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RESEARCH ARTICLE

Moss-inhabiting diatom communities from Ile Amsterdam (TAAF, southern Indian Ocean)

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Background and aims – Despite the ongoing taxonomical revision of the entire (sub)-Antarctic diatom flora, our knowledge on the ecology and community associations of moss-inhabiting diatoms is still rather limited. In the present study, our research aim was to survey the diversity together with the environmental factors structuring the epiphytic moss diatom communities on Ile Amsterdam (TAAF), a small volcanic island in the southern Indian Ocean.
Material and methods – A morphology-based dataset and (physico)chemical measurements were used for the ecological and biogeographical analysis of moss-inhabiting diatom flora from Ile Amsterdam. In total, 148 moss samples were examined using light microscopy.
Key results – The analysis revealed the presence of 125 diatom taxa belonging to 38 genera. The uniqueness of the Ile Amsterdam diatom flora is mainly reflected by the species composition of the dominant genera *Pinnularia*, *Nitzschia*, *Humidophila*, and *Luticola*, with a large number of unknown and often new species. This highly specific diatom flora, together with differences in the habitats sampled and the isolated position of the island, resulted in very low similarity values between Ile Amsterdam and the other islands of the Southern Ocean. From a biogeographical point of view, 40% of the taxa have a typical cosmopolitan distribution, whereas 22% of all observed species can be considered endemic to Ile Amsterdam, with another 17% species showing a restricted sub-Antarctic distribution. The NMDS analysis, based on a cluster dendrogram, divides the samples into six main groups. For each group, indicator species were determined. Both environmental data and diatom distributions indicate that apart from elevation, specific conductance, pH, and moisture are the major factors determining the structure of moss-inhabiting diatom communities on Ile Amsterdam.
Conclusion – The isolated geographic position and unique climatological and geological features of the island shaped the presence of a unique diatom flora, characterised by many endemic species. The results of the study are of prime importance for further (palaeo-)ecological and biogeographical research.

Keywords – Bacillariophyta; diatoms; ecology; mosses; Ile Amsterdam; southern Indian Ocean; sub-Antarctic region.

INTRODUCTION

Diatoms (Bacillariophyceae) are one of the most abundant and diverse algal groups in the (sub-)Antarctic region (Jones 1996; Van de Vijver & Beyens 1999a; Sabbe et al. 2003). Although the majority of diatom species are restricted to aquatic habitats, a large number of diatom taxa is able to survive in non-submerged or even dry habitats, such

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as dry mosses, bark, litter, lichens, wet rocks, and soils (Van de Vijver et al. 2002a; Pfister et al. 2017; Foets et al. 2020). Diatom communities can be strongly influenced by environmental differences in their habitat. Within the (sub-) Antarctic region, there are several studies on local factors controlling the diatom community structure. The structure of moss-inhabiting diatom communities determined by water availability was demonstrated on several sub-Antarctic localities such as Heard Island (Van de Vijver et al. 2004b) and the Prince Edward Islands (Van de Vijver et al. 2008b). The soil diatom communities on Ile de la Possession (Iles Crozet) appeared to be structured by available moisture, phosphate and sulphate content (Van de Vijver et al. 2002b). Furthermore, the moss-inhabiting diatom communities in the Maritime Antarctic Region also appeared to be strongly influenced by water availability (Kopalová et al. 2014). In addition, the endurance and survival strategies of diatoms have been intensively studied in the form of controlled laboratory experiments, focusing mainly on their tolerance to extreme conditions such as freezing and desiccation (Souffreau et al. 2010, 2013a; Hejduková et al. 2019).

The present study is the second in a series of three papers characterising the non-marine diatom diversity from freshwater, moss, and soil habitats on Ile Amsterdam, one of the most remote islands in the world, located north of the sub-Antarctic islands Iles Crozet and the Prince Edward Islands in the southern Indian Ocean, halfway between South Africa and Australia. The first paper described the ecological preferences of the freshwater diatom flora (Chattová et al. 2014), while a third paper discussing the soil diatom communities on Ile Amsterdam is currently being prepared. These ecological analyses of the Ile Amsterdam diatom communities followed a thorough morphological and taxonomical revision that led to the description of many new species (Van de Vijver et al. 2008a, 2012, 2014b, 2017; Lowe et al. 2013; Van de Vijver & Cox 2013; Chattová et al. 2017, 2018).

Chattová et al. (2014) presented a history of diatom research on Ile Amsterdam, starting in 1999 with a first small study on the diatom flora in a handful of samples around the scientific station, where almost 100 different taxa were observed (Van de Vijver & Beyens 1999c). Most of these samples were taken from dry moss vegetation, rehydrated by rain.

Bryophyte communities represent an important part of the sub-Antarctic vegetation. *Sphagnum* peatlands are absent from all sub-Antarctic islands in the southern Indian Ocean, except for Ile Amsterdam and Ile Saint-Paul where several (endemic) *Sphagnum* species, forming extensive peatlands above 500 m a.s.l., have been discovered (Flatberg et al. 2011). The moss vegetation in the sub-Antarctic region is clearly inhabited by highly diverse diatom communities. One of the first papers discussing the sub-Antarctic moss-inhabiting diatom flora provided an analysis of epiphytic diatom communities from Campbell Island (Hickman & Vitt 1974), reporting the presence of 59, mostly cosmopolitan, diatom species. In recent years, the moss diatom flora of sub-Antarctic islands has been increasingly well studied, with 104 taxa reported from terrestrial mosses of South Georgia (Van de Vijver & Beyens 1997), more than 190 taxa found on aquatic and terrestrial mosses of Ile de la Possession in the Crozet archipelago (Van de Vijver & Beyens 1999b), and 192 taxa reported from aquatic and terrestrial mosses of Heard Island (Van de Vijver et al. 2004b). A highly diverse diatom flora (170 taxa) was reported in a combined dataset of freshwater samples and aquatic moss samples from Iles Kerguelen (Van de Vijver et al. 2001), another archipelago in the southern Indian Ocean. Moreover, Gremmen et al. (2007) examined the distribution of moss-inhabiting diatoms (130 species) along an altitudinal gradient on Iles Kerguelen. A final paper, describing the diversity and distribution patterns of freshwater and moss-inhabiting diatoms on the Prince Edward Islands, was published a year later and lists 214 diatom taxa (Van de Vijver et al. 2008b). The results of the aforementioned studies together with recent taxonomic revisions of the sub-Antarctic diatom flora (e.g. Van de Vijver et al. 2004a, 2011, 2014a, 2014b) have uncovered a number of endemic species previously misidentified as cosmopolitan taxa, due to "force-fitting" of species into American or European names (Tyler 1996; Sabbe et al. 2003).

The main objective of the present study is to characterise and discuss the diatom communities living on aquatic and terrestrial mosses on Ile Amsterdam, in order to reveal the principal factors influencing the moss-inhabiting diatom diversity. Furthermore, we aim to compare the moss diatom flora of Ile Amsterdam with the floras of other sub-Antarctic islands to add to our biogeographical knowledge of the sub-Antarctic diatom flora.

MATERIAL AND METHODS

Study site

Ile Amsterdam (77°30′E, 37°50′S) (supplementary file 1), with a total surface area of 55 km^2, has the shape of a small cone culminating at 881 m a.s.l. (Mont de la Dives) and is geologically very young, with its main part appearing during the period 400–200 ka (Giret 1987; Doucet et al. 2003). Permanent waterbodies are restricted to the higher plateau (Caldera, Plateau des Tourbières) in the centre and the west-southwestern part of the island (Falaises d'Entrecasteaux, Grandes Ravines). Almost all other areas lack (semi-) permanent waterbodies due to the steepness of the slope and the extreme permeability of the substrate and underground, composed of numerous lava tunnels, holes, and fissures. Due to frequent fog, low clouds, and a high relative humidity in the upper areas (from 500 m a.s.l.), extensive peat formations have developed, especially in the volcanic caldera (Heger et al. 2009). On the higher central plateau, the vegetation has a typical sub-Antarctic character, composed of mosses, small ferns (e.g. *Austroblechnum penna-marina* (Poir.) Gasper & V.A.O.Dittrich), grasses, sedges such as *Uncinia brevicaulis* (Mack.) Thouars, and several *Lycopodium* species (Tréhen et al. 1990). Reflecting the isolation of the island, the number of native spermaphyte species is low (17) but 56 species were introduced (Frenot et al. 2001). The lichen flora is still incompletely known but in 2011, Aptroot et al. reported 77 species, including the newly described *Caloplaca amsterdamensis* Aptroot & Ertz (Aptroot et al. 2011).

Sampling

In total, 148 moss samples were collected during a field campaign in November and December 2007. Both aquatic and terrestrial mosses were sampled spanning a broad range of moisture content (as expressed by the F-values of Jung 1936). The sampling sites are shown in supplementary file 1. Each sample consisted of at least 10 cm^3 of the living part of the moss, without rhizomes. Samples were collected in PVC bottles and fixed with 3% formaldehyde. When possible, the samples were geographically localised using GPS, accompanied by a detailed site description. When possible, pH, conductivity, and water temperature were measured in situ using a WTW 340i Multimeter. For 25 samples, which were all aquatic mosses collected from pools and rivers, water was collected 10 cm below the water surface, filtered in situ, and deep-frozen to be subsequently analysed. The nutrients $(NO_2^-+NO_3^-)N$, NH_4^+-N, PO_4^{3-}-P, SO_4^{2-}, Cl^-, Na^+, K^+, Mg^{2+}, and Ca^{2+} were analysed at the Laboratory for Ecosystem Management (University of Antwerp, Belgium) using a continuous flow analysis (CFA–SKALAR). Supplementary file 2 list all samples used for further analyses, together with their characteristics.

The moisture content of each sample was determined using the F-classification of Jung (1936). It is a humidity scale based on water content: FI = submerged mosses, FII = free floating mosses, FIII = very wet (water drips from the samples without pressure), FIV = wet (water drips with a slight pressure), FV = quasi-wet (water drips after moderate pressure), FVI = moist (little water produced after high pressure), FVII = quasi-dry (only a few drops of water can be squeezed out), FVIII = dry (contains no water).

Sample preparation and diatom counting

Sample contents were randomised before preparation and prepared for light microscopy analysis following the method described in van der Werff (1955): small subsamples (± 2 cm^2) of moss fragments, with an addition of distilled water, were cleaned by adding 37% H_2O_2 and heated to 80°C for about 1 h. The reaction was completed by addition of an excessive amount of saturated $KMnO_4$. Following digestion and centrifugation (three times 10 min at 3700 rpm), cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom valves were mounted in Naphrax®. Samples and slides are stored at the BR-collection (Belgium). In each sample, 400 diatom valves were identified and enumerated on random transects at 1000× magnification (oil-immersion), using an Olympus BX53 microscope, equipped with Differential Interference Contrast (Nomarski) optics and the Olympus UC30 Imaging System. Slides were scanned after counting 400 valves in order to find rare species. For identification of Antarctic and sub-Antarctic species, the following publications were consulted: Van de Vijver et al. (2002a, 2002b, 2004a, 2008a, 2012, 2014b); Van de Vijver & Cox (2013); Lowe et al. (2013); Wetzel et al. (2015).

Data analysis

For a pairwise comparison of the diatom flora of Ile Amsterdam with those of the other sub-Antarctic islands, the Community Coefficient of Sørensen (1948) was used with the following formula: 2c/(a+b+2c), where a and b are the number of species observed exclusively in each of the two sites and c is the number of species shared between these sites. The Ile Amsterdam moss inhabiting diatom flora was compared with terrestrial and aquatic moss diatom flora from Heard Island (Van de Vijver et al. 2004b), Ile de la Possession (Van de Vijver & Beyens 1999b), Prince Edward Islands (Van de Vijver et al. 2008b), and with aquatic moss diatom flora from Iles Kerguelen (Van de Vijver et al. 2001). Datasets were made taxonomically consistent prior to the similarity analysis.

To evaluate the extent to which our sampling effort represented the moss-inhabiting diatom flora of Ile Amsterdam, the incidence-based species richness estimator (ICE, Chao et al. 2000) and the mean Chao2 richness estimator (Chao 1984) were calculated, both using the EstimateS program v.9.1.0. (Colwell 2013).

Non-metric Multidimensional Scaling (NMDS) was performed to reduce the multidimensional species data matrix into two dimensions best reflecting site dissimilarities given by diatom species composition. NMDS was based on Bray-Curtis (Sørensen) dissimilarity calculated on square root transformed species data.

Classical agglomerative clustering was used to group diatom assemblages according to the same Bray-Curtis distances using the unweighted per group average algorithm (UPGMA). Resulting groups were projected onto the NMDS ordination as well as best indicator species of the (combinations of) site groups. Indicator species were identified using the extended Indicator Species Analysis. The indicator value (IV) of an indicator species is a number calculated as the product of two quantities, called A and B, ranging from 0 to 1. Quantity A gives the probability of a site being a member of the site-group combination when the species was found at that site. Quantity B informs how frequently (and hence how easily) the species is found at sites of the site-group combination under study (De Cáceres et al. 2010). Unless otherwise indicated, statistical analyses were performed in the R statistical environment (R Core Team 2017; RStudio Team 2015) using the packages vegan v.2.4-6 (Oksanen et al. 2018) and ggplot2 (Wickham 2016).

RESULTS

Species composition and diversity

The analysis of 148 samples revealed the presence of 122 diatom taxa belonging to 38 genera. Three additional taxa were observed outside the counts bringing the total number of moss-inhabiting diatoms to 125 taxa. Twenty-one samples contained (almost) no diatoms, even after scanning entire slides, and have therefore been removed from further analysis. The distribution of the species numbers per sample (supplementary file 3A) showed that most samples contained between 11 and 15 taxa per sample. The average number (and standard deviation) of taxa per sample was 12 ± 7, with a median of 11. The asymptotic flattening towards the end of the species accumulation curve (supplementary file 3B) indicates that a large part of the moss-inhabiting diatom

Table 1 – Taxonomical list of all observed taxa in this study. Unidentified species are given a provisional letter code. C = cosmopolitan, SA = sub-Antarctic region, U = unknown, AMS = Ile Amsterdam, (AMS) = Ile Amsterdam but yet undescribed.

Taxon	Distribution
Achnanthes coarctata (Bréb.) Grunow	C
Achnanthes muelleri G.W.F.Carlson	SA
Achnanthes naviformis Van de Vijver & Beyens	SA
Achnanthidium sieminskae Witkowski, Kulikovskiy & Riaux-Gob.	SA
Achnanthidium sp.	U
Angusticopula aff. *dickiei* (Thwaites) Houk, Klee & H.Tanaka	U
Caloneis bacillum (Grunow) Cleve	C
Craticula submolesta (Hust.) Lange-Bert.	C
Denticula cf. *sundaysensis* C.G.M.Archibald	U
Diatomella balfouriana Grev.	C
Eunotia aff. *minor* (Kütz.) Grunow	U
Eunotia cf. *arcus* Ehrenb.	U
Eunotia cf. *pectinoides* J.R.Carter	U
Eunotia clotii Van de Vijver, de Haan & Lange-Bert.	SA
Eunotia cocquytiae Van de Vijver	AMS
Eunotia lecohui Van de Vijver	SA
Eunotia manguinii Van de Vijver & Jüttner	SA
Eunotia paludosa Grunow group	C
Eunotia pugilistica Van de Vijver	AMS
Ferocia setosa (Grev.) Van de Vijver & Houk	C
Fistulifera sp.	U
Fragilaria neoproducta Lange-Bert.	C
Frustulia lebouvieri Van de Vijver & Gremmen	SA
Frustulia vulgaris (Thwaites) De Toni	C
Geissleria sp.	U
Gomphonema aff. *exilissimum* Grunow	U
Gomphonema cf. *montanum* (Schum.) Grunow	U
Gomphonema parvulum (Kütz.) Kütz. group	C
Halamphora compereana Van de Vijver & Levkov	AMS
Halamphora dagmarobbelsiana Van de Vijver & Levkov	AMS
Halamphora veneta (Kütz.) Levkov	C
Hantzschia abundans Lange-Bert.	C
Hantzschia amphioxys (Ehrenb.) Grunow	C
Hantzschia possessionensis Van de Vijver & Beyens	SA
Hantzschia sp.	U
Humidophila amsterdamensis Chattová & Van de Vijver	AMS
Humidophila brekkaensis (J.B.Petersen) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bert. & Kopalová	C
Humidophila contenta (Grunow) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bert. & Kopalová	C
Humidophila crozetikerguelensis (Le Cohu & Van de Vijver) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bert. & Kopalová	SA
Humidophila gallica (W.Sm.) R.L.Lowe, Kociolek, You, Wang & Stepanek	C
Humidophila rouhaniana Chattová & Van de Vijver	AMS

Table 1 (continued) – Taxonomical list of all observed taxa in this study. Unidentified species are given a provisional letter code. C = cosmopolitan, SA = sub-Antarctic region, U = unknown, AMS = Ile Amsterdam, (AMS) = Ile Amsterdam but yet undescribed.

Taxon	Distribution
Humidophila vidalii (Van de Vijver, Ledeganck & Beyens) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bert. & Kopalová	SA
Chamaepinnularia aerophila Van de Vijver & Beyens	SA
Chamaepinnularia evanida (Hust.) Lange-Bert.	C
Chamaepinnularia soehrensis var. *muscicola* (J.B.Petersen) Lange-Bert. & Krammer	C
Kobayasiella subantarctica Van de Vijver & Vanhoutte	SA
Lecohuia geniculata (H.Germ.) Lange-Bert. & U.Rumrich	C
Luticola beyensii Van de Vijver, Ledeganck & Lebouvier	SA
Luticola ivetana Chattová & Van de Vijver	AMS
Luticola subcrozetensis Van de Vijver, Kopalová, Zidarova & Levkov	SA
Luticola vancampiana Chattová & Van de Vijver	AMS
Mayamaea atomus var. *permitis* (Hust.) Lange-Bert.	C
Mayamaea cavernicola Van de Vijver & E.J.Cox	AMS
Mayamaea cf. *agrestis* (Hust.) Lange-Bert.	U
Mayamaea fossalis (Krasske) Lange-Bert. group	C
Melosira aff. *varians* C.Agardh	U
Microfissurata australis Van de Vijver & Lange-Bert.	AMS
Navicula aff. *shackletonii* West & G.S.West	U
Navicula cf. *bicephala* Hust.	U
Navicula cf. *cryptotenella* Lange-Bert.	U
Navicula gregaria Donkin	C
Navicula longicephala Hust. group	C
Navicula veneta Kütz.	C
Nitzschia communis Rabenh.	C
Nitzschia commutata Grunow	C
Nitzschia debilis (Arn. ex O'Meara) Grunow in Cleve & Grunow	C
Nitzschia fonticola (Grunow) Grunow	C
Nitzschia frustulum (Kütz.) Grunow	C
Nitzschia palea (Kütz.) W.Sm. group	C
Nitzschia soratensis E.Morales & M.L.Vis	C
Nitzschia sp.	(AMS)
Orthoseira roeseana (Rabenh.) O'Meara	C
Orthoseira verleyenii Van de Vijver	AMS
Pinnularia acidicola var. *acidicola* Van de Vijver & Beyens	SA
Pinnularia aff. *acidicola* var. *elongata* Van de Vijver & Beyens	U
Pinnularia aff. *amsterdamensis* Chattová, Van de Vijver & Metzeltin	U
Pinnularia aff. *microstauron* (Ehrenb.) Cleve	U
Pinnularia amsterdamensis Chattová, Van de Vijver & Metzeltin	AMS
Pinnularia australogibba Van de Vijver, Chattová & Metzeltin	AMS
Pinnularia australogibba var. *subcapitata* Van de Vijver, Chattová & Metzeltin	AMS
Pinnularia borealis Ehrenb. complex	C
Pinnularia bottnica Krammer	C

Table 1 (continued) – Taxonomical list of all observed taxa in this study. Unidentified species are given a provisional letter code. C = cosmopolitan, SA = sub-Antarctic region, U = unknown, AMS = Ile Amsterdam, (AMS) = Ile Amsterdam but yet undescribed.

Taxon	Distribution
Pinnularia lindanedbalovae Van de Vijver & Moravcová	SA
Pinnularia microcapitata Van de Vijver, Chattová & Metzeltin	AMS
Pinnularia microstauron (Ehrenb.) Cleve	C
Pinnularia myriamiae Van de Vijver, Chattová & Metzeltin	AMS
Pinnularia perminor Kulikovskiy, Lange-Bert. & Metzeltin	C
Pinnularia pseudohilseana Van de Vijver, Chattová & Metzeltin	AMS
Pinnularia rabenhorstii var. *subantarctica* Van de Vijver & Le Cohu	SA
Pinnularia robrechtii Van de Vijver	AMS
Pinnularia sinistra Krammer	C
Pinnularia sp.1	U
Pinnularia sp.2	U
Pinnularia sp.3	U
Pinnularia sp.4	U
Pinnularia subacoricola Metzeltin, Lange-Bert. & García-Rodríguez	C
Pinnularia subcommutata Krammer	C
Pinnularia subsinistra Van de Vijver, Chattová & Metzeltin	AMS
Pinnularia sylviae Van de Vijver	AMS
*Pinnularia vixconspicu*a Chattová, Metzeltin & Van de Vijver	AMS
Pinnularia vlaminghi Van de Vijver, Chattová & Metzeltin	AMS
Pinnularia whinamiae Van de Vijver	SA
Pinnunavis gebhardii (Krasske) Van de Vijver	SA
Pinnunavis sp.	(AMS)
Placoneis anglica (Ralfs) Cox	C
Planothidium pericavum (J.R.Carter) Lange-Bert.	C
Planothidium subantarcticum Van de Vijver & C.E.Wetzel	SA
Platessa oblongella (Østrup) C.E.Wetzel, Lange-Bert. & Ector	C
Psammothidium investians (J.R.Carter) Bukht.	C
Psammothidium manguini (Hust.) Van de Vijver	C
Psammothidium stauroneioides (Manguin) Bukht.	C
Pseudostaurosira naveana (Le Cohu) E.Morales & M.B.Edlund	C
Pseudostaurosira trainorii E.Morales	C
Rhopalodia rupestris (W.Sm.) Krammer	C
Sellaphora arvensis (Hust.) C.E.Wetzel & Ector	C
Sellaphora barae Van de Vijver	AMS
Sellaphora cf. *atomoides* (Grunow) C.E.Wetzel & Van de Vijver	U
Sellaphora cf. *seminulum* (Grunow) D.G.Mann	U
Sellaphora sp.	(AMS)
Stauroforma aff. *exiguiformis* (Lange-Bert.) R.J.Flower, V.J.Jones & Round	U
Stauroneis kriegeri Patrick	C
Stauroneis pseudomuriella Van de Vijver & Lange-Bert.	SA
Stauroneis thermicola (J.B.Petersen) Lund	C
Stauroneis bertrandii Van de Vijver & Lange-Bert.	SA
Tryblionella debilis Arn. ex O'Meara	C

Table 2 – Similarity analysis (Sørensen index) between Ile Amsterdam and other sub-Antarctic islands. References to original datasets used for the similarity analysis: Prince Edward Islands (Van de Vijver et al. 2008b); Crozet (Van de Vijver & Beyens 1999b); Heard Island (Van de Vijver et al. 2004b); Iles Kerguelen (Van de Vijver et al. 2001); Gough Island (P. Vinšová unpubl. res.); Ile Saint-Paul (Chattová 2017). Datasets were made taxonomically consistent prior to the similarity analysis.

	Ile Amsterdam	Prince Edward Islands	Crozet	Heard Island	Kerguelen	Gough Island	Saint-Paul
Number of taxa	125	198	160	181	210	141	60
Sørensen index		0.29	0.33	0.30	0.31	0.24	0.48

flora was collected. Using species richness estimators, it is possible to evaluate how well the sampling effort reflected the true diatom species richness of the area. The expected total number of taxa in all moss samples is 139 (ICE) or 137 (Chao2), suggesting that the counting protocol detected between 88 and 90% of the theoretical total taxa present in the samples. Species richness per sample ranged from 1 to 40. Two samples were entirely monospecific, composed only of *Eunotia paludosa* Grunow (M026 and M157). The highest species richness was recorded in sample M203 (40 taxa). The five most abundant species accounted for 64.3% of all counted valves. The dominant species include *Eunotia paludosa* with more than 35% of all counted valves, *Frustulia lebouvieri* Van de Vijver & Gremmen (10.5%), *Planothidium subantarcticum* Van de Vijver & C.E.Wetzel (7.4%), *Eunotia manguinii* Van de Vijver & Jüttner (5.6%), and *Kobayasiella subantarctica* Van de Vijver & Vanhoutte (5.6%). On the other hand, 108 taxa (more than 87% of all counted taxa) had a total relative abundance of less than 1%. Table 1 provides an alphabetical list of all observed species together with their biogeographical distribution. The genera *Pinnularia* (28 taxa), *Eunotia* (nine taxa), *Nitzschia* (eight taxa), and *Humidophila* (seven taxa) were the most species-rich genera. Other species-rich genera include *Sellaphora* (five taxa) and *Hantzschia*, *Luticola*, *Psammothidium*, *Stauroneis* (four taxa each). Supplementary file 4 lists all genera arranged according to their species number. Eleven taxa (9%) could only be identified to the genus level. Some of these are most likely new to science and will have to be formally described (mainly in the genera *Nitzschia*, *Navicula*, *Pinnunavis*, and *Sellaphora*).

Forty percent of all observed taxa showed a typical cosmopolitan distribution, 17% had a restricted sub-Antarctic distribution, while another 22% can be considered endemic to Ile Amsterdam (supplementary file 3C). The similarity analysis based on presence/absence data indicates that the moss diatom flora of Ile Amsterdam only showed a limited affinity to other sub-Antarctic islands, with Sørensen index values ranging from 0.24 to 0.48 (table 2). The highest similarity was noted with Ile Saint-Paul, whereas the lowest similarity was observed with Gough Island. The latter is part of the Tristan da Cunha archipelago and located in the southern Atlantic Ocean, at approximately the same latitude as Ile Amsterdam.

Community analysis

The NMDS analysis, based on a cluster dendrogram (supplementary file 5), divided the samples into six main groups (fig. 1), clearly reflecting the species composition. For better classification of the groups, indicator species were used to characterise the community types of the individual groups. A strong relation between the indicator species and the groups was observed with an Indicator Value (IV) ranging from 0.8 to 0.99 (fig. 2) (De Cáceres et al. 2010).

The first group contained samples taken mostly from wet, moist to dry mosses and liverworts growing in cracks on wet rocks. The indicator species included terrestrial taxa such as *Humidophila brekkaensis* (J.B.Petersen) Lowe et al. (IV 0.94), *H. contenta* (Grunow) R.L.Lowe et al. (IV 0.83), and *Pinnularia borealis* Ehrenb. complex (IV 0.89). Due to the habitat of the samples, the physico-chemical data were only available for one sample, indicating an acidic pH, slightly elevated conductivity, and low nutrient values. The relevant ecological parameters together with the mean number of taxa for each group are listed in table 3.

Five samples formed a second group composed of acidic, species-poor, mostly dry samples with low specific conductance, nutrient and ion values. The indicator species was *Pinnularia whinamiae* Van de Vijver (IV 0.99), a species described from small, acidic (pH 4.7–5.0), almost dystrophic pools near the Museau de Tanche crater in the caldera at the top of the island. The samples were further dominated by *Eunotia paludosa* and *Pinnularia microstauron* (Ehrenb.) Cleve.

The third group, composed of samples from the Del Cano region in the southern part of the island, was characterised by a dominance of *Platessa oblongella* (Østrup) C.E.Wetzel, Lange-Bert. & Ector (IV 0.9), *Psammothidium investians* (J.R.Carter) Bukht. (IV 0.99), and by high occurrence of *Eunotia paludosa*, *Sellaphora* cf. *seminulum* (Grunow) D.G.Mann, *Sellaphora arvensis* (Hust.) C.E.Wetzel & Ector, and *Eunotia manguinii*. The samples were characterised by a slightly acidic pH, higher specific conductance values, and higher Cl^- and Na^+ values, possibly the result of sea spray.

The fourth group was exclusively composed of high-elevation acidic samples with very low specific conductance, nutrient and ion values. This group was characterised by extremely high abundances of its indicator species *Frustulia lebouvieri* (IV 0.84) and *Eunotia paludosa* (IV 0.97). The samples are further dominated by *Kobayasiella subantarctica* and various *Eunotia* (*E. manguinii*, *E. lecohui* Van de Vijver) and *Pinnularia* taxa (*P. amsterdamensis* Chattová et al., *P. vixconspicua* Chattová et al., *P. myriamiae* Van de Vijver et al.).

Table 3 – Water chemistry features in the different sample groups identified by the NMDS analysis (mean and standard deviation).

	1	2	3	4	5	6
number of samples (with pH and conductivity/with physico-chemical data)	8 (1/1)	5 (3/1)	11 (6/3)	79 (55/16)	14 (6/3)	10 (1/1)
number of taxa	12 ± 5	7 ± 2	17 ± 7	9 ± 5	17 ± 6	24 ± 8.9
number of genera	7 ± 3	5 ± 1	10 ± 3	5 ± 2	12 ± 4	16 ± 5.2
moisture category	VI–VII	III–VI	III–VII	I–VIII	I–VII	IV–VII
elevation	73–675	386–398	121–600	295–759	48–711	59–715
pH	6.2	4.3 ± 0.1	6 ± 0.3	5.3 ± 0.7	7.6 ± 0.9	5.81
specific conductance (µS/cm)	444	158 ± 14	399 ± 136	109 ± 81	642 ± 360	239
$(NO_2^-+NO_3^-)N$ (mg/l)	0.02	0.29	0.02	1.2 ± 2.5	0.9 ± 0.7	0.31
NH_4^+-N (mg/l)	0.05	0.05	0.05	0.2 ± 0.1	0.05	0.09
PO_4^{3-}-P (mg/l)	0.01	0.01	0.01	0.04 ± 0.05	0.03 ± 0.05	0.06
SO_4^{2-} (mg/l)	7	6	9.3 ± 2	6.6 ± 3	20 ± 0.9	10
Cl^- (mg/l)	28	42	60 ± 28	34 ± 37	59.3 ± 89	63
Na^+ (mg/l)	16.2	24.2	35.2 ± 15	9.5 ± 3.5	42.1 ± 13.5	35.5
K^+ (mg/l)	0.4	1.8	1.1 ± 0.5	1 ± 3	2.8 ± 1.3	1.3
Ca^{2+} (mg/l)	1.1	1.6	3.1 ± 2	0.6 ± 0.2	15.1 ± 7.5	4.1
Mg^{2+} (mg/l)	1.6	2.48	4 ± 1.9	0.8 ± 0.4	10.9 ± 2.2	4.6

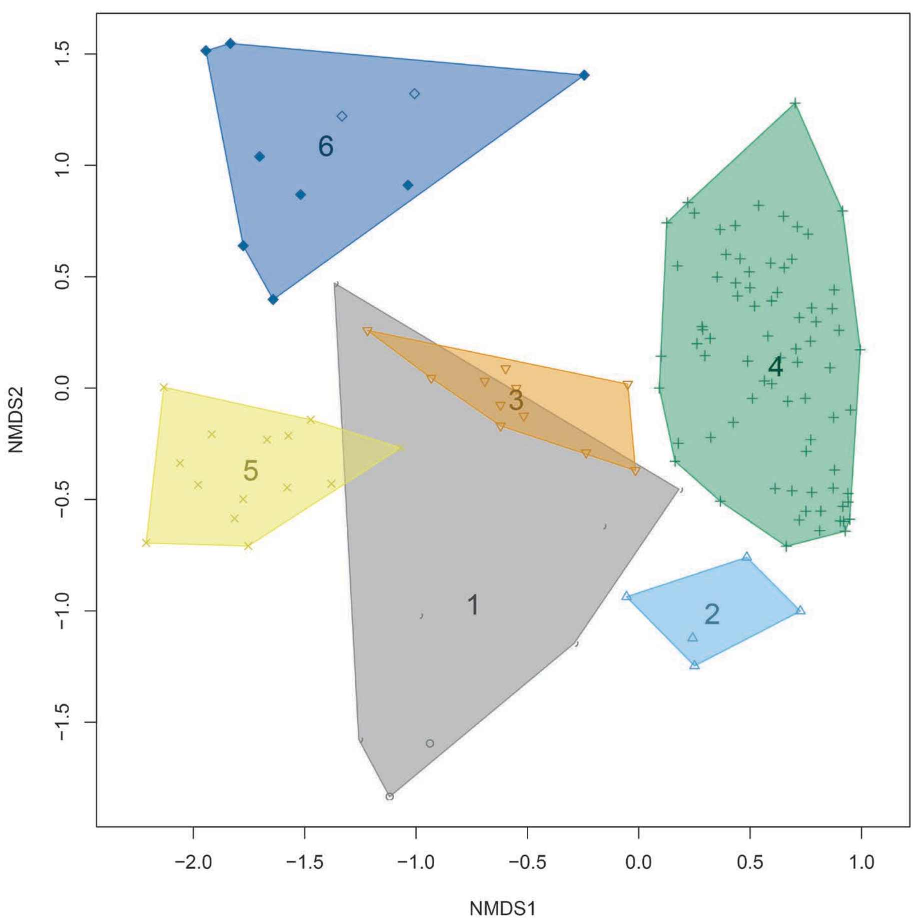

Figure 1 – Results of the Non-metric Multidimensional Scaling (NMDS) analysis, displaying the 6 main groups of the samples. The groups reflect site dissimilarities given by diatom species composition. The NMDS analysis is based on a cluster dendrogram (supplementary file 5). Final stress value of the successful NMDS run is 0.158.

The fifth group contained samples collected mostly in the coastal ravines of the Falaises d'Entrecasteaux (southern part of the island) and Del Cano, often taken from mosses or liverworts growing near or in a waterfall. These samples had higher pH values (7.6 ± 0.9) and a higher conductivity and SO_4^{2-}, Mg^{2+}, Ca^{2+}, and K^+ values. The amount of Cl^- and Na^+ was also high, reflecting the vicinity of the ocean and the possible effect of sea spray. The samples were almost exclusively dominated by *Planothidium subantarcticum* (IV 0.97) with *Sellaphora* cf. *seminulum*, *Nitzschia soratensis* E.Morales & M.L.Vis, and *Halamphora veneta* (Kütz.) Levkov as co-dominant taxa.

The last group comprised of moist and dry samples (moisture categories FIV–FVII), collected mainly from caves in the lava tunnel. The samples were slightly acidic with elevated Na^+ and Cl^- values and were dominated by *Angusticopula* aff. *dickiei* (IV 0.99), *Ferocia setosa* (Grev.) Van de Vijver & Houk (IV 0.94), *Orthoseira verleyenii* Van de Vijver (IV 0.89), *Chamaepinnularia aerophila* Van de Vijver & Beyens, *Mayamaea cavernicola* Van de Vijver & E.J.Cox, *Luticola ivetana* Chattová & Van de Vijver, and various *Humidophila* taxa (*H. rouhaniana* Chattová & Van de Vijver, *H. amsterdamensis* Chattová & Van de Vijver, *H. crozetikerguelensis* (Le Cohu & Van de Vijver) R.L.Lowe et al., and *H. gallica* (W.Smith) R.L.Lowe et al.). Figure 3 shows micrographs of typical taxa in the groups 1–5, while fig. 4 illustrates the cave-inhabiting diatom community of group 6.

The relationship between species richness and environmental variables was analysed with the samples divided into two main groups, according to elevation (fig. 5). The majority of the samples (84) were found on higher elevations (above 500 m a.s.l.), whereas the rest of the samples originated from lower elevations (0–500 m a.s.l.). The species richness clearly increased with increasing pH and conductivity in the samples of the lower elevations, whereas no apparent pattern could be observed in samples of higher elevations.

DISCUSSION

Species composition and general biogeography

Based on the relative abundance data, the most reported taxon in the moss vegetation of Ile Amsterdam is *Eunotia paludosa*, a cosmopolitan species frequently reported from sub-Antarctica and typically found in semi-wet terrestrial mosses or in small acidic pools with low conductivity values (Van de Vijver et al. 2014a). However, within the five most abundant taxa, four taxa (*Frustulia lebouvieri*, *Eunotia manguinii*, *Planothidium subantarcticum*, and *Kobayasiella subantarctica*) are only present on the southern Indian Ocean

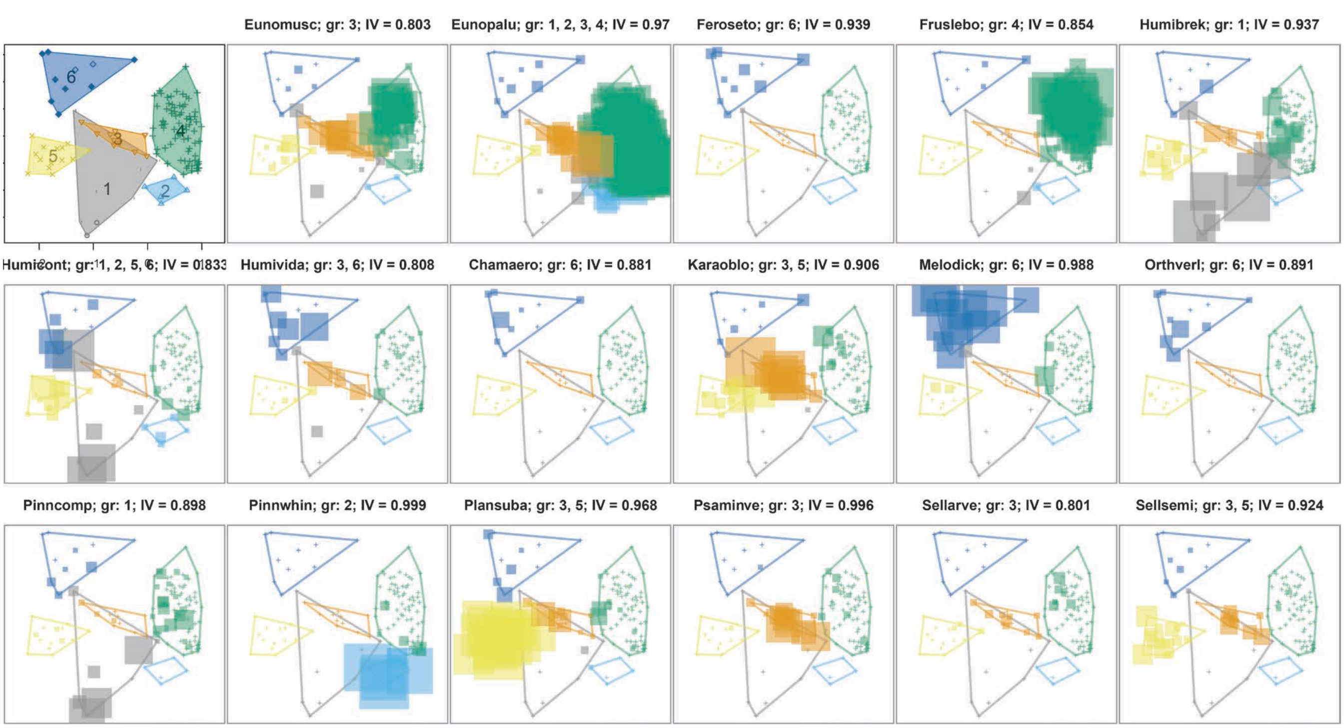

Figure 2 – Indicator species for the different groups of the samples, used to characterise the community types of the individual groups. A strong relation between the indicator species and the groups is evident, with Indicator Values (IV) ranging from 0.8 to 0.99. The relative abundance of the indicator species in each sample of the different groups is coded by the square size (the bigger the square, the higher the abundance). Eunomusc = *Eunotia manguinii*; Eunopalu = *Eunotia paludosa*; Feroseto = *Ferocia setosa*; Fruslebo = *Frustulia lebouvieri*; Humibrek = *Humidophila brekkaensis*; Humicont = *Humidophila contenta*; Humivida = *Humidophila vidalii*; Chamaero = *Chamaepinnularia aerophila*; Karaoblo = *Platessa oblongella*; Melodick = *Angusticopula* aff. *dickiei*; Orthverl = *Orthoseira verleyenii*; Pinncomp = *Pinnularia borealis complex*; Pinnwhin = *Pinnularia whinamiae*; Plansuba = *Planothidium subantarcticum*; Psaminve = *Psammothidium investians*; Sellarve = *Sellaphora arvensis*; Sellsemi = *Sellaphora* cf. *seminulum*.

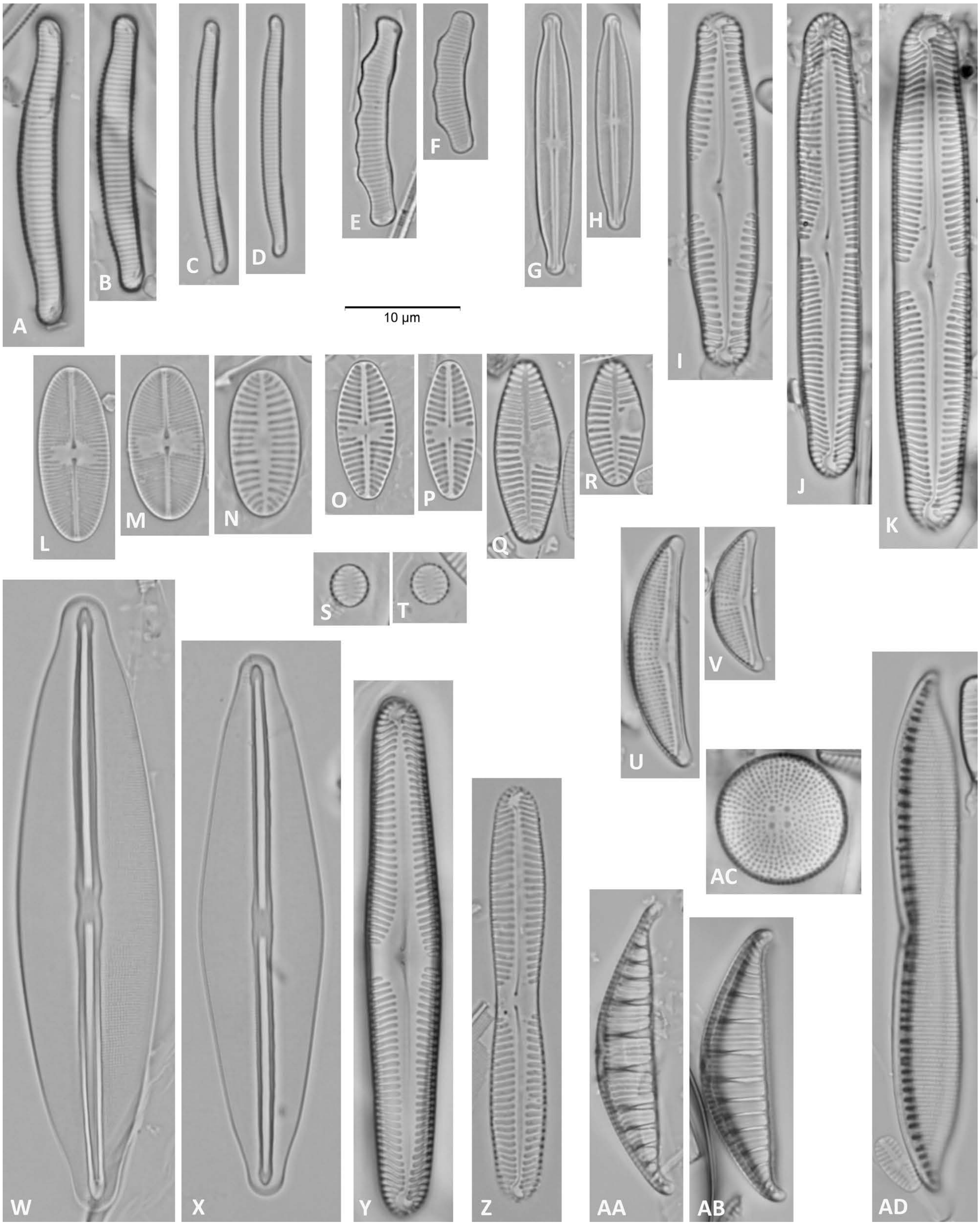

Figure 3 – LM micrographs of the typical taxa of the high-elevation acidic (A–H, W–Z), and slightly acidic to subalkaline (L–V, AA–AD) diatom communities of Del Cano and d'Entrecasteaux. **A**–**B**. *Eunotia lecohui*. **C**–**D**. *Eunotia paludosa* **E**–**F**. *Eunotia manguinii.* **G**–**H**. *Kobayasiella subantarctica*. **I**. *Pinnularia australogibba* var. *subcapitata*. **J**–**K**. *Pinnularia microstauron*. **L**–**M**. *Platessa oblongella* raphe valves. **N**. *Platessa oblongella* rapheless valve. **O**–**P**. *Planothidium subantarcticum* raphe valves. **Q**–**R**. *Planothidium subantarcticum* rapheless valves. **S**–**T**. *Pseudostaurosira* cf. *trainorii*. **U**–**V**. *Halamphora veneta*. **W**–**X**. *Frustulia lebouvieri*. **Y**. *Pinnularia amsterdamensis*. **Z**. *Pinnularia myriamiae.* **AA**–**AB**. *Rhopalodia rupestris*. **AC**. *Orthoseira roeseana*. **AD**. *Nitzschia commutata*.

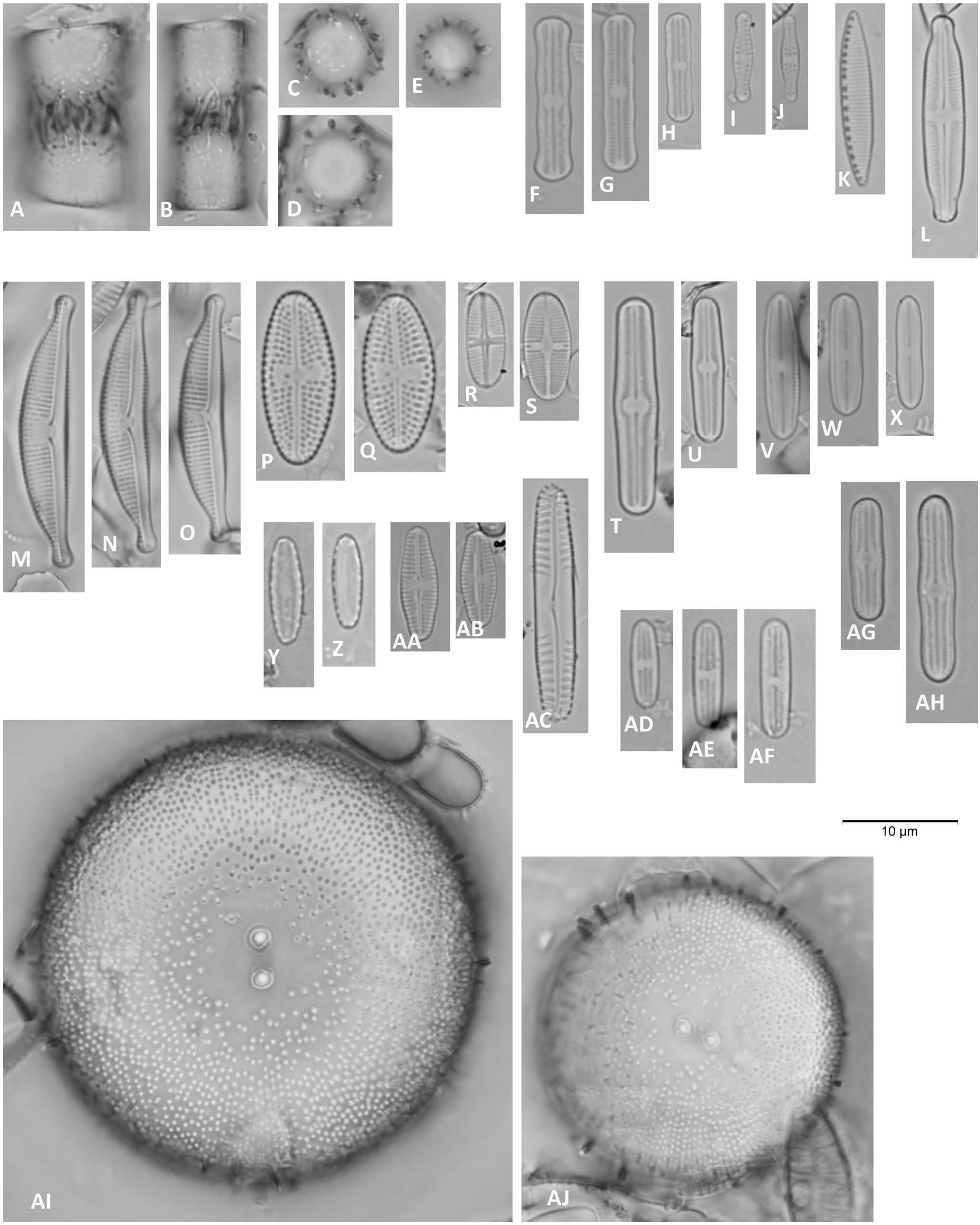

Figure 4 – LM micrographs of taxa found on mosses growing in caves in the lava tunnel. **A**–**B**. *Ferocia setosa*, valves connected via linking spines. **C**–**E**. *Ferocia setosa*, valve view. **F**–**H**. *Humidophila crozetikerguelensis*. **I**–**J**. *Chamaepinnularia aerophila*. **K**. *Nitzschia frustulum*. **L**. *Stauroneis kriegeri*. **M**–**O**. *Halamphora compereana*. **P**–**Q**. *Luticola ivetana*. **R**–**S**. *Psammothidium abundans*. **T**–**U**. *Humidophila amsterdamensis*. **V**–**X**. *Humidophila vidalii*. **Y**–**Z**. *Humidophila gallica*. **AA**–**AB**. *Sellaphora barae*. **AC**. *Pinnularia subsinistra*. **AD**–**AF**. *Humidophila rouhaniana*. **AG**–**AH**. *Humidophila brekkaensis*. **AI**–**AJ**. *Orthoseira verleyenii*.

islands and even absent from all other studied Antarctic localities (Zidarova et al. 2016 and references therein). The second most abundant taxon, *Frustulia lebouvieri*, was so far only found on the Prince Edward Islands, the most northerly of the sub-Antarctic Islands (Van de Vijver et al. 2008b). It is at the same time the most abundant taxon (30.8% of all counted valves) in the freshwater diatom communities on Ile Amsterdam (Chattová et al. 2014).

The uniqueness of the Ile Amsterdam's diatom flora is reflecting one of the most typical features of oceanic islands: the fact that the flora and fauna of these islands are usually disharmonic (Gillespie 2007) with some genera tending to be overrepresented whereas others are missing or only show a reduced diversity. The genus *Pinnularia* accounts for more than 22% of all recorded taxa whereas other typical species-rich genera such as *Navicula* or *Nitzschia* are less abundantly present on the island. Nineteen genera are represented by only one species and cymbelloid taxa, common in the Arctic region, are even completely absent. Typical terrestrial genera such as *Humidophila* and *Luticola* are quite diversified on Ile Amsterdam. *Humidophila* species are present worldwide, with a large number of endemic taxa restricted to the (sub)-Antarctic region (Le Cohu & Van de Vijver 2002; Van de Vijver et al. 2002c; Kopalová et al. 2015). Recently, two new *Humidophila* taxa were described from Ile Amsterdam (Chattová et al. 2018): *Humidophila amsterdamensis*, found in a sample taken from semi-dry mosses (FVI) that were collected from a small cave bog pond, and *Humidophila rouhaniana*, which was observed in an almost dry moss sample (FVII) collected from the Jardin Météo in the vicinity of the base Martin-de-Viviès. Both *Humidophila* taxa were frequently reported with other endemic taxa that were typically found in caves and lava tunnels on Ile Amsterdam, such as *Halamphora dagmarobbelsiana* Van de Vijver & Levkov, *Mayamaea cavernicola*, *Microfissurata australis* Van de Vijver & Lange-Bert., and *Orthoseira verleyenii*. The other genus, *Luticola*, is one of the dominant components of the terrestrial diatom flora in Antarctic terrestrial habitats. The genus has one of the highest levels of endemism of any diatom genus in Antarctica, both in terms of total number of species (taxon endemism) and the percentage of the entire genus (phylogenetic endemism) (Kociolek et al. 2017). The *Luticola* records on Ile Amsterdam confirm this high level of endemism, with three recently described taxa *L. beyensii* Van de Vijver et al., *L. ivetana*, and *L. vancampiana* Chattová & Van de Vijver (Chattová et al. 2017) confined to Ile Amsterdam and/or Ile Saint-Paul. The high diversity of the terrestrial genera is most likely linked to the large diversity in aerophilic microhabitats (moss vegetation on the moist rock faces or in caves) on the island.

The moss-inhabiting diatom flora of Ile Amsterdam is more species-rich (125 species) compared to the 104 taxa recorded from the freshwater samples on the same island by Chattová et al. (2014), and to the 60 taxa observed in the terrestrial samples from Ile Saint-Paul (Chattová 2017). The high species richness is confirmed with the results of the incidence-based species richness estimator, clearly demonstrating that the moss sampling effort reflected the true diatom species richness, with the best results among investigated habitats (between 88 and 90%). The expected total number of taxa in the freshwater samples on Ile Amsterdam is 110 (ICE) or 113 (Chao2) and 72 (ICE) or 69 (Chao2) in the terrestrial samples collected on Ile Saint-Paul, suggesting that the counting protocol scored between 87 and 89% of the total taxa present in the freshwater samples and between 83 and 86% in the case of the terrestrial flora

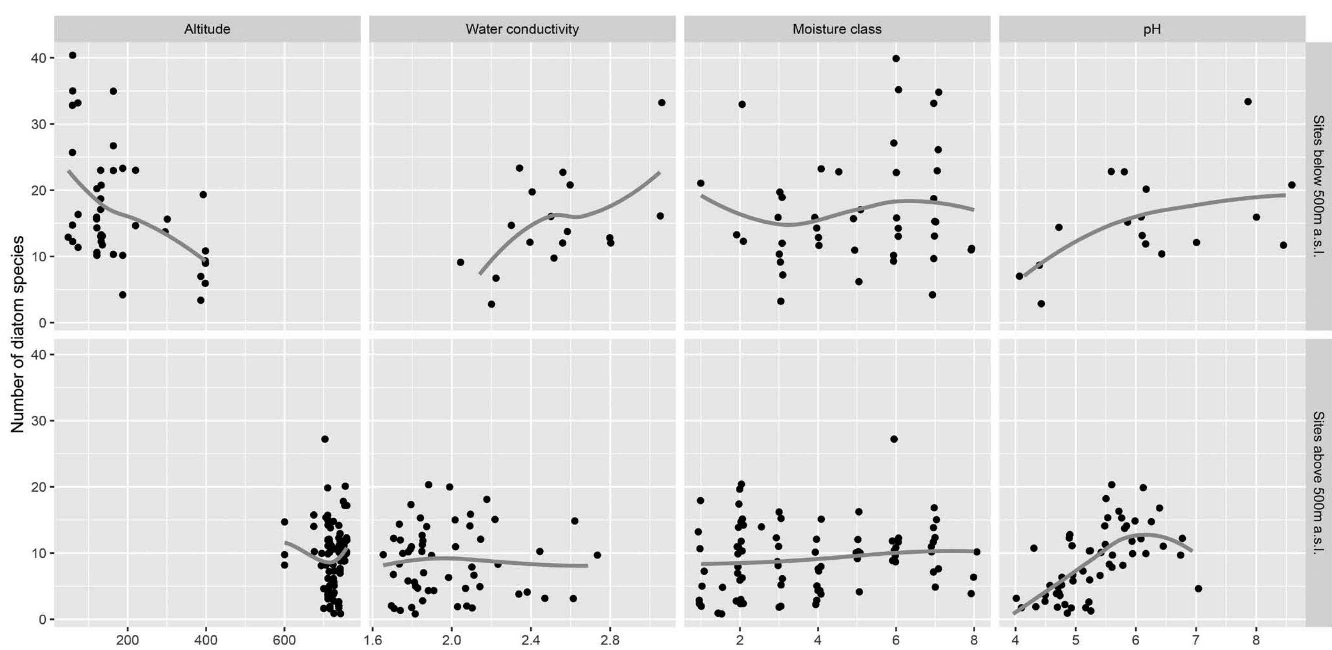

Figure 5 – A scatterplot showing the relation between species richness and environmental variables (elevation, pH, moisture, and conductivity), with the samples divided into two groups, according to elevation (0–500 m a.s.l. and above 500 m a.s.l.). Note that the species richness is clearly increasing with increasing pH and conductivity in the samples of the lower elevations.

of Ile Saint-Paul. This higher species richness of the moss-inhabiting diatom flora is most likely the result of a higher diversity of moss (micro) habitats but can also be the result of undersampling and underreporting in the other habitats.

When comparing the species composition of the freshwater (Chattová et al. 2014) and the moss-inhabiting diatom flora, clear differences can be observed. The main dissimilarities are reflected in the proportion of terrestrial species. The freshwater dataset contained only two *Hantzschia* species, whereas our moss dataset included four different *Hantzschia* taxa. Moreover, *Microfissurata australis* Van de Vijver & Lange-Bert., *Chamaepinnularia soehrensis* var. *muscicola* (J.B.Petersen) Lange-Bert. & Krammer, or *Geissleria* sp. were exclusively observed in mosses.

The low similarity values based on presence/absence data between Ile Amsterdam and the other islands are not surprising, considering the differences in microhabitat diversity, the rather large distances between the islands, the isolated position of Ile Amsterdam, and the relatively young geological age of the island. The most similar diatom flora (Sørensen Index = 0.48) was found on the neighbouring Ile Saint-Paul (at 80 km distance), followed by Ile de la Possession (Iles Crozet), which is located more than 1000 km to the south (table 2). The samples on Ile Saint-Paul are dominated by typical terrestrial species (two cosmopolitan *Humidophila* species: *Humidophila brekkaensis* and *H. contenta*, and *Luticola vancampiana*, so far only observed on Ile Amsterdam and Ile Saint-Paul) (Chattová 2017). The two most abundant species on Ile Amsterdam, *Eunotia paludosa* and *Frustulia lebouvieri*, are however lacking on Ile Saint-Paul. This situation is not surprising considering the lack of waterbodies on Ile Saint-Paul. The situation is different on Ile de la Possession, where species of monoraphid genera, such as *Psammothidium* and *Planothidium*, dominate the flora (Van de Vijver & Beyens 1999b). The observed similarity is restricted to more common, often cosmopolitan species, such as *Pinnularia microstauron*, *Rhopalodia rupestris* (W.Sm.) Krammer, and *Humidophila contenta*. Typical sub-Antarctic species shared between the islands include *Humidophila vidalii* (Van de Vijver, Ledeganck & Beyens) R.L.Lowe et al., *Humidophila crozetikerguelensis*, and *Pinnularia acidicola* var. *acidicola* Van de Vijver & Beyens. The low similarity also confirms the highly specific status of the diatom flora on Ile Amsterdam. A large number of taxa are only unequivocally identified on genus level and are listed in table 1 as cf. or sp. This high number of unidentified taxa is the result of the more fine-grained taxonomy that is nowadays applied when characterising the (sub-)Antarctic diatom flora. Those species show some affinity with known taxa but at the same time have sufficient differences to allow separation as independent taxa. In the past, these unidentified species would most probably have been given European or North American names as a result of a too broad interpretation of the original species descriptions. This historic “force-fitting” (Tyler 1996) had severe consequences for our understanding of the ecology, diversity, and biogeographical distribution of diatoms, as it not only stretched the morphological boundaries of many species, but also reinforced the idea that most diatom species have cosmopolitan distributions and are ecologic generalists.

Similarly, recent molecular studies of the diatom flora from the sub-Antarctic islands and the Maritime Antarctic Region indicate that the cosmopolitan nature of many non-marine (sub-)Antarctic diatoms might be overestimated. Distinct Antarctic lineages have been confirmed within two widely distributed diatom species complexes, *Pinnularia borealis* and *Hantzschia amphioxys* (Souffreau et al. 2013b; Pinseel et al. 2019). Pinseel et al. (2020) included several samples of *P. borealis* from Ile Amsterdam and Ile Saint-Paul in their analysis, revealing multiple distinct *P. borealis* species present on both islands. Based on the dataset of Pinseel et al. (2020) (their Supplementary Fig. 5), those distinct *P. borealis* species have only been found in Patagonia, Tasmania, and on other sub-Antarctic islands in the southern Indian Ocean. These data, showing high levels of hidden species-level diversity of *P. borealis* in sub-Antarctica including Ile Amsterdam, suggest the presence of several endemic *P. borealis* species in the area. It is therefore likely that the true species-level diversity and endemicity of the Ile Amsterdam’s diatom flora remain hidden and underestimated. Further molecular research is needed to shed a more detailed light on the cryptic diversity and biogeography of other presumed cosmopolitan diatom species in (sub-)Antarctica, to unravel the true nature of such cosmopolitan morphospecies.

Moss-inhabiting diatom communities

Both environmental data and diatom distributions indicate that apart from the effect of elevation, conductivity, pH, and moisture are the major factors determining the structure of moss-inhabiting diatom communities on Ile Amsterdam. The effect of nutrients and ions as determining factors remains unclear as only a small part of the samples (25) was analysed for physico-chemical parameters and drawing any conclusions should be done with caution.

No elevated phosphorous values were detected in the samples included in this study, all samples showed low PO_4^{3-}-P values (0.01–0.06 mg/l). This is in contrast to an elevated phosphorous value (1.58 mg/l) reported by Chattová et al. (2014) from one sample (W031) taken from a pool in the middle of a fur seal colony, where the presence of marine mammals together with soil erosion might have caused a higher phosphorous load in that sample. None of the moss samples was taken from areas heavily influenced by animals, which is a possible explanation of the generally quite low nutrient values. The high levels of Cl^- and Na^+ in the coastal samples of groups 3, 5, and 6 most likely result from sea spray that is continuously deposited in the streams overflowing the moss vegetation, combined with soil erosion and strong winds.

The mosses in the region near the Falaises d’Entrecasteaux and Pointe Del Cano were taken from waterbodies showing an almost circumneutral to clearly alkaline pH, whereas the waterbodies in the upper Caldera are strictly (very) acidic. The areas of d’Entrecasteaux and Del Cano (groups 3 and 5) represent a similar habitat of very steep cliffs with small ravines and their diatom communities show some clear similarities. Samples of both groups are dominated by taxa preferring circumneutral to alkaline conditions such as *Sellaphora* cf. *seminulum*, *Rhopalodia rupestris*, and several *Nitzschia* taxa (Hofmann et al. 2011). However, the groups significantly differ in their dominant (indicator) species, with *Platessa oblongella* and *Psammothidium investians* characterising the third group of the slightly acidic to circumneutral samples from Del Cano, while *Planothidium subantarcticum* almost exclusively dominates the alkaline samples of the fifth group. In contrast, the alkaline moss-inhabiting diatom communities on Ile de la Possession (Van de Vijver & Beyens 1999b) and Iles Kerguelen (Van de Vijver et al. 2001, Gremmen et al. 2007), have very high abundances of various fragilarioid taxa such as *Frankophila maillardii* (Le Cohu) Lange-Bert., *Fragilaria* aff. *vaucheriae* (Kütz.) J.B.Petersen, and *Distrionella germainii* (E.Reichardt & Lange-Bert.) E.Morales, Bahls & Cody, whereas the diatom flora on Ile Amsterdam is extremely poor in fragilarioid taxa. The only araphids on Ile Amsterdam are *Pseudostaurosira naveana* (Le Cohu) E.Morales & M.B.Edlund, *Pseudostaurosira* cf. *trainorii* E.Morales, *Stauroforma* aff. *exiguiformis* (Lange-Bert.) R.J.Flower, V.J.Jones & Round, and *Fragilaria* cf. *neoproducta* Lange-Bert., found in the caves or the coastal habitats.

The acidic diatom communities represented by the high elevation samples from the fourth group are dominated by *Frustulia lebouvieri* and *Eunotia paludosa*. This group is typical for locations found on Ile Amsterdam at higher elevations (above 500 m a.s.l.) characterised by peat bogs with higher moisture levels and acidic pH. Similar communities characterised by the dominance of *Eunotia paludosa* were reported from Gough Island (P. Vinšová, Charles University, Prague, Czechia, unpubl. res.), South Georgia (Van de Vijver & Beyens 1997), and Ile de la Possession (Van de Vijver & Beyens 1999b). However, differences can be found in the associated diatom flora of the dominant species. On Ile de la Possession, the *Eunotia paludosa* dominated assemblages were co-dominated by *Chamaepinnularia soehrensis* var. *muscicola* (J.B.Petersen) Lange-Bert. & Krammer, *Aulacoseira principissa* Van de Vijver (reported as *A. alpigena* (Grunow) Krammer), and *Adlafia bryophyla* (J.B.Petersen) Lange-Bert., whereas on Gough Island, they were co-dominated by *Eunotia* cf. *fallax* (Cleve) and *Chamaepinnularia* cf. *begeri* (Krasske) Lange-Bert. (Van de Vijver & Beyens 1999b; P. Vinšová unpublished results).

A major habitat difference between the Caldera region on Ile Amsterdam and the other sub-Antarctic islands is the dominance of *Sphagnum* taxa as peat-forming mosses on Ile Amsterdam, while *Sphagnum* taxa are completely absent from the sub-Antarctic islands (Flatberg et al. 2011). *Sphagnum* is well known for acidifying its environment (Munson & Gherini 1993; Siegel et al. 2006) and this activity in the isolated Caldera region in the combination with the flat geomorphology of the Caldera most likely created the highly acidic and oligotrophic habitat where the acidic diatom community could develop (Chattová et al. 2014). Those relatively uniform and species-poor high elevation diatom communities in the Caldera region are in strong contrast to the diatom communities from the coastal areas of Del Cano and Falaises d'Entrecasteaux. The explanation can be found in the geological history of the island. Ile Amsterdam has been shaped by two consecutive volcanic episodes resulting in a formation of mostly subalkaline, magnesium-rich tholeiitic basalt bedrock (Doucet et al. 2004). This geochemical composition probably influenced the development of the slightly acidic and subalkaline diatom communities of Del Cano and d'Entrecasteaux. Those areas most likely represent the original habitat for diatom communities on Ile Amsterdam.

The typical terrestrial taxa such as *Hantzschia amphioxys* complex, *Humidophila brekkaensis*, *Pinnularia borealis* complex, or *Orthoseira roeseana*, forming the driest assemblages of group 1, play only a minor role or are completely absent from Ile de la Possession and Gough Island (Van de Vijver & Beyens 1999b; P. Vinšová unpubl. res.). The only similar feature of the terrestrial diatom flora on Ile Amsterdam with those on Ile de la Possession is the dominance of *Humidophila* cf. *contenta*. Differences can be found in the associated diatom flora of these communities, mainly composed of *Planothidium aueri* (Krasske) Lange-Bert. and *Fragilaria* cf. *vaucheriae*. The most similar terrestrial diatom flora was found on dry mosses from South Georgia, with the samples dominated mainly by well-known, cosmopolitan taxa, such as *Hantzschia amphioxys* complex, *Pinnularia borealis* complex, *Orthoseira roeseana*, and *Humidophila* cf. *contenta* (Van de Vijver & Beyens 1997).

Moisture content is one of the principal factors determining the diatom assemblages in moss communities in the (sub-)Antarctic region (Van de Vijver & Beyens 1999b; Kopalová et al. 2014) and it is one of the factors co-responsible for the classification of the main groups of moss-inhabiting diatom communities on Ile Amsterdam. A clear difference between diatom communities growing on wet versus dry mosses was found (figs 1, 2). Moisture can therefore be considered as an important factor, even when the wettest samples are not the most species-rich on the island, resulting most likely from the fact that the majority of the wet samples are the most acidic, with lower conductivity values. Moreover, the highly diverse cave samples represent at the same time some of the driest habitats on the island. Future diatom research on Ile Amsterdam should focus on the influence and specificity of the cave and lava tube microhabitat. To accomplish this, a large set of new lava tube and cave samples was recently (austral summer of 2016; B. Van de Vijver pers. comm.) collected on Ile Amsterdam and are currently being investigated.

CONCLUSION

The isolated geographic position and physical features of the island have resulted in the presence of a unique diatom flora, characterised by many species found to be endemic to Ile Amsterdam or sub-Antarctica. This study revealed a high number of diatom taxa unknown to science that will need formal description in the future. Future molecular research could lend another perspective and help to reveal the true extent of the likely underestimated diatom diversity and endemism on Ile Amsterdam. The moss-inhabiting diatom flora on Ile Amsterdam showed a limited affinity to the moss-inhabiting diatom flora from several other sub-Antarctic islands, indicating the presence of clear biogeographical patterns in the area. Our findings provide useful information for future investigations, including research on the influence and specificity of the cave and lava tube microhabitat on diatoms, the application of diatoms as proxy in palaeo-ecological research, and biogeographic or molecular studies.

SUPPLEMENTARY FILES

Supplementary file 1 – Location of Ile Amsterdam in the Southern Hemisphere, indication of the main sampling sites and the main topographic features.

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Supplementary file 2 – Characteristics (when available) of samples collected on Ile Amsterdam.

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Supplementary file 3 – Figures related to methods and results.

https://doi.org/10.5091/plecevo.2021.1767.2361

Supplementary file 4 – Genera ordered by decreasing percental portion (%) calculated on the number of taxa (n).

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Supplementary file 5 – Cluster diagram (Bray-Curtis dissimilarity calculated on square root transformed species data) of the total sample set with indication of the six groups.

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