of treeless areas of the Arctic, such as Svalbard and Greenland, where EPT taxa are species poor or even absent. It is also important to include a wide range of sites that span the biogeographic gradients present in Fennoscandia north of the Arctic Circle in order to capture the changes that are ongoing in the Arctic. These guidelines can also be used in the conservation planning and bioassessment of Arctic riverine systems.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that are analysed in this study were taken from the CBMP database. Restrictions apply to the availability of these data.

ORCID

John E. Brittain  <https://orcid.org/0000-0001-5457-8260>
 Jani Heino  <https://orcid.org/0000-0003-3183-772X>
 Nikolai Friberg  <https://orcid.org/0000-0003-4128-7303>
 Maria Kahlert  <https://orcid.org/0000-0001-9643-4281>
 François Keck  <https://orcid.org/0000-0002-3323-4167>
 Jennifer Lento  <https://orcid.org/0000-0002-8098-4825>
 Susanne C. Schneider  <https://orcid.org/0000-0002-9545-3023>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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