

Running title: **Greenland moss diatoms**

Title: **Local and regional, not latitudinal, variation in microclimate and bedrock shapes moss-associated diatom communities in Greenland**

### **Abstract**

**Aim:** The Arctic is among the most rapidly changing regions on Earth, with climate change having a profound impact on its terrestrial ecosystems. Arctic moss-associated diatoms hold great potential to be used as sensitive biological indicators to monitor responses to climate change, but their diversity, community structure and biogeography remain virtually unexplored in Greenland. Our study aims to (1) explore the diversity and community structure of moss-associated diatoms in Greenland and (2) assess the environmental and spatial variables driving their geographic distribution, establishing a baseline for their use as bio-indicators of climate change.

**Location:** Greenland, spanning a gradient from High to Subarctic regions.

**Taxon:** Moss-associated diatoms (Bacillariophyta).

**Methods:** LM and SEM analysis was conducted on 175 terrestrial moss samples collected from preserved herbarium material and fresh samples (1988-2021) from High, Low, and Subarctic localities in Greenland. Biogeographical distributions, biodiversity patterns and community structures were examined in relation to environmental and spatial factors using Kruskal-Wallis, Spearman's Rank, ordination, SIMPROF and variation partitioning analyses.

**Results:** A total of 544 diatom taxa (66 genera) were identified, with nearly half potentially new to science. Community structure was predominantly influenced by moisture, pH, conductivity, and temperature. Local variation in microclimate and bedrock thus explained more variation in the diatom communities than latitude-related environmental gradients.

Surprisingly, temperature had a negative impact on diatom richness, probably due to its adverse effect on moisture, highlighting the vulnerability of Arctic moss diatoms to global warming.

**Main Conclusions:** This study provides the first comprehensive analysis of Greenland's moss-associated diatoms, highlighting their high diversity and sensitivity to environmental changes. Our findings underscore their potential as indicators for monitoring climate change in the Arctic, with moisture, pH, conductivity, and temperature being critical factors influencing their communities. This work lays the groundwork for future research and monitoring efforts using moss diatoms as bio-indicators in the Arctic.

**Keywords:** Arctic region, Bacillariophyta, climate change, diatoms, ecology, Greenland, mosses

### **Statements and Declarations**

The authors declare no competing interests that are (in)directly related to this work submitted for publication.

## Introduction

Soil protists are essential in the functioning of terrestrial ecosystems given their role in nutrient cycling, primary production, and decomposition (Bruni et al., 2024; Crowther et al., 2019; Geisen et al., 2018; Oliverio et al., 2020; Rodriguez-Caballero et al., 2018). Yet, how terrestrial protists will respond to climate change, and how this will affect their role within ecosystems is hardly known. Diatoms are an important component of terrestrial protist communities, especially in moss-dominated systems such as tundra, where they often exhibit high abundances and species diversities (Kopyrina et al., 2021; Morison et al., 2019; Pienitz & Smol, 1993; Pinseel et al., 2021; Rühland et al., 2003; Shinneman et al., 2016). Moss diatoms live on moss thalli and are an agglomeration of euterrestrial, lithophytic, and a few predominantly bryophytic species (Johansen, 1999). They hold an enormous potential as bio-indicators, since they are sensitive to a suite of ecological variables, including moisture, pH, and conductivity (Pouličková et al. 2013, Kopalová et al. 2014, Das et al. 2020, Chattová et al. 2021). In addition, as temperature impacts species distributions and community composition, diatoms are a promising tool to study the impact of climate change on terrestrial ecosystems (Bigler & Hall, 2003; Gremmen et al., 2007; Lotter et al., 1997; Vyverman & Sabbe, 1995).

Arctic tundra is one of the most rapidly changing terrestrial ecosystems in response to recent climate change (Arctic Climate Impact Assessment, 2005). With 80% of its surface area covered in ice, most of which concentrated in the Greenland Ice Sheet, the environmental characteristics of terrestrial Greenland (including liquid water availability) are a function of temperature and proximity to the coast and outlet glaciers (Henderson et al., 2021). Climate projections suggest that if we fail to address climate change, Greenland's climate may become similar to, or even surpass, warm conditions encountered during the Last Interglacial period (ca. 125,000 years ago) by the end of this century (Masson-Delmotte et al., 2012), with large

implications for resident communities. While freshwater diatoms are regularly applied to study climate change in Greenland (Hobbs et al., 2010; Perren et al., 2009; Weckström et al., 2023), the use of moss diatoms is a novel approach. Mosses are often the dominant vegetation in the Arctic since they have a high tolerance to freezing and drought compared to vascular plants. In addition, extensive moss herbarium collections from the Arctic are widely available and the application of collection-based material in diatom research has already proved to be successful in the past (Goeyers et al., 2022; Kohler et al., 2021). However, research on Greenland's moss diatoms is extremely scarce. An exception is the work of Foged, who included them in his works on West Greenland, Peary Land and Southwest Greenland. Foged was one of the first to study the link between environmental variables (e.g., pH, temperature, geological region) and diatom ecology in Greenland (Foged, 1953, 1955, 1958, 1973, 1977). Aside from this, additional records are scattered, and the most recent study was published more than two decades ago (Van Kerckvoorde et al., 2000).

The objectives of our study are to (1) provide a detailed taxonomic description of moss diatom communities from Greenland, and (2) assess which spatial and environmental variables are the most important in driving their diversity, community structure, and biogeography. As such, this work will establish a reference point for future research on Arctic moss diatoms, enabling their use as bio-indicators for past, present and future climate change. Using recent (> 1988) moss herbarium specimens, together with recently collected materials, we investigated communities from High, Low, and Subarctic localities including the transition zone between High and Low Arctic in Greenland. Given the lack of studies on Arctic moss diatoms, and adopting a fine-grained, up-to-date taxonomic approach, we expect to uncover a unique flora with many novel species, of which a significant portion could be restricted to the Arctic or even Greenland. Moss diatoms are generally influenced by moisture level, pH, and conductivity (Chattová et al., 2021; Das et al., 2020; Goeyers et al., 2022; Pouličková et al., 2004; Pouličková

et al., 2013; Van de Vijver & Beyens, 1997). We therefore expect to find an impact of these factors on community structure. We hypothesize that moss diatom diversity follows a latitudinal diversity gradient (LDG) (Hillebrand, 2004), decreasing from Sub- to High Arctic, following gradients observed in Greenland mosses (Daniëls et al., 2013) and Antarctic diatoms (Verleyen et al., 2021).

## **Materials and Methods**

### *Study area and environmental data*

Greenland (Kalaallit Nunaat; 59°—83 °N, 11°—74° W) covers >20 degrees of latitude, resulting in different climatic conditions (Engels & Helmens, 2010). Mean January temperatures increase from -32 °C (north) to -5° C (south). An average annual precipitation of <100 mm is observed in the north and on the ice sheet, increasing to max. 2,500 mm/year in the south (Cappelen et al., 2001; Stendel et al., 2008). Soil pH (related to precipitation, bedrock, and vegetation cover) (Nielsen 2010, Jakobsen 2013, Canini et al. 2019) follows a N-S gradient as well, with the most northern parts having the highest pH (>7.2) and the southernmost and south-western parts having the lowest pH (<5.5); areas with circumneutral pH are restricted to the east and west (Walker et al., 2005). A gradient is observed from a maritime climate near the coast to more continental further inland (Cappelen et al. 2001). In addition, Greenland is climatologically divided into an eastern and western zone, due to the effect of ocean currents associated with thermohaline circulation on regional climates (Engels & Helmens, 2010). Consequently, vegetation in West Greenland is more maritime compared to East Greenland. The five main oceanic currents driving this gradient (Andresen et al., 2004) are illustrated in Fig. 1.

Greenland is divided into 5 bioclimatic subzones based on mean July temperatures (Walker et al., 2005), largely following the N-S gradient. High Arctic Greenland has an open vegetation cover and is divided into subzones A, B, and C: Subzone A, characterized by a mean July temperature of 0–3°C, a dominant lichen/moss layer (<2cm tall), and an absence of woody plants; subzone B with a mean temperature of 3–5°C, a moss layer of 1–3 cm thick, a herbaceous layer (5–10 cm) and prostrate dwarf shrubs (<5 cm); and subzone C with a mean temperature of 5–7°C, a moss layer of 3–5 cm thick, a herbaceous layer (5–10 cm) and (hemi)prostrate dwarf shrubs (<15 cm). The Low Arctic is densely vegetated and divided into subzones D, which has a mean temperature of 7–9°C, a moss layer of 5–10 cm thick, a herbaceous and erect dwarf shrub layer of <40 cm, and Subzone E, which has a mean temperature of 9–12°C, a moss layer of 5–10 cm thick, and a herbaceous/dwarf-shrub layer of 20–50 cm (Daniëls, 2015; Walker et al., 2005). Included in this group is one of the most expansive areas of terrestrial Greenland, located at the head of Kangerlussuaq fjord, characterized by well-drained sandy soils with steppe-like plant communities (Engels & Helmens, 2010). Lastly, the inland area in the southernmost part of Greenland, including Narsarsuaq, is considered Subarctic. Due to the lack of meteorological and vegetation data, this part has not been categorized into a subzone (Daniëls, 2008). Overall, mosses follow the latitudinal diversity gradient, with species diversity increasing with decreasing latitudes (Daniëls et al., 2013). Around 670 bryophyte species have been reported, with *Bryum* (42 species) and *Sphagnum* (24 species) as most species-rich genera.

Geologically, half of the ice-free regions in Greenland are composed of Precambrian crystalline rocks (Toyokuni et al., 2020). In Northeast Greenland, bedrock and sediment consist of basaltic cores and intrusions, carbonate rocks, and gneiss and granite formations (Kroon et al., 2010). Coastal areas of West Greenland are underlain by gneiss, granite, quartzite, schist, marble, siltstone, and sandstone (St-Onge et al., 2009). Southern West Greenland consists

mainly of gneiss and granite (Hawkings et al., 2021; Piazzolo & Jaconelli, 2014; St-Onge et al., 2009), while East Greenland is predominantly underlain by gneiss, granite, and sedimentary and volcanic rocks (Hartz et al., 2002).

### ***Sample collection, preparation & counting***

A total of 175 moss samples were collected from a variety of habitats, including barren ground, fens, peat bogs, dry and wet heaths, and shrub (see below). Mosses from preserved herbarium material and fixed samples were used (Table 1). Sampling periods range from 1988–2021. Herbarium mosses were retrieved from the Meise Botanic Garden collection. All samples with associated metadata are summarized in Appendix S1.

Moss diatoms were prepared for light microscopy (LM) following Van der Werff (1953). For the Zackenberg 1998 dataset, moss fragments were sourced from the mosses utilized by Van Kerckvoorde et al. (2000), although new slides were prepared. Moss fragments were cleaned by adding 37% H<sub>2</sub>O<sub>2</sub> and heating to 80 °C for one hour. The reaction was completed with saturated KMnO<sub>4</sub>. After digestion and centrifugation (3 times for 10 minutes at 3700 g), the cleaned material was diluted with distilled water and mounted in Naphrax®. Samples and slides were stored in the BR collection (Meise, Belgium). Slides were analyzed using an Olympus BX53 microscope with Differential Interference Contrast (Nomarski) and UC30 camera connected to CellSens (Olympus) Standard. 400 valves were identified and enumerated at 1000× magnification.

Scanning electron microscopy (SEM) was used to aid identification of smaller taxa. Stubs were prepared by filtering oxidized suspension drops through 5 µm pore polycarbonate membrane filters (Whatman Cyclopore PC circles, 25 mm diameter). Filters were air-dried and affixed to 12.7 mm aluminum specimen (Agar) stubs covered with double-sided carbon stickers

(Agar Carbon Tabs). Stubs were placed in a fine sputter coater for FE-SEM (JFC-2300HR Coating Unit, JEOL) and coated 10 nm platinum (Argon-gas, 0.05 mbar pressure). SEM observations were performed using a JEOL JSM-7100FLV Field Emission SEM (1 kV, working distance 3.5–6.0 mm).

Identification of Greenland taxa was mainly based on Foged (1953, 1955, 1977, 1974), Antoniadou et al. (2008), Kulikovskiy et al. (2010), Lange-Bertalot et al. (2017), Furey et al. (2020), Heudre et al. (2021), Van de Vijver et al. (2022). Taxa that could not be identified are indicated by ‘sp’, followed by an identifying number, e.g., ‘sp1’, ‘sp2’, etc. Several unidentified taxa in the genera *Humidophila* and *Brachysira* have been formally described as new species (Goeyers et al. 2024a, 2024b).

### ***Data analysis***

Data analysis was performed in R version 2022.7.1.554 (RStudio Team, 2020), with key packages including ‘vegan’ 2.6-6.1 (Oksanen et al., 2019), ‘BiodiversityR’ (Kindt & Coe, 2005), ‘dendextend’ (Galili, 2015), and ‘ggOceanMaps’ (Vihtakari, 2022). The basic diversity unit we used is any subgeneric taxon (i.e. species, subspecies, or varieties). In the diversity and community analyses, we used the term ‘species’ to refer to any subgeneric taxon. Species accumulation curves (SAC) were constructed to assess sampling effort and evaluate regional and overall diversity using ‘specaccum’ (vegan). Species richness, Shannon-Wiener diversity, and Shannon’s equitability (evenness) indices were calculated. Bray-Curtis similarities were summarized in boxplots.

To compare  $\alpha$ -diversity components between locations and environmental variables, Kruskal–Wallis tests followed by Dunn’s Test with Holm–Bonferroni correction were used for categorical variables, and Spearman’s rank correlation for continuous variables. The



environmental variables included bioclimatic subzones, bedrock types, habitat, moss genera, F-values, conductivity, pH, annual precipitation, mean annual air temperature, mean summer air temperature (June-August) and mean winter air temperature (December-February). Due to the combination of materials from different sampling campaigns, missing values are present for numerous samples. Statistical analyses were performed on subsets with complete data.

Bioclimatic subzones were extracted from Walker et al. (2005). Bedrock types (basalt, batholith, gneiss, granite) were derived from geological maps (Guarnieri et al., 2022; Hawkings et al., 2021; Kroon et al., 2010; Piazzolo & Jaconelli, 2014; St-Onge et al., 2009). Habitat classification was based on high-resolution land cover maps: (1) abrasion (low amount of snow in winter, dry with very low vegetation activity during growing season, very sparse *Dryas* plants and/or grasses); (2) dry (barren ground, not covered by vegetation during growing season, mostly rocks or wind-blown surfaces in high elevations); (3) dry heath & grassland (*Betula* and *Vaccinium*, almost no *Salix*, relatively low amount of snow during winter resulting in low amount of melt water in growing season); (4) fen (water logged areas located in depressions covered with grasses and mosses); (5) shrub (mostly *Salix* and *Betula*, >40 cm, fair amount of snow during winter, wet during growing season); and (6) wet heath (mix of *Betula*, *Vaccinium*, *Salix*, and *Empetrum*, more snow in winter compared to dry heath, <40 cm in height) (Karami et al., 2018; Rudd et al., 2021). Moss identifications were based on the following literature when the preserved material was of sufficient quality: (Crum & Anderson, 1981; Hill et al., 2006; Smith & Smith, 2004), and on field notes. F-values, which estimate the moisture content of mosses by squeezing, were defined on the Jung-scale (F1 = submerged to F8 = completely dry). F-values, pH, and conductivity ( $\mu\text{S cm}^{-1}$ ) were measured in the field. Conductivity and pH were obtained from squeezing water out of the mosses and/or from waterbodies next to where mosses were sampled, using calibrated probes. Conductivity, F-values, moss species, and pH were only available for a smaller subset and analyses were conducted on these. Annual

precipitation and mean annual, summer and winter air temperatures were calculated in Python with data derived from the Danish Meteorological Institute (DMI) and the European Climate Assessment & Dataset (ECA&D).

### *Community analysis*

Ordination and SIMPROF analyses were applied to elucidate patterns in community composition. SIMPROF (Clarke et al., 2008) was used to group samples into clusters using Bray-Curtis distance dissimilarity, with 999 iterations, Ward clustering, and alpha on 0.05. Indicator species for each cluster were derived by calculating indicator values (IndVal) (Roberts, 2023), based on the method of Dufrière & Legendre (1997), using 'indval' in 'labdsv'. Indval uses relative abundance and relative frequency of occurrence to measure the exclusiveness of species and to calculate indicator values. Kruskal-Wallis with Dunn's Test was used to compare clusters in terms of  $\alpha$ -diversity and continuous environmental variables (annual precipitation, conductivity, mean annual, summer and winter air temperature, and pH). Fisher's Exact test was applied on categorical variables (bedrock type, bioclimatic subzones, F-value, habitat, and region).

For ordination analyses, Detrended Correspondence Analysis (DCA) (Hill & Gauch, 1980) was performed on species abundance data to estimate the gradient length of the first axis (in standard deviation units). This gradient length is used to decide whether data should be analyzed by linear (axis < 3SD) or unimodal (axis > 4SD) methods. As the gradient length of the first axis of a DCA analysis on the complete dataset corresponded to 6 SD, we opted for unimodal ordination methods. To reduce the arch effect of correspondence analysis (CA), DCA was used. Continuous environmental variables were afterwards plotted passively onto the

diagram using ‘envfit’, whereas categorical variables were plotted as centroids. The 5% best fitted species, calculated with ‘ordiselect’, were added.

Variation partitioning (Peres-Neto et al., 2006) (function ‘varpart’ in ‘vegan’) was used to determine how much of the variation in community composition could be attributed to purely spatial variables, environmental variation, bedrock variation, and their joint effect (i.e. spatially structured environmental variation). Four matrices were created: (1) a biotic matrix with species abundance data, (2) a bioclimatic matrix with environmental and climatic variables, bioclimatic subzones, habitat, and F-values (3) a bedrock matrix with bedrock types, conductivity, and pH, and (4) a spatial matrix, containing principal coordinates of neighbor matrices (PCNM) vectors (Borcard & Legendre, 2002; Dray et al., 2006) generated by principal coordinates analysis (PCoA) of a truncated Euclidean distance matrix and based on geographical coordinates. The latter allow to identify and quantify spatial patterns over a wide range of spatial scales (Borcard & Legendre, 2002). As not all explanatory variables were available for all samples, analyses were performed on three different sample subsets (131 samples for which most variables were available, 88 samples for which conductivity and pH were available, and 110 samples for which F-values were available). The truncation threshold value corresponds to the largest value in the minimum spanning tree linking the sites (Legendre & Legendre, 2012). The function ‘ordistep’ in ‘vegan’ was used for forward selection to include only those variables (and PCNMs) that significantly contribute to explaining variation. Variables with variance inflation factor (VIF) higher than 20 were removed to decrease multicollinearity.

## **Results**

### *Biodiversity analysis*

### ***Species composition***

Microscopic analysis of 175 samples revealed 544 subgeneric diatom taxa (249 species, 13 varieties, and 282 taxa that could not be identified to species level) belonging to 66 genera. Figure 2 shows the 25 most important taxa (in terms of average relative abundance across all samples). An overview of all taxa can be found in Appendix S2. Appendix S3 lists the taxa which were also observed in Van Kerckvoorde et al. (2000b), the only other recent study on moss diatoms in Greenland.

*Pinnularia* and *Eunotia* were the most species-rich genera in every region, followed by *Humidophila* for Zackenberg, Disko Island, and Kobbefjord, *Gomphonema* for Narsarsuaq, and *Nitzschia* for Kangerlussuaq and Nuuk. The 10 most dominant genera together represented more than 70% of all counted diatom valves in all samples. In terms of relative abundance, *Tabellaria acidodelicata* and *Nitzschia cf. alpina* were dominant in all Greenland samples. *Nitzschia cf. alpina* was also prevalent, being observed in 80% of the samples, followed by *Tabellaria acidodelicata* (61%) and *Rossithidium petersenii* (51%).

### ***Diversity patterns***

Species richness per sample varied from 2–69 (median of 25, mean of 36). The highest richness was found in sample ZACK98-M460, while ZACK99-ZM76 and KANG17-48 contained the lowest richness with only two taxa each. The asymptotic flattening towards the end of the species accumulation curves (Figure 3b) demonstrates that moss habitats were generally well sampled, and a significant part of Greenland's moss diatom flora is represented in the complete dataset (Figure 3b). Overall, regional taxon richness did not differ much between sampling

regions (Fig. 3a), but note that for Nuuk, Narsarsuaq, and Kobbefjord, the limited number of samples limits our ability to estimate their ‘true’ diversity.

Comparisons of species richness, Shannon-Wiener diversity, and evenness between locations and between different categories of environmental variables (bedrock, bioclimatic subzones, F-values, habitat, moss genera) revealed significant differences in richness between locations (with richness being significantly lower in Disko and Kangerlussuaq than in Zackenberg) (see Figure 4a). Mean species richness was highest in Zackenberg and lowest in Nuuk (33 and 20, respectively). The highest mean values for diversity and evenness were found in Narsarsuaq (2.65 and 0.77, respectively), and the lowest mean values in Nuuk (1.72 and 0.58, respectively). Figure 4d demonstrates that overall, Kobbefjord has the highest sample similarity, and Nuuk the lowest.

Other differences in richness were found between bedrock types (significantly higher on gneiss than on granite) (see Appendix S4 a), and bioclimatic subzones (significantly higher in Subzone C than D and E) (see Appendix S4 d). Significant differences in diversity and evenness were found between bedrock types (significantly lower diversity on granite than other bedrock types, and significantly lower evenness on gneiss than on basalt) (see Appendix S4 b-c).

Spearman’s rank correlation identified a significant positive correlation between conductivity and evenness ( $\rho=0.29$ ,  $p<0.01$ ) and a significant negative correlation between conductivity and richness ( $\rho=-0.42$ ,  $p<0.001$ ). A significant negative correlation between mean annual ( $\rho=-0.19$ ,  $p<0.05$ ), summer ( $\rho=-0.30$ ,  $p<0.001$ ) and winter ( $\rho=-0.19$ ,  $p<0.05$ ) air temperature and richness was found.

## ***Biogeography***

Comparison with literature showed that 65% of the taxa that could be identified to species level have a cosmopolitan distribution; 25% are so far only known from the Northern Hemisphere, and 10% only from the Arctic (see Appendix S2). Assuming the unidentified taxa have distributions restricted to the Arctic (as to date they have never been documented outside this region), the number of taxa with an Arctic distribution would increase to a maximum of 55%, whereas the proportion of taxa with cosmopolitan and Northern Hemisphere distributions would decrease to 32 and 12%, respectively. In addition, 33% of all taxa (both identified and unidentified) have a distribution restricted to only one of the studied locations. Most were confined to Disko (11%), followed by Zackenberg (8%), Kangerlussuaq (7%), and Kobbefjord (3%). Nuuk and Narsarsuaq had the lowest number of unique taxa (1%).

### *Community analysis*

#### ***SIMPROF***

SIMPROF separated samples into clusters based on Bray-Curtis dissimilarities. Seven clusters can be distinguished (Figure 5), differing in species composition, richness, diversity, and evenness (see Figure 6 a-c) and showing significant differences in annual precipitation, bedrock, bioclimatic subzone, conductivity, habitat, mean annual, summer and winter air temperature, and pH (see Appendix S5 a-i).

Cluster 1 primarily contains samples from Zackenberg and Kobbefjord and exhibits a relatively high species richness (see Figure 6 a). IndVal identified 22 indicator species, of which *Tabellaria acidodelicata* had the highest indicator value (0.74) (see Figure 6 d). In terms of relative abundance, *T. acidodelicata* was also dominant (see Figure 6e). Cluster 2 mainly represents Zackenberg. *Eunotia zackenbergensis*, *Pinnularia* sp5, and *Encyonema*

*groenlandica* had the highest indvals (0.9, 0.6, and 0.55, respectively) (see Figure 6 d). *Eunotia zackenbergensis* also had the highest relative abundance (see Figure 6 e). Cluster 3 is the smallest cluster with the lowest species richness and diversity and consists of samples from Kangerlussuaq and Disko. Fifteen indicator species were defined, with *Pinnularia cf. borealis* as most important (0.9, see Figure 7 d) and abundant taxon (see Figure 6 e). In cluster 4, mainly Kangerlussuaq samples are found. *Nitzschia cf. alpina* was dominant as indicator species and in relative abundance (see Figure 6 d-e). Cluster 5 consists of samples from Disko, Kangerlussuaq, Kobbefjord, and Zackenberg and had the highest species richness and diversity (see Figure 6 a-b). 32 indicator species were identified, although none had indicator values exceeding 0.5. Both *Tabellaria acidodelicata* and *Nitzschia cf. alpina* were dominant in terms of relative abundance (see Figure 6 e). In cluster 6, only Disko samples are grouped. *Adlafia suchlandtii*, *Caloneis cf. tenuis*, *Planothidium lanceolatum*, *Encyonema procerum*, and *Sellaphora* sp9 had the highest indval (see Figure 6 d). Cluster 7 contains samples from all locations. *Humidophila perpusilla*, *H. eldfjallii*, and *Pinnularia lunata* were identified as indicator species, but all had indvals lower than 0.5.

Cluster 5 had significantly higher pH values than clusters 1 and 7 (see Appendix S5 a). Cluster 1 had a significantly lower conductivity compared to clusters 6 and 7, while the conductivity of cluster 6 was higher than cluster 5 (see Appendix S5 b). In terms of mean winter air temperature, cluster 1, 6 and 7 had significantly higher values than cluster 2, whereas in cluster 5 it was lower than in clusters 6 and 7 (see Appendix S5 c). Cluster 1, 2 and 5 had significantly lower mean summer air temperatures than cluster 3, 4 and 7 (see Appendix S5 d). In terms of mean annual air temperature, cluster 2 and 5 had significantly lower values compared to cluster 6 and 7 (see Appendix S5 e). Annual precipitation was significantly higher in cluster 6 compared to cluster 3, 4 and 5 (see Appendix S5 f). Most clusters significantly

differed from each other in terms of bioclimatic subzone, habitat, and bedrock (Appendix S5 g-i).

### ***Ordination***

DCA axes 1 and 2 captured 59% of the total variation in the species data (Figure 5 b-e). Along the first axis, ‘abrasion’ and ‘dry/barren’ samples from granite bedrock (Appendix S6) in Kangerlussuaq and Disko (cluster 3, and part of 4 and 7), characterized by the higher abundance of especially *Pinnularia* and *Luticola* species, are separated from the other samples. The other Kangerlussuaq and Disko samples are mainly on the positive side of axis 2 (higher temperatures, pH and conductivity, corresponding to clusters 4, 6, and partly 7), characterized by higher abundances of *Chamaepinnularia* and *Nitzschia* spp. Most Kobbefjord samples lie on the negative side of both axes, together with most samples from Zackenberg (corresponding to clusters 1, 2, and partly 5), indicative of low mean summer temperatures and conductivity. Nuuk samples are mostly situated around the negative side of axis 1 (higher precipitation), whereas most samples from Narsarsuaq are positioned in the center. Cluster 7 is the least defined cluster, comprising samples from all localities and spread out across the diagram.

Variation partitioning analysis and forward selection conducted on the first subset of 131 samples from Disko, Kangerlussuaq, Kobbefjord, and Zackenberg (see Appendix S7 a) identified annual precipitation, bioclimatic subzones C and D, wet heath habitat, and mean summer and winter air temperatures (bioclimatic matrix), basalt and gneiss (bedrock matrix), and PCNM 1, 3, 4 and 5 (spatial matrix) as significant explanatory variables, together explaining 22% ( $p < 0.001$ ) of the total variation. Most variation explained was shared between two or three categories of explanatory variables, with only bioclimatic variables having a significant but low unique contribution (1%,  $p < 0.05$ ). The overlap between spatial and



bioclimatic variables accounted for 9% ( $p < 0.001$ ), between spatial and bedrock variables for 3% ( $p < 0.001$ ), and between bedrock and bioclimatic variables for 4% ( $p < 0.001$ ). The overlap between all variables equaled 3%. A second variation partitioning analysis on a subset of 88 samples was conducted to include pH and conductivity (see Appendix S7 b). Only annual precipitation, mean annual air temperature and bioclimatic subzone D were selected as significant variables in the bioclimatic matrix, whereas basalt, conductivity, and pH were included in the bedrock matrix. PCNM3, 4, and 5 were selected as spatial variables. All variables together explained 21% ( $p < 0.001$ ), with the unique contributions being non-significant. The overlap between spatial and bioclimatic variables accounted for 10% ( $p < 0.001$ ) and between bioclimatic and bedrock variables 3% ( $p < 0.001$ ). There was no overlap between spatial and bedrock variables. A third variation partitioning (110 samples, Appendix S7 c) was run to assess the effect of moisture (F-values). The total effect of all variables equaled 14% ( $p < 0.001$ ). The bioclimatic matrix, with annual precipitation, bioclimatic subzones C and D, F-value 6, mean annual and summer air temperature uniquely explained 3% ( $p < 0.01$ ). The spatial matrix with PCNM2, 3, 4 uniquely accounted for 2% ( $p < 0.01$ ), whereas the bedrock matrix (basalt and gneiss) had no unique contribution. The joint effect of bioclimatic and bedrock variables was 1% ( $p < 0.001$ ), whereas the overlap between spatial and bioclimatic variables accounted for 4% ( $p < 0.001$ ).

## **Discussion**

Our study provides the first large-scale taxonomic, ecological and biogeographical analysis of moss diatoms in Greenland, and contributes to advancing our understanding of the biodiversity and biogeography of the Arctic moss diatom flora in general. The exceptionally high taxonomic diversity of 544 subgeneric taxa highlights Greenland as a polar hotspot for moss diatom

biodiversity, with species richness exceeding that reported from comparable moss diatom studies in the Antarctic, where values ranged between 49–191 (in 99-148 samples) (Bishop et al., 2021; Chattová et al., 2021; Van de Vijver & Beyens, 1999). Our mean richness was 36 taxa per sample, exceeding the numbers reported globally (4-26) (Van Kerckvoorde et al., 2000; Buczkó 2006; Van de Vijver et al., 2008; Kopalová et al., 2014; Chattová et al., 2021, 2022b, a; Goeyers et al., 2022; Radhakrishnan et al., 2022). Only Iles Kerguelen had a similar richness (average of 36 taxa per sample) (Gremmen et al. 2007). The high diversity underscores the need for further research on Arctic moss diatoms, which have been underexplored relative to their Antarctic counterparts.

In Greenland, *Eunotia* and *Pinnularia* are the most species-rich genera, while *Nitzschia*, *Pinnularia*, *Navicula*, and *Luticola* are the most species-rich in the Antarctic (Chattová et al., 2021; Kopalová et al., 2014; Vinocur & Maidana, 2010). This may be due to the fact we exclusively included terrestrial mosses from barren ground, fens, peat bogs, heaths and shrub, which are characterized worldwide by a dominance of *Pinnularia* and *Eunotia* (Buczkó, 2006; Chen et al., 2012; Kapetanović et al., 2011), while Antarctic studies often included mosses collected in/near aquatic habitats. Another explanation is that some genera, such as *Luticola*, have undergone unique regional diversifications in the Antarctic, resulting in high diversity and endemism (Kociolek et al., 2017; Pinseel et al., 2021). At species-level, the Antarctic moss diatom flora also differs from the Arctic flora, with for example *Achnanthes confusa* Manguin, *A. aueri* Krasske, *Adlafia bryophila* (J.B.Petersen) Lange-Bertalot, *Eunotia paludosa* Grunow, *Fragilaria germainii* Reichardt & Lange-Bertalot, *Frustulia lebouvieri* Van de Vijver & Gremmen, *Humidophila gallica* (W.Smith) R.L. Lowe et al., *Humidophila australis* (Van de Vijver & Sabbe) R.L.Lowe et al., *Navicula gregaria* Donkin and *Planothidium renei* (Lange-Bert. & Rol.Schmidt) Van de Vijver as most abundant Antarctic taxa (Bishop et al., 2021; Chattová et al., 2021; Goeyers et al., 2022; Kopalová et al., 2014; Van

de Vijver, Beyens, Vincke, et al., 2004; Van de Vijver & Beyens, 1999). This agrees with comparative data of Arctic and Antarctic freshwater diatoms, which show a low degree of overlap (Pinseel et al., 2021).

Our data suggest that an estimated 65-32% of all taxa in our study has a cosmopolitan distribution, 25-12% is restricted to the Northern Hemisphere, and 55–10% to the Arctic, with the second values representing estimates which include unidentified taxa, and assuming these are restricted to the Arctic (as they have not yet been documented from other locations worldwide). This assumption is contentious, as many taxa remain unidentified, likely due to limited research on Arctic diatoms (Antoniades et al., 2008; Pinseel et al., 2017). Future studies in underexplored areas worldwide (e.g. in alpine regions) may reveal broader distributions. However, these unidentified taxa could also include many potential Arctic endemics. In the Antarctic, recent taxonomic revisions have uncovered numerous new endemic species (Goeyers et al., 2022; Kociolek et al., 2017; Kopalová et al., 2014; Lange-Bertalot & Werum, 2001; Van de Vijver, Beyens, & Lange-Bertalot, 2004; Van de Vijver et al., 2002; Van de Vijver & Beyens, 1997), with an estimated 44% of freshwater diatom species being Antarctic endemics and even mostly confined to one Antarctic subregion (Verleyen et al., 2021). This might be similar in the Arctic, where recent studies uncovered many new species (Furey et al., 2020; Lange-Bertalot & Genkal, 1999; Pinseel et al., 2014; M. Potapova et al., 2014; M. G. Potapova et al., 2020; Van de Vijver, Beyens, & Lange-Bertalot, 2004; Veselá & Potapova, 2014). If similar, our findings would be in line with Verleyen et al. (2021) and earlier studies reporting that diatoms generally have restricted biogeographic distributions (Vanormelingen et al., 2007; Vyverman et al., 2007).

Variation in community structure was significantly related to different sets of environmental variables, many of which are intercorrelated and spatially structured. Variation partitioning analysis revealed moisture (captured by F-values, habitat, and precipitation), pH,

conductivity, bedrock, bioclimatic subzone, and mean annual, summer and winter temperature as key variables, explaining 14–22% of the variation (depending on the dataset analyzed), which is comparable to other studies, e.g., 10% in a global stream diatom dataset (Soininen et al., 2016), 24% in Swedish freshwater diatoms (Keck et al., 2018), and 15–35% in Subarctic stream diatoms (Lindholm et al., 2018). The large overlap between all variables shows that most explained variation is spatially structured (Keck et al., 2018), indicating that factors influencing moss diatoms are not acting independently but are interrelated and co-vary across the Arctic landscape. The low and non-significant unique contributions of spatial variables suggest most unexplained variation is not captured by the spatial variables used. The relatively low amount of explained variation might be related to (1) stochastic factors affecting species distributions, which may be especially relevant given the high diversity of our dataset, with many rare species, and (2) potential important environmental drivers not included in our study, e.g., nutrients and biotic factors such as grazing. Variation along the second DCA axis, which correlates with pH, conductivity and temperature, may also be explained by nutrient status, with species preferring high nutrient habitats (e.g., *Chamaepinnularia krookii* and *C. krookiformis*) situated on the positive side, and species adapted to oligotrophic conditions (e.g., *Pseudostaurosira* and *Frustulia* spp.) on the negative side.

In agreement with findings from other moss diatom studies (Van de Vijver & Beyens 1997, Poulíčková et al. 2004, Goeyers et al. 2022), moisture was a prime determinant of community structure, with especially the driest habitats (abrasion, dry/barren) and low precipitation locations having distinct, low diversity communities. *Hantzschia abundans*, *H. amphioxys*, and *Pinnularia borealis* (Lange-Bertalot et al., 2017) were typical of such dry, aerial habitats. Temperature, pH and conductivity (both related to bedrock) were also important, separating low pH, conductivity, and temperature sites from sites with high values. Characteristic species for wet, electrolyte-poor habitats, such as undisturbed peat bogs, include

*Eunotia fennica*, *Frustulia saxonica* and *Brachysira wygaschii* (Lange-Bertalot et al., 2017), while species typical for wet, electrolyte-rich environments include *Chamaepinnularia krookiformis* and *C. krookii* (Lange-Bertalot & Genkal, 1999). The influence of pH and conductivity aligns with prior research, showing both as key drivers of moss diatom communities (Chattová et al., 2021; Das et al., 2020; Pouličková et al., 2013).

Mean annual, summer and winter temperature had small, albeit significant impacts on species richness, which decreased with increasing temperature. In marine diatoms, temperature was reported as a dominant driver of richness patterns, especially at its extremes, i.e., the Arctic and tropical regions (Busseni et al., 2020). Multiple studies also indicated that temperature likewise affects freshwater diatom distributions and community composition (Bigler & Hall, 2003; Gremmen et al., 2007; Lotter et al., 1997; Vyverman & Sabbe, 1995). The absence of a latitudinal richness gradient in our study however contradicts with previous studies on Arctic freshwater diatoms where an increasing trend in biodiversity with higher temperatures was explained by longer growing seasons and a wider range of available habitats in warmer regions, favoring richness and diversity (Michelutti et al., 2003; Weckström et al., 2023). In contrast, in habitats where water is limited, such as tundra soils, higher temperatures may result in drier conditions, which might negatively impact diatom communities as their richness generally strongly correlates with moisture (Das et al., 2020; Kopalová et al., 2014). Our findings thus suggest that global warming might adversely affect Arctic terrestrial diatom richness in the future, particularly through increased temperatures and their effect on moisture. We found no support for a latitudinal decline in local diversity from Sub- to High Arctic Greenland, despite a strong influence of bioclimatic (e.g., temperature, precipitation) and related (e.g., moisture) variables on species richness, suggesting that bioclimatic forcing mainly relates to local and/or regional microclimatic scales. In general, the latitudinal diversity gradient seems to be less strong for microbiota (Soininen et al., 2016; Soininen & Teittinen, 2019) and in freshwater

diatoms, U-shaped (Passy, 2010), inverse (Soininen et al., 2016), non-significant (Schiaffino et al., 2016), and very weak (Hillebrand & Azovsky, 2001) gradients have been identified. Interestingly, while freshwater diatoms display a latitudinal diversity gradient in the Southern Hemisphere (Vyverman et al., 2007) and within the Antarctic (Verleyen et al., 2021), a hump-shaped gradient was observed in the Northern Hemisphere (Vyverman et al., 2007). This was attributed to the present-day higher degree of isolation and low lake connectivity with increasing latitude in the Southern Hemisphere, and a high number of lakes in previously glaciated temperate and Subarctic regions in the Northern Hemisphere (Vyverman et al., 2007). This suggests that diatoms adhere to the theory of island biogeography (MacArthur & Wilson, 1967) and that highly connected habitats contain more species due to recolonizations after local extinctions. The lack of a latitudinal diversity gradient in our dataset might be related to the shorter latitudinal gradient studied, small-scale habitat variability masking larger patterns, or the interaction of local microclimatic conditions and geographic factors such as the distribution of ice-free land in Greenland. Indeed, ice-free land and hence the availability of suitable habitats for mosses and associated diatoms is, excluding the southernmost regions, nearly equally distributed along Greenland's coastline, which might result in the observed similar species richness in our study regions. One exception is the low richness and diversity in Nuuk, which might be explained by the high anthropogenic disturbance where the mosses were collected (some were taken near roads with regular traffic). The negative effect of anthropogenic disturbance on richness has been shown by multiple studies, e.g., on terrestrial diatoms in Luxemburg, Poland, sub-Antarctica, and Greenland (Foets et al., 2021), spring diatoms in Italy (Angeli et al., 2010), and epipelagic diatoms in Argentina (Gómez, 1998).

## **Figure legends**

**Fig. 1:** Overview of the sampling locations in Greenland. Bioclimatic subzones, based on the Circumpolar Arctic Vegetation Map (CAVM) (Walker et al. 2005), are indicated as colors. The arrows indicate ocean currents. NAC = North Atlantic Current, EGC = East Greenland Current, IC = Irminger Current, WGC = West Greenland Current, LC = Labrador Current.

**Fig. 2:** The 25 most abundant diatom taxa in Greenland (based on overall average relative abundance). A. *Eunotia* sp7, B. *Eunotia fennica*, C. *Eunotia zackenbergensis*, D. *Pinnularia* cf. *borealis*, E. *Pinnularia* sp5, F. *Pinnularia* sp30, G. *Eunotia curtagrunowii*, H. *Eunotia* sp30, I. *Rossethidium petersenii*, J. *Pinnularia humilis*, K. *Caloneis fusus*, L. *Meridion circulare*, M. *Tabellaria acidodelicata*, N. *Encyonema groenlandica*, O. *Humidophila perpusilla*, P. *Planothidium lanceolatum*, Q. *Staurosirella* cf. *martyi*, R. *Diatomella balfouriana*, S. *Meridion constrictum*, T. *Nitzschia* cf. *alpina*, U. *Psammothidium helveticum*, V. *Odontidium mesodon*, W. *Pinnularia* sp35, X. *Pinnularia* sp6, Y. *Achnanthisidium* cf. *minutissimum*.

**Fig. 3:** Species Accumulation Curves for (a) the different sampling locations in Greenland and (b) the complete Greenland dataset.

**Fig. 4:** Boxplots of (a) species richness, (b) Shannon-Wiener diversity, and (c) evenness (Shannon Equitability index). Kruskal-Wallis identified a significant difference in richness, with lower richness in Disko and Kangerlussuaq than in Zackenberg. In (d), boxplots of Bray-Curtis sample similarities within locations are shown. (e) shows the most species-rich genera per location. The regions are ordered from high to low latitude. Significance levels (Dunn's Test) are indicated by asterisks (\*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$ ).

**Fig. 5:** (a) Circle dendrogram with 7 clusters of samples resulting from SIMPROF analysis. (b-e) DCA ordination with (b) locations; (c) SIMPROF clusters; (d) 5% best fitted species; and (e) continuous environmental variables plotted with envfit (arrows were doubled in length for clarity) and centroids of categorical environmental variables. Bedrock: BA = batholith, BS = basalt, GN = gneiss, GR = granite; Habitat: AB = abrasion, D = dry/barren, DH = dry heath, F = fen, SH = shrub, WH = wet heath; Vegetation: Bioclimatic subzone C = SC, subzone D = SD, subzone E = SE.

**Fig. 6:** (a-c) Species richness, Shannon-Wiener diversity, and Shannon's Equitability (evenness) for the different SIMPROF clusters; (d) balloon plot showing indicator species per cluster. The size of the symbols corresponds to the indicator values resulting from IndVal analysis and reflects the 'exclusiveness' of a species to a cluster. Only indvals higher than 0.5 are included. For species labels, see Appendix S6; (e) barplot showing the most important species per cluster.

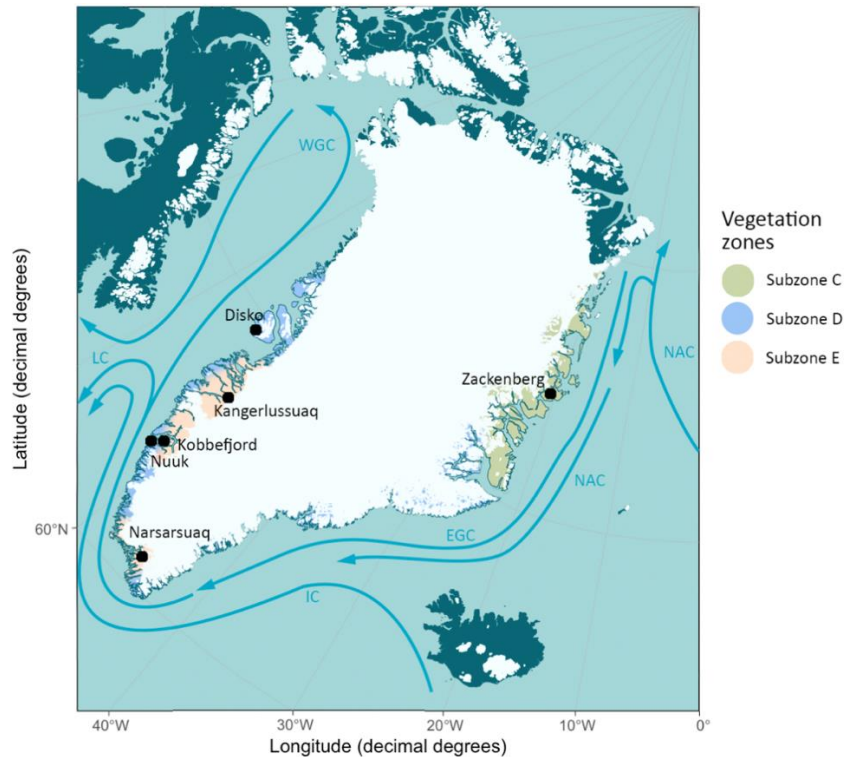
## Figures & tables

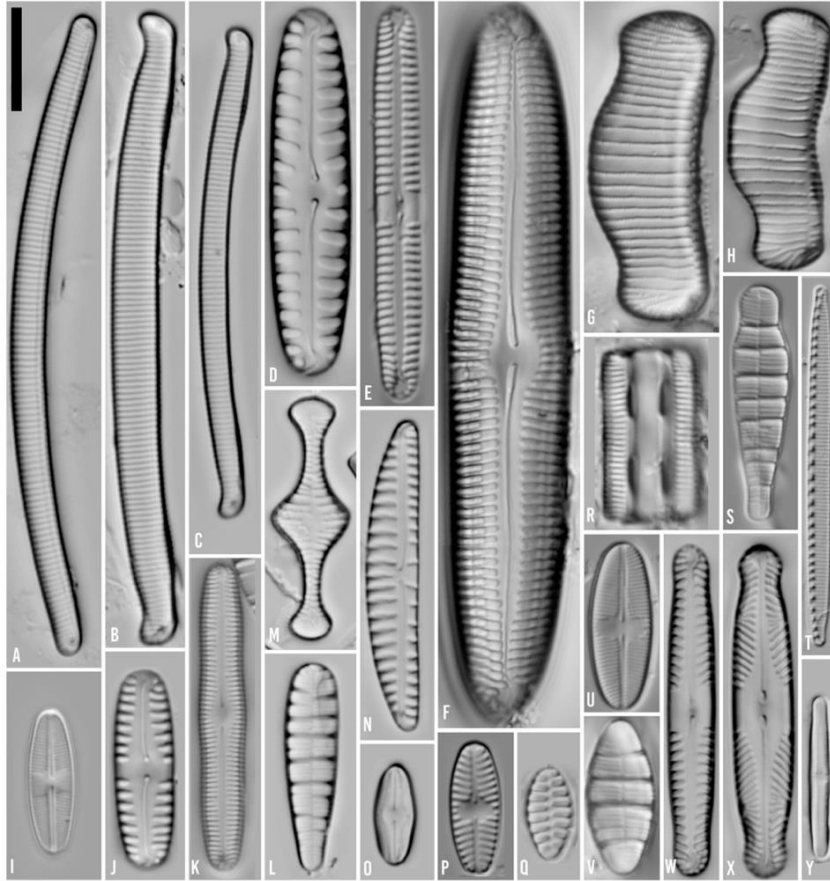
**Table 1** Overview of the different sampling campaigns with number of moss sample slides used in this study, preservation methods of the samples, coordinates, information on geology and bedrock, bioclimatic subzones ('BC subzones'), and weather, with mean summer air temperature ('MSAT'), mean winter air temperature ('MWAT'), mean annual air temperature ('MAAT'), and annual precipitation ('AP'). Herbarium material is indicated with an asterisk.

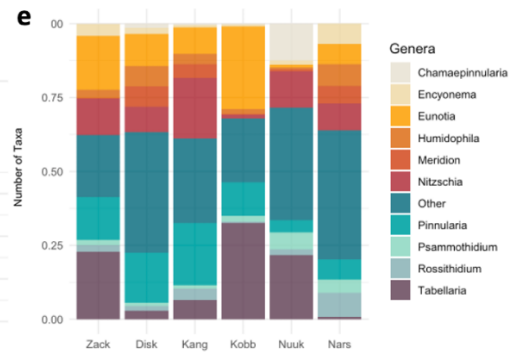
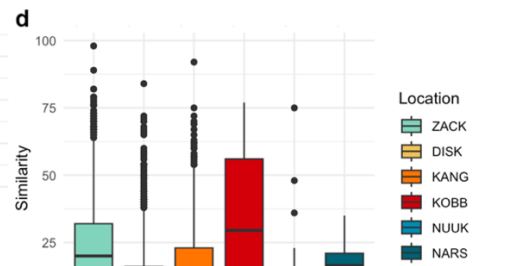
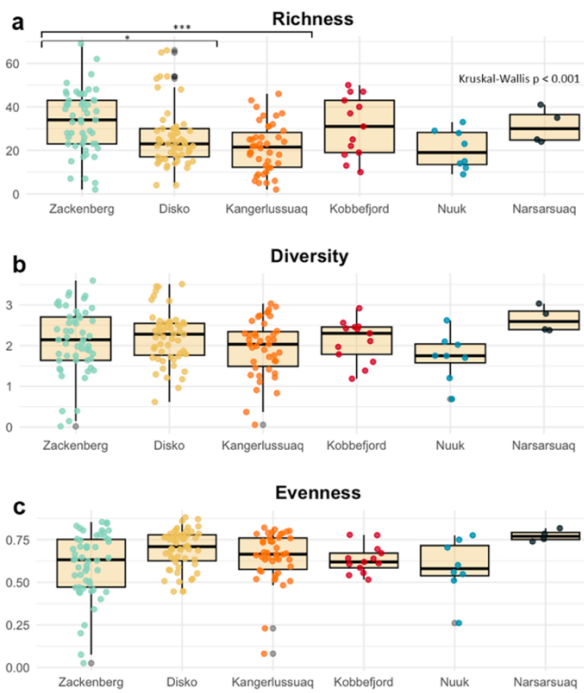
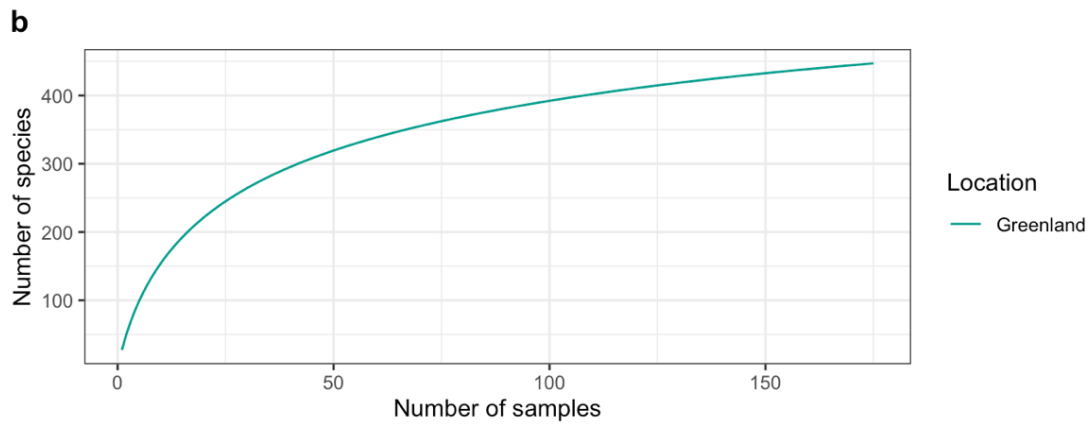
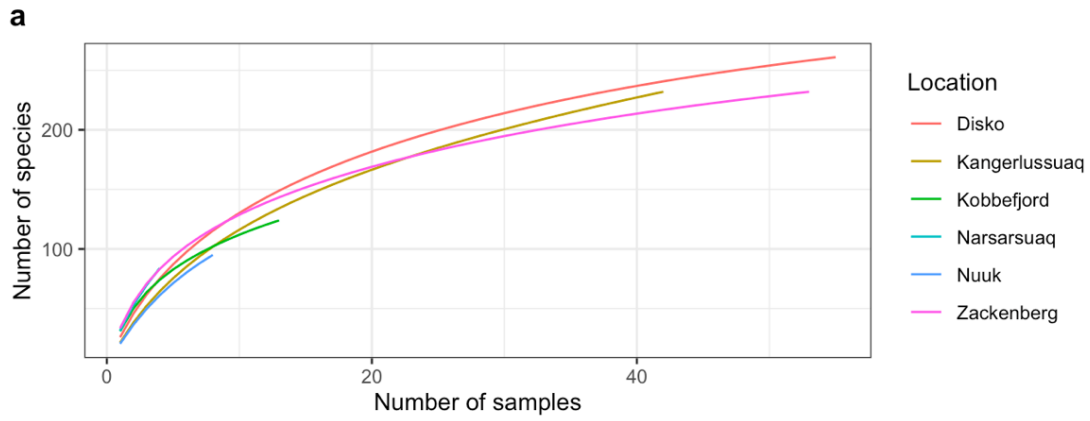
Locations	Samples	Preservation	Coordinates	Geology	BC subzones	Weather
Zackenbergl (1998*,1999*, 2000*)	53	Dry, ethanol, 3% formaldehyde	74°28'N, 20°34'W	Cretaceous and Tertiary sandstones with basalt (East), Caledonian gneissic	Subzone C	MSAT: 2.04°C MWAT: -22.24°C MAAT: -11.43°C AP: 218.67 mm

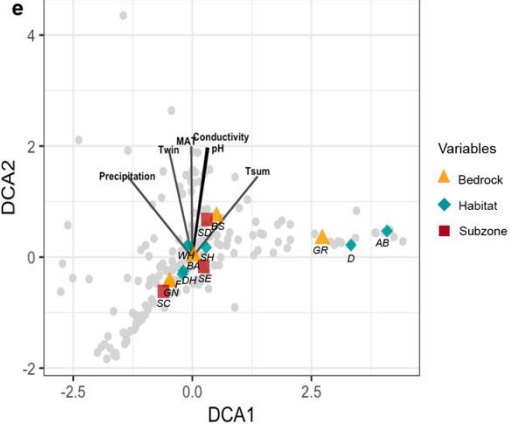
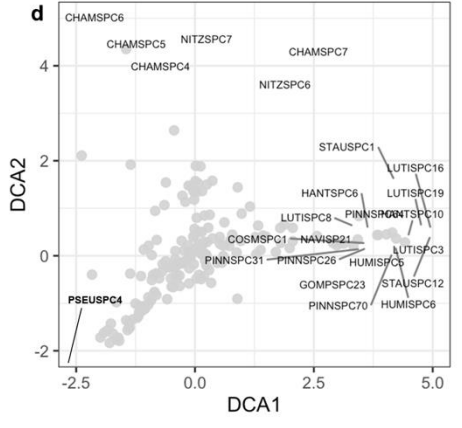
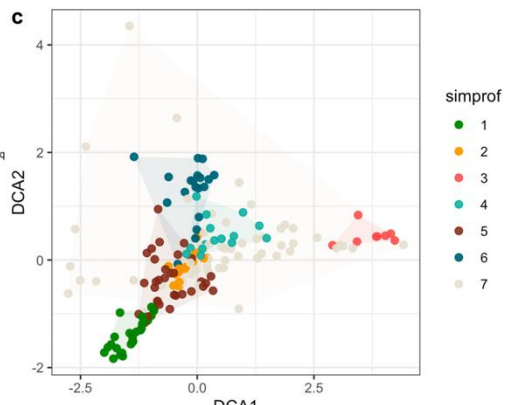
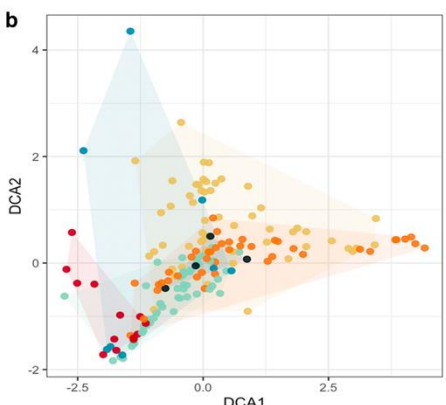
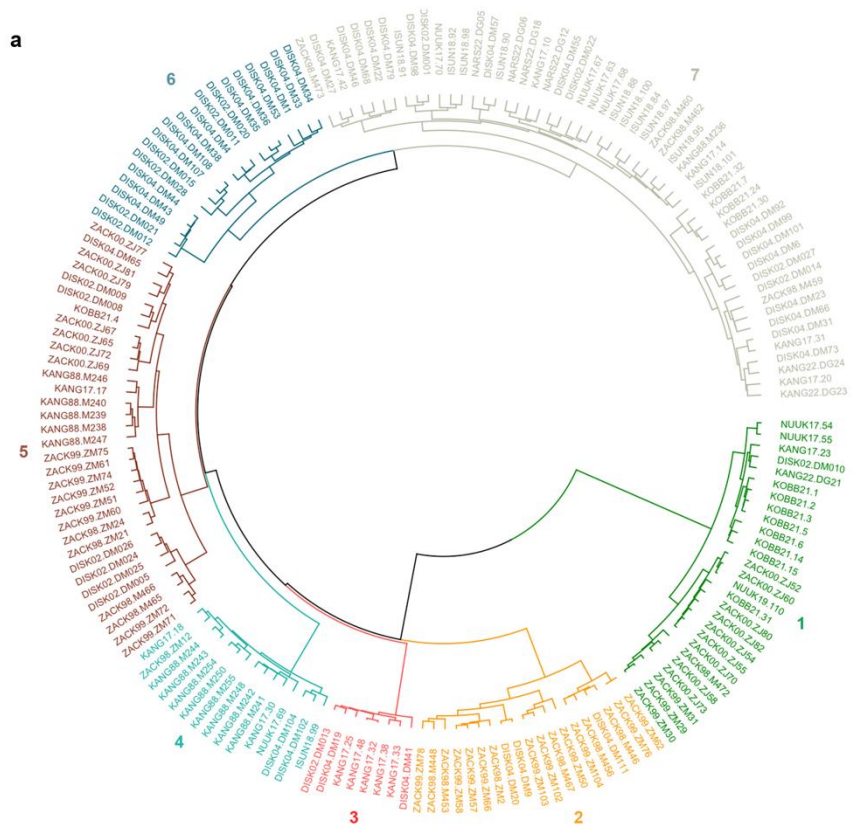


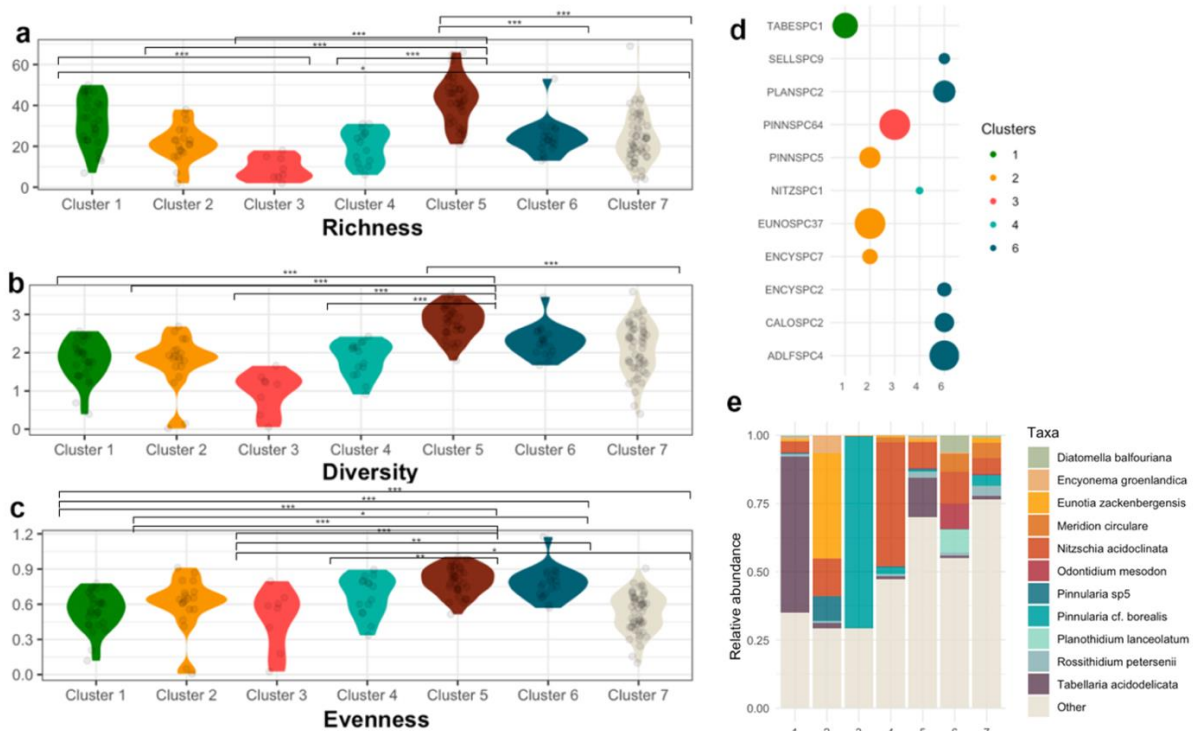
				and granite bedrock (West)		
Disko (2002*, 2004*)	55	Dry & ethanol	70°N, 54°W	Tertiary plateau basalt	Subzone D	MSAT: 5.6°C MWAT: -10.25°C MAAT: -3.05°C AP: 435 mm
Kangerlussuaq (1988*, 2017, 2018, 2022)	42	Ethanol	67°01'N, 50°40'W	Archaean granodiorite gneiss, local mica schists and metasediments	Subzone E	MSAT: 7.88°C MWAT: -15.45°C MAAT: -4.48°C AP: 169 mm
Nuuk (2017, 2019)	8	Ethanol	64°07'N, 51°21'W	Archaean terranes bounded by faults/mylonite zones, rocks with contrasting origin	Subzone D	MSAT: 6.52°C MWAT: -5.9°C MAAT: -0.15°C AP: 867.5 mm
Kobbefjord (2021)	13	Ethanol	64°09'N, 51°34'W	Archaean tonalitic to granodioritic gneiss and Qorqût granite	Subzone E	MSAT: 6.7°C MWAT: -4.4°C MAAT: 0.1°C AP: 908 mm
Narsarsuaq (2022)	4	Ethanol	61°09'N, 45°25'W	Granodiorite and diorite with local nepheline syenite intrusives	/	MSAT: 9.6°C MWAT: -9.1°C MAAT: 1°C AP: 729 mm











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*Palaeogeography, Palaeoclimatology, Palaeoecology*, 189(3-4), 147-160.

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