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Diatom communities differ among Antarctic moss and lichen vegetation types

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Abstract

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Diatom communities differ among Antarctic moss and lichen vegetation types

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Abstract: Continental Antarctica is a polar desert containing sparse pockets of vegetation within ice-free areas. Despite the recognized association between lichens, mosses, and epiphytic diatoms, environmental factors controlling diatom community structure are poorly understood. We investigated the association between diatom communities and host vegetation characteristics by experimentally adding nutrients and/or water to two bryophyte (healthy and moribund) and two lichen (crustose and *Usnea*) vegetation types in the Windmill Islands. Diatom communities were morphologically characterized, diversity indices calculated, and differences between treatments, vegetation type, and vegetation characteristics tested. We identified 49 diatom taxa, 8 of which occurred >1% relative abundance. Bryophyte and lichen vegetation harbored significantly different diatom communities, both in composition and diversity indices. Specifically, *Luticola muticopsis* was more prevalent in moribund bryophytes and crustose lichens, and *Usnea* lichens showed lower species richness than other types. While nutrient and water additions did not significantly alter diatom communities, diversity indices and some species showed relationships with vegetation physiological characteristics, notably %N and δ^{13}C, suggesting the importance of ambient gradients in water and nutrient availability. Collectively, this work suggests that future conditions favoring the dominance of a particular vegetation type may have a homogenizing effect on the terrestrial diatom communities of East Antarctica.

Key words: Bryophyte, climate change, Bacillariophyceae, algae, Antarctic Region, East Antarctica

Introduction

Despite Antarctica's vast area, less than 1% of the continent is ice-free (Convey and Peck 2019). While these ice-free 'oases' are largely free of vascular plants, mosses and lichens are common (Convey et al. 2014), as well as an increasingly studied "microflora" of protists, bacteria, and fungi (Zhang et al. 2019). Antarctic bryophytes (including mosses and liverworts) and lichens are limited in growth and distribution by extremes in wind, temperature, and photoperiod (Wasley et al. 2006a, b, Clarke et al. 2012, Robinson et al., 2018), as well as bioavailable (liquid) water and nutrients (Convey et al. 2014). Nonetheless, Antarctica features about 100 bryophyte and 200 lichen species (Chown et al. 2015), which have been extensively studied throughout East Antarctica (Schroeter et al. 2011, Ball and Virginia 2014). Additionally, terrestrial Antarctic mosses in particular have long been understood to provide suitable microclimates that harbor a diverse community, including arthropods (Nielsen and King 2015), green algae, cyanobacteria, and diatoms (Ohtani 1986).

Diatoms are ubiquitous across Antarctica, present within both the marine environment, as well as terrestrial and benthic freshwater habitats (Kellogg and Kellogg 2002). The non-marine Antarctic diatom flora is composed of a high number of endemic taxa specific to particular bioregions, reflecting both sensitivity to physiochemical parameters and their geographic isolation (Sakaeva et al. 2016, Zidarova et al. 2016). Because of the species-specific responses of diatoms to their environment, diatoms have been used to assess the ecological status of Antarctic lakes (Spaulding et al. 2010) and streams (Stanish et al. 2011). Moss-associated diatoms have been well-characterized on the Sub-Antarctic islands, such as the Prince Edward Islands (Van de Vijver et al. 2008) and Ile de la Possession (Crozet Archipelago, Van de Vijver et al. 002). Further work has focused on the Maritime Antarctic Region, such as Livingston Island and James Ross Island (Kopalová et al. 2014). However, despite the wealth of historical sources, biogeographical and ecological studies on the Antarctic Continent have generally examined diatoms and mosses separately (Opalinski 1972), without investigating potential relationships between mosses and their associated diatom communities. Even less is known about diatoms inhabiting lichens, which have been largely unexplored save for the recent work of Chattová (2018) on James Ross Island in the Antarctic Peninsula.

The formation of ‘microclimates’ within the vegetation matrix may be a major factor supporting diatom inhabitation of mosses and lichens by providing sufficient water availability and shelter from the external environment (Beyer et al. 2000 and references therein). Previous work has found moisture content to be an influential variable for epiphytic diatom communities within the Maritime Antarctic (Kopalová et al. 2014) and the Sub-Antarctic islands (Van de Vijver et al. 2002, 2008). Increased water availability and associated habitat connectivity is anticipated for Antarctica in the future through a reduction of ice and permafrost cover within coastal areas (Lee et al., 2017), which is likely to also coincide with increased nutrient liberation (Convey & Peck 2019). A warmer, wetter climate in the Windmill Islands, East Antarctica may furthermore result in the regeneration and expansion of moss beds based on species-specific differences and indirect effects of climate change (Wasley et al. 2012, Robinson et al. 2018).

Within close proximity to Casey Station, Wasley et al. (2006a) tested for bryophyte and lichen community responses to *in situ* water and nutrient additions based upon projected changes in these resources due to climate change. The test area originated at the edge of a meltwater lake, spanning from bryophyte-dominated to lichen-encrusted moss communities up a hill, and included four vegetation types: 1) healthy bryophytes, 2) moribund bryophytes, 3) crustose lichens, and 4) lichens belonging to the genus *Usnea* Dillenius ex Adanson. Vegetation responses were examined by measuring chlorophyll *a*, total water content, carbon (C), nitrogen (N) and phosphorus (P) content, and δ^{13}C and δ^{15}N stable isotope ratios, among other variables (Wasley et al. 2006a). Increased productivity was observed for healthy bryophyte and *Usnea* lichen vegetation with the combined addition of water and nutrients, and nutrient additions appeared to illicit a stronger response than water (Wasley et al. 2006a). This suggests that Antarctic bryophyte communities will respond to anticipated changes to their environment, and may in turn create carry-over effects to their associated epiphytes (Robinson et al. 2018) such as diatoms, though these impacts have not been investigated.

In the current study, we characterize diatom communities inhabiting the bryophyte and lichen samples from the experiment conducted by Wasley et al. (2006a) to gain further insights into the potential impacts of increases in water and nutrient availability in East Antarctica. Our objectives were threefold: First, do diatom communities differ among different bryophyte and lichen vegetation types; secondly, do nutrient and water additions impact diatom communities; and third, do diatom communities correspond to differences in bryophyte and lichen physiological characteristics? Given the results of Wasley et al. (2006a), as well as past studies linking epiphytic diatoms community structure to the characteristics of their environment (Kopalová et al. 2014), we expected that water and nutrient additions should have a strong structuring effect on epiphytic diatoms growing on mosses and lichens in this experiment.

Methods

Study area and sampling

The study site was located within Antarctic Specially Protected Area (ASPA) 135, about 1 km away from Casey Station on Bailey Peninsula, Windmill Islands (Wilkes Land), East Antarctica. The Windmill Islands are collectively one of the most extensively studied areas on the continent and are known for their well-developed lichen and bryophyte vegetation (Robinson et al. 2018). This vegetation is due to a long history of nutrient and salinity inputs by numerous penguin colonies, creating strong gradients of both water and nutrient availability (Melick et al. 1994). At present, there are a number of penguin breeding sites in the area which strongly impact the surrounding flora due to increased nutrient inputs (Melick et al. 1994, Beyer et al. 2000).

The experimental site was located nearby an abandoned penguin rookery on the western edge of a meltwater lake originating from a snow slope, of northeasterly aspect, above Thala Valley (66°116.03’S, 110°132.53’E) located at the northern boundary of ASPA 135. This site featured a vegetation gradient starting at the edge of a meltwater lake and continuing up a ridge, with an eastern aspect, away from the lake. Vegetation was categorized based on the percent coverage of four major types: healthy bryophytes, moribund bryophytes, crustose lichens, and lichens of the genus *Usnea* (Table I). The order of these four vegetation types reflects their proximity to the meltwater lake, respectively, with healthy bryophytes more common at the edge of the lake, whereas the *Usnea* community was located closer to the ridge, farthest from the lake. The dominant bryophyte across the site was the Antarctic endemic *Schistidium antarctici* Card. (Wasley et al. 2006a), previously identified as *Grimmia antarctici* (Cardot) L.I. Savicz & Smirnova (Robinson et al. 2018).

Our samples originated from a field manipulation experiment (supplemented nutrient and water regimes along the transect) performed by Wasley et al. (2006a) to simulate predicted water and nutrient increases due to climate change, and examine the physiological responses generated within each bryophyte and lichen community across treatments. In the present study, we retain the overall experimental design, and the sample coding scheme indicated in parentheses originates from Wasley et al. (2006a) (Fig. 1).

Table I. Characteristics of the bryophyte and lichen vegetation types within the experimental site, including “color coding” and descriptions of individual attributes.

Community Type	Description
Bryophyte	Healthy, "Green" brophytes are dominant at >90% cover
Moribund	Mixed Community. Approximately 50% cover of moribund bryophytes, occuring predominantly within upon ridges and 50% cover of healthy bryophytes, occuring predominantly in valleys
Crustose	Mixed Community. Dominance of Moribund bryophytes with 50% cover encrusted with both yellow and white lichens
Usnea	Mixed Community. Thin moribund bryophyte crust with dominant cover (>50%) of macrolichen *Usnea*

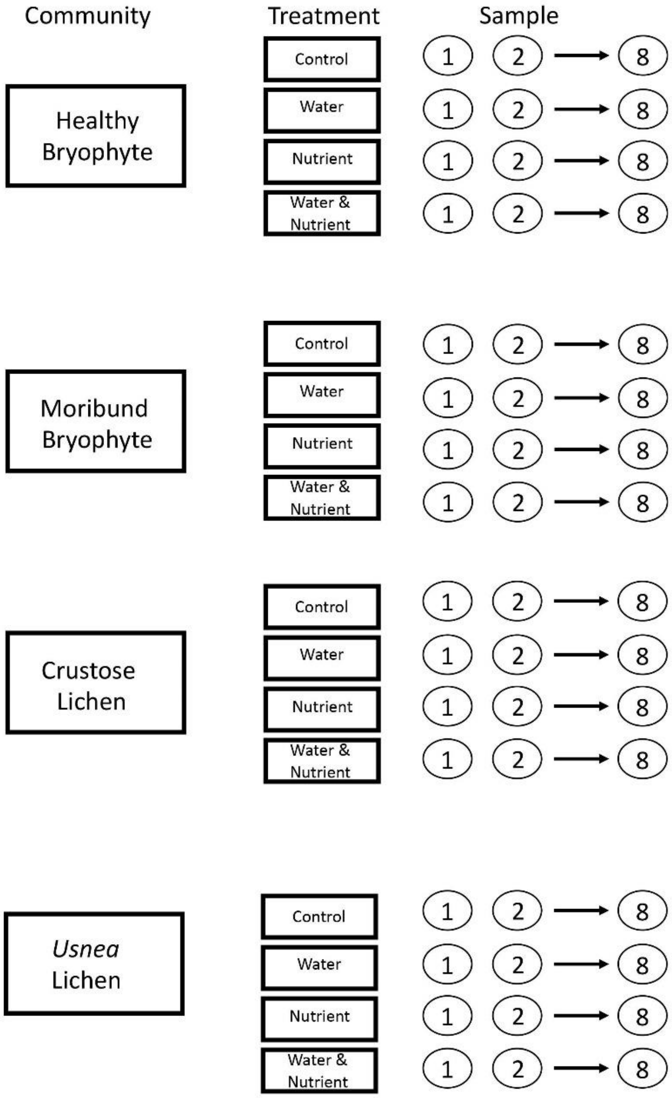

Fig. 1. Experimental design displaying the four vegetation types (healthy bryophyte, moribund bryophyte, crustose lichen, and *Usnea* lichen) alongside randomly assigned treatments (Control, Water, Nutrients, and Water + Nutrients).

Briefly, thirty-two quadrats (25 x 25 cm) within each community were randomly assigned one of the following four treatments: (1) Control (no treatment, C), (2) Water only (W), (3) Nutrient only (N), or (4) Water + Nutrient (WN). From December to February over two consecutive summer seasons (1998-1999 and 1999-2000), the two water addition treatments (W and WN) received applications of 500 mL of lake water approximately every two days. At the start of the treatment period (15 December 1999), 10 g of slow release fertilizer beads (Osmocote, Scotts Australia Pty. Ltd., Castle Hill, NSW, Australia) was applied to quadrats marked to receive nutrient additions. A low phosphorous Osmocote variety was chosen, which was composed of 18% nitrogen, 4.8% phosphorous and 9.1% potassium.

Representative community samples were collected at the end of the treatment period (3-8 March 2000). A sample from each of the 16 treatment and community groups was collected, one sample from each replicate from each community and treatment type. Samples of approximately 4 cm^2 were collected from the center of each quadrat. To quantify the physiological responses of the vegetation within the transect, total water content (TWC), chlorophyll *a* concentration, nutrient content (%N, %C, and %P), and stable isotopes (δ^{13}C and δ^{15}N) were measured. For a more detailed description of experimental and analytical methods, see Wasley et al. (2006a). An aliquot for diatom community characterization was also taken, dried, and archived until analysis. Thus, for our diatom study, one sample is equal to one quadrat.

Sample preparation and analyses

A total of 128 samples were originally collected (Table S1), but only 99 of these were successfully analyzed due to limited amounts of material and processing failures for several samples. Samples were prepared for light microscopy (LM) observation following the method described in van der

Werff (1955). Subsamples of dried bryophytes or lichens were transferred into 50 mL beakers and soaked for 10 – 14 days in 37% (v/v) H_2O_2. Once organic matter was oxidized, the sample was boiled for about 1 h, or until total volume was reduced to <10 mL. The liquid was left to cool for 1 h before the addition of $KMnO_4$ to remove undigested moss material. This resultant liquid was then "cleaned" with approximately 2-5 mL of 10% (v/v) HCl to complete the reaction. Following digestion and centrifugation (three times for 10 minutes at 3,500 *g*), cleaned diatom valves were mounted on glass microscope slides using Naphrax for further LM observation.

Light Microscopy was performed on an Olympus BX43 equipped with a Differential Interference Contrast (Nomarski) optic at 1000x magnification with oil immersion. Images were taken using an Olympus PD27 Color camera with CellSens Entry 1.15 software. Diatom valves were counted in full fields of view along random transects, with at least 400 valves counted per sample (Table S2). Only in two samples was it not possible to reach 400 valves: Sample 84 (63 valves) and Sample 9 (36 valves). Due to the low overall diversity observed in the samples, these were nonetheless included in the analyses.

Taxonomic affiliations and biogeographic data were compiled based primarily on Sabbe et al. (2003), Van de Vijver et al. (2002, 2012), Kohler et al. (2015) and Zidarova et al. (2016). In the event of ambiguous or uncertain taxa, images were taken and corresponding measurements of valve length, valve width at mid-valve, and stria density per 10 μm. When the identity of a taxon could not be confirmed based on the existing literature, the designations "cf." or "sp." were indicated alongside a proposed generic and/or species affiliation. In the study, a large number of *Luticola* D.G.Mann specimens were encountered as complete valves within girdle view, making them impossible to definitively attribute to a particular known taxon. During data collection, these specimens were thus only identified to the genus level. During data analysis, these unidentified

Luticola were assigned to species (if possible) by multiplying them by the proportion of positively identified co-occurring *Luticola* taxa in the sample. In samples where unidentified *Luticola* did not co-occur alongside other *Luticola* taxa, they remain identified only to the genus level (<1% of counts).

Statistical analyses

Count data were first transformed to relative abundances by dividing individual counts by the total number of valves counted for the corresponding sample. From these, diversity indices including genera and species richness, Evenness, and Shannon's diversity ($\log_{10}$ – based) were calculated as described previously (Sakaeva et al. 2016). A series of two-factor analysis of variance (ANOVA) tests were performed to examine if the treatments (C, W, N, and WN), vegetation type (healthy bryophytes, moribund bryophytes, crustose lichens, and lichens of the genus *Usnea*), or their interactions significantly influenced diversity metrics. Significant results were followed by applying Tukey's Honest Significant Differences (HSD) to directly compare the means between categories. Statistical significance was designated at $\alpha = 0.05$ and p values are reported.

Four genera dominated the dataset, and accounted for a large majority of the total valves counted. As such, the relative abundances of these four genera were extracted for each sample to test their response to the different treatments and vegetation types using ANOVA and Tukey's HSD as described above. The dataset is comprised of *Luticola* D.G.Mann (12 taxa), *Humidophila* Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot & Kopalová (5 taxa), *Psammothidium* Buhtkiyarova & Round (3 taxa), and *Pinnularia* Ehrenberg (1 taxon).

Initial exploration of community data began with the creation of dot plot diagrams and continued with the creation of ordinations. Rare taxa were filtered from the dataset, excluding taxa occurring at < 1% relative abundance. Diatom relative abundance data were Hellinger transformed (Legendre and Gallagher 2001), and redundancy analyses (RDA) constrained the dataset separately by treatment and for each individual vegetation type to quantify their role in explaining community structure using the *vegan* package, version 2.5-6 (Oksanen et al. 2019) in R. To test whether diatom community structure differed significantly between vegetation types and treatments, permutational analysis of variance (PERMANOVA, Anderson 2001) was performed, with significance designated at $\alpha = 0.05$.

In order to determine if physiological characteristics of bryophyte and lichen vegetation would influence diatom communities, 76 samples of the total 99 included in this study, which contained the full suite of variables examined by Wasley et al. (2006a), were analyzed further. These raw data (Table S3) were examined and, if needed, transformed in order to induce a normal distribution. TWC and δ^{15}N underwent a logarithmic transformation ($\log_{10}$ – based) whereas %N, %P, and chlorophyll *a* concentration were transformed using the natural logarithm ($\log_e$ – based). Lastly, δ^{13}C data were transformed by taking the absolute value of the term, applying $\log_{10}$ – transformation, and multiplying values by negative one (-1) in order to maintain the sign and directionality from the original data. Only one variable, %C was left untransformed.

A principal components analysis (PCA) was performed to investigate large scale relationships among the variables with the calculated diversity indices. To investigate individual relationships of measured vegetation characteristics with diatom communities, a distance-based redundancy analysis (db-RDA) using Hellinger transformed relative abundance data was performed using *vegan*. An analysis of variance (ANOVA) test was performed on the individual terms of the db-RDA using 999 permutations to test statistical significance of the individual terms within the model. All visualizations and statistical analyses were performed using the R console, version 3.5.0 (R Core Team 2018).

Results

Diatom flora

Overall, 49 taxa belonging to 20 genera were observed. Table II presents all diatom taxa, as species, forms, and varieties encountered within the study. The genera *Luticola* (12 taxa) and *Humidophila* (five taxa) were the most diverse, and together with *Pinnularia* and *Psammothidium* constituted the four most abundant genera. The five most abundant taxa, representing approximately 92% of all valves counted within the analysis, are: *Humidophila gallica* (W.Smith) Lowe, Kociolek, Q.You, Q.Wang & Stepanek (59%), *Humidophila australis* (Van de Vijver & Sabbe) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová (~11%), *Pinnularia borealis* Ehrenberg (~11%), *Luticola muticopsis* (Van Heurck) D.G.Mann (8%), and *Luticola austroatlantica* Van de Vijver, Kopalová, Spaulding & Esposito (4%). At least one of these five most abundant taxa occurred in each sample (Fig. 2), and only eight taxa occurred with a relative abundance >1% in the study as a whole (Fig. 3).

Diversity metrics

Boxplots displaying species richness, Shannon’s diversity, and Evenness, grouped by vegetation type and separated by treatment (Fig. 4), show species richness ranged between 4 – 12 taxa per sample. An average of seven taxa (median = 7) was observed across the samples. Shannon’s diversity ranged between 0.4 to 1.8 for all samples, and the majority possessed a value of approximately 1. Evenness scores for the majority of samples were between approximately 0.2 to 0.8, with the upper extreme value of 0.8 observed only once.

Table II. Diatom species, authorities and geographic distribution for taxa observed within the study. Distribution data codes are as follows: Continental Antarctica (CA), Maritime Antarctica (MA), Sub-Antarctica (SA) Globally distributed (Cosmopolitan), Southern Hemisphere (SH), and marine species (Marine).

Species & Authority	**Species Code**	**Distribution**	**Relative Abundance (%)**
Achnanthes Bory sp. 1	Acn_Sp1	—	0.233
Achnanthes taylorensis D.E.Kellogg, Stuiver, T.B.Kellogg & G.H.Denton	Ach_Tay	CA	0.018
Centric unidentified	Cnt_Xxx	—	0.043
Chamaepinnularia cymatopleura (West & G.S.West) Cavacini	Cha_Cym	CA	0.005
Cocconeis cf. *fasciolata* (Ehrenberg) N.E.Brown	Ccf_Fas	—	0.089
Cocconeis Ehrenberg	Coc_Sp1	—	0.010
Fragilaria Lyngbye	Fra_Xxx	—	0.003
Fragilariopsis Hustedt sp. 1	Fop_Sp1	—	0.010
Fragilariopsis Hustedt sp. 2	Fop_Sp2	—	0.015
Fragilariopsis Hustedt sp. 3	Fop_Xxx	—	0.003
Genus uncertain 1	Gen_Xx	—	0.476
Genus uncertain 2	Smt_Xxx	—	0.003
Gomphonema Ehrenberg	Gom_Sp1	—	0.005
Humidophila australis (Van de Vijver & Sabbe) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová	Hum_Aus	MA/CA	10.562
Humidophila cf. *gallica* (W.Smith) Lowe, Kociolek, Q.You, Q.Wang & Stepanek	Dcf_Gal	—	0.757
Humidophila cf. *inconspicua* (Kopalová & Van de Vijver) R.L. Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová	Hcf_Inc	—	0.122
Humidophila gallica (W.Smith) Lowe, Kociolek, Q.You, Q.Wang & Stepanek	Hum_Gal	Cosmopolitan	59.129
Humidophila inconspicua (Kopalová & Van de Vijver) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová	Hum_Inc	MA	0.053
Luticola austroatlantica Van de Vijver, Kopalová, Spaulding & Esposito	Lut_Aus	MA/CA	4.323
Luticola cf. *katkae* Van de Vijver & Zidarova	Lcf_Kat	—	0.028
Luticola D.G. Mann	Lut_Xxx	—	0.114
Luticola D.G. Mann sp. 2	Lut_Sp2	—	0.020
Luticola D.G. Mann sp. 3	Lut_Sp3	—	0.117
Luticola D.G. Mann sp. 4	Lut_Sp4	—	0.327
Luticola D.G. Mann sp. 5	Lut_Sp5	—	0.063
Luticola dolia Spaulding & Esposito	Lut_Dol	CA	0.038
Luticola elegans (West & West) Kohler & Kopalová	Lut_Ele	CA	1.003
Luticola muticopsis (Van Heurck) D.G. Mann	Lut_Mut	SH	7.659
Luticola permuticopsis Kopalová & Van de Vijver	Lut_Per	MA/CA	0.154
Luticola pseudomurrayi Van de Vijver & Tavernier	Lut_Psu	CA	0.018
Nanofrustulum shiloi (Lee, Reimer & McEnery) Round, Hallsteinsen & Paache	Nan_Shi	Marine	0.020
Navicula Bory sp. 1	Nav_Sp1	—	0.005
Navicula cf. *cremeri* Van de Vijver & Zidarova	Ncf_Cre	—	0.003
Nitzschia Hassall sp. 1	Nit_Sp1	—	0.005
Nitzschia Hassall sp. 2	Nit_Sp2	—	0.005
Nitzschia Hassall sp. 3	Nit_Sp3	—	0.005
Pinnularia borealis Ehrenberg	Pin_Bor	Cosmopolitan	10.597
Planothidium Round & L.Bukhtiyarova sp. 1	Pla_Sp1	—	0.005
Planothidium Round & L.Bukhtiyarova sp. 2	Pla_Sp2	—	0.010
Planothidium Round & L.Bukhtiyarova sp. 3	Pla_Sp3	—	0.003
Planothidium Round & L.Bukhtiyarova sp. 4	Pla_Sp4	—	0.005

Species & Authority	Species Code	Distribution	Relative Abundance (%)
Planothidium renei (Lange-Bertalot & Schmidt) Van de Vijver	Pla_Ren	Southern Hemisphere	0.020
Psammothidium papilio (D.E. Kellogg, M. Stuiver, T.B. Kellogg & G.H. Denton) Kopalová & Van de Vijver	Psa_Pap	MA/CA	3.472
Psammothidium rostrogermainii Vam de Vijver, Kopalová & Zidarova	Psa_Ros	MA/CA	0.023
Psammothidium stauroneioides (Manguin) Buhktiyarova	Psa_Sta	SA/CA	0.291
Pseudostaurosira D.M.Williams & Round sp. 1	Pse_Sp1	—	0.003
Stauroforma inermis Flower, Jones & Round	Sta_Ine	MA/CA	0.122
Stauroneis Ehrenberg	Sta_Sp1	—	0.005
Staurosirella D.M.Wiliams & Round sp. 1	Str_Sp1	—	0.003

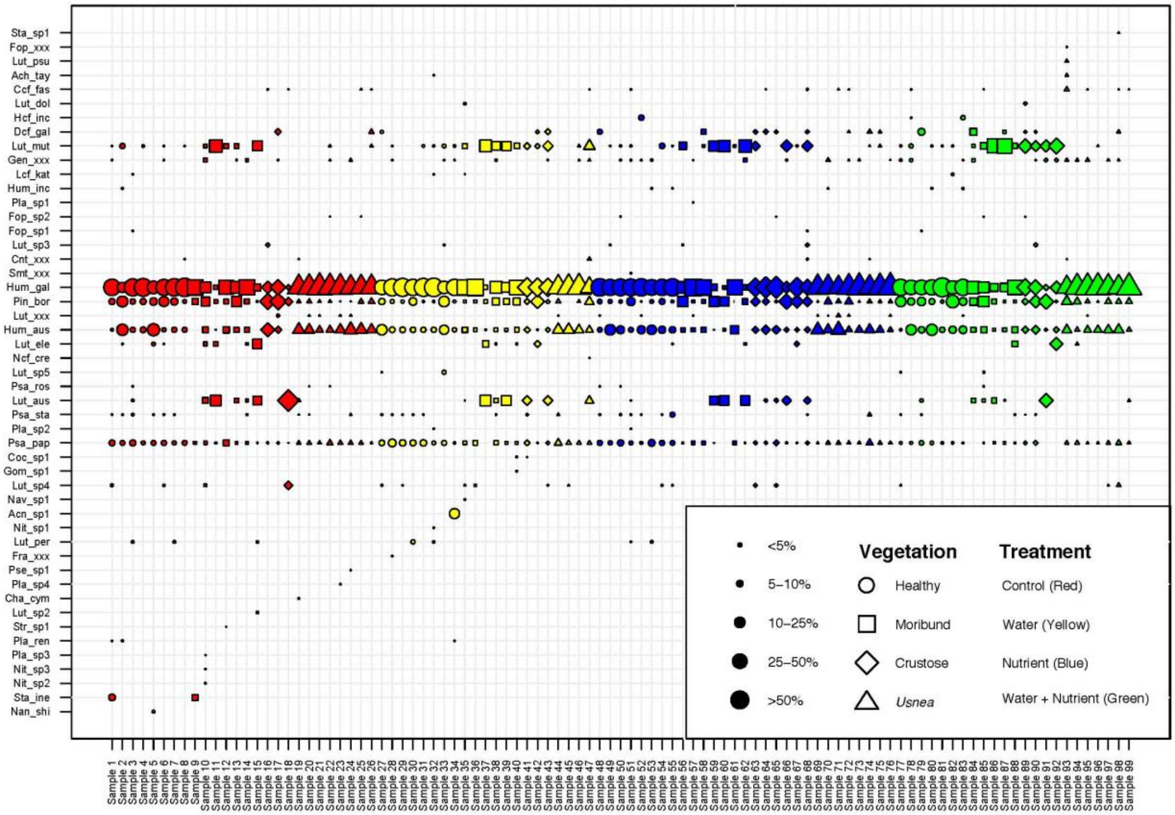

Fig. 2. Dot plot diagram of all diatom taxa across all samples within the study. Diatom species codes shown on the y-axis are defined in Table II. Treatments are color coded within the plot, Control (Red), Water (Yellow), Nutrients (Blue) and Water + Nutrients (Green). Vegetation type is coded by shape: "Circle" (healthy bryophyte), "Square" (moribund bryophyte), "Diamond" (crustose lichen), and "Triangle" (*Usnea* lichen).

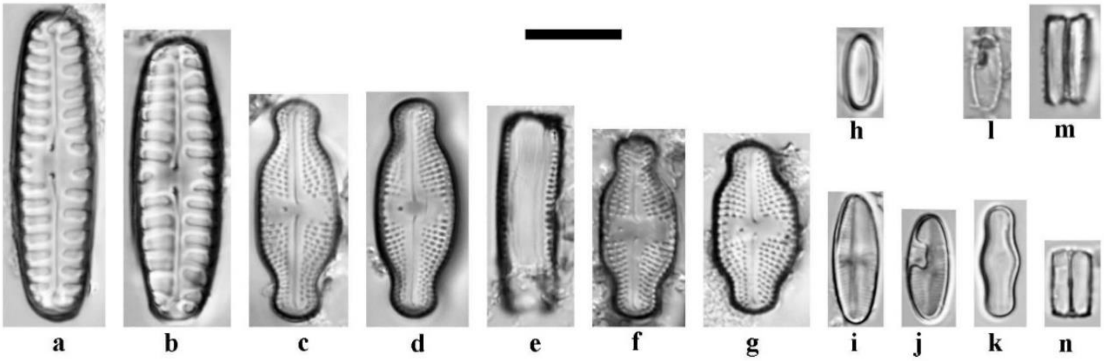

Fig. 3. Common diatom species associated with bryophyte and lichen vegetation types. All taxa shown occurred at greater than or equal to 1% relative abundance across samples. **a, b.** *Pinnularia borealis*. **c, d.** *Luticola austroatlantica*. **e.** *Luticola* in girdle view. **f, g.** *Luticola. muticopsis*. **h.** *Humidophila* cf. *gallica*. **i**, **j** *Psammothidium papilio*. **l**, **m.** *Humidophila gallica*. **k, n.** *Humidophila. australis*. Central 10 µm scale bar applies to all images.

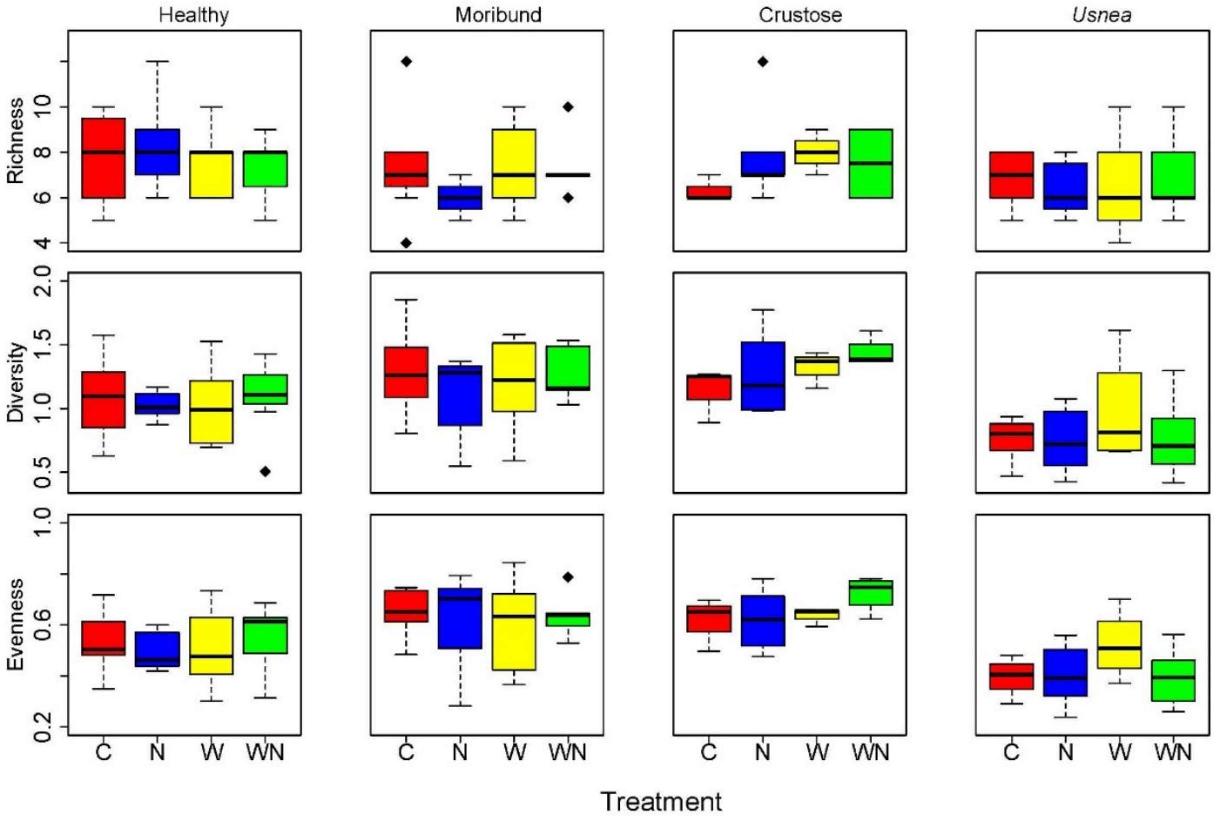

Fig. 4. Box plots of species richness, Shannon's diversity index and Evenness arranged by vegetation type and treatment. Treatments are color coded, with abbreviations, within the plot, Control (Red)-"C", Water (Yellow)-"W", Nutrients (Blue)-"N", and Water + Nutrients (Green)-"WN". Vegetation types follow the designation: "Healthy" (healthy bryophyte), "Moribund" (moribund bryophyte), "*Usnea*" (*Usnea* lichen), and "Crustose" (crustose lichen).

Across all three diversity metrics, neither treatment nor the interaction between treatment and vegetation type were significant (Table III). While vegetation type also did not have a significant effect on species richness, it did have a significant effect on Shannon's diversity ($p<<0.01$), and Evenness ($p<<0.01$). Specifically, *Usnea* vegetation had lower Shannon diversity than healthy ($p=0.003$) and moribund ($p<<0.01$) bryophytes, and crustose lichens had significantly greater Shannon's diversity than *Usnea* ($p<<0.01$). *Post hoc* analysis of Evenness between vegetation types showed that both moribund bryophytes ($p=0.007$) and crustose lichens ($p=0.004$) had significantly greater values than healthy bryophytes. Crustose lichen diatom community Evenness was also greater than in *Usnea* ($p<<0.001$), and *Usnea* Evenness values were lower than in healthy bryophytes ($p=0.007$).

Patterns between the four most abundant genera

Relative abundances of the genera *Luticola, Pinnularia*, and *Humidophila* were significantly different between vegetation types, though there were no significant differences among treatments when examined with two-way ANOVA (Table III). Only the genus *Psammothidium* showed significantly different relative abundances between vegetation types and among treatments. Specifically, healthy bryophytes contained more *Psammothidium* taxa than did moribund ($p<<0.01$), *Usnea* ($p<<0.01$), and crustose ($p<<0.01$) vegetation types. *Post hoc* analysis of treatment categories showed that the Water + Nutrient treatment had lower relative abundances of *Psammothidium* than the Water-only treatment ($p<<0.01$).

Table III. The results of the analysis of variance (ANOVA), permutational analysis of variance (PERMANOVA) and redundancy analysis (RDA) models. Significant results are in bold.

Statistical Test	Variable	Transformation	Test	DF (model, error)	*F* Ratio	P Value	Post Hoc Comparison	diff	P Value
ANOVA	Species Richness	log 10	Whole Model	15, 83	9.40E-01	5.30E-01			
			Treatment	3	8.00E-02	9.70E-01			
			Community	3	2.24E+00	9.00E-02			
			Treatment x Community	9	7.90E-01	6.30E-01			
ANOVA	Shannon Diversity	none	Whole Model	15, 83	3.23E+00	3.00E-04	Crustone - *Usnea*	4.90E-01	5.00E-07
			Treatment	3	5.60E-01	6.40E-01	*Usnea* - Healthy	-2.60E-01	3.00E-03
			Community	**3**	**1.39E+01**	**1.91E-07**	*Usnea* - Moribund	-4.10E-01	3.20E-06
			Treatment x Community	9	5.60E-01	8.30E-01	Crustose - Healthy	2.43E-01	2.00E-02
ANOVA	Evenness	none	Whole Model	15, 83	4.09E+00	1.50E-05	Moribund - Healthy	1.06E-01	7.00E-03
			Treatment	3	4.20E-01	7.30E-01	Crustose - Healthy	1.30E-01	4.00E-03
			Community	**3**	**1.81E+01**	**4.10E-09**	Crustone - *Usnea*	2.20E-02	1.00E-08
			Treatment x Community	9	6.60E-01	7.40E-01	*Usnea* - Healthy	-1.04E-01	7.00E-03
							Usnea - Moribund	-0.212	1E-08
ANOVA	*Luticola*	square root	Whole Model	15, 83	5.77E+00	6.11E-08	Moribund - Healthy	3.02E-01	3.00E-07
			Treatment	3	9.51E-01	4.20E-01	Crustose - Healthy	2.41E-01	4.77E-04
			Community	**3**	**2.64E+01**	**4.30E-12**	Crustone - *Usnea*	2.46E-01	4.89E-04
			Treatment x Community	9	5.39E-01	8.42E-01	*Usnea* - Moribund	-3.08E-01	4.00E-07
ANOVA	*Pinnularia*	square root	Whole Model	15, 83	2.72E+00	1.96E-03	Crustose - Healthy	8.34E-02	4.08E-02
			Treatment	3	1.86E+00	1.42E-01	Crustone - *Usnea*	1.49E-01	5.00E-05
			Community	**3**	9.15E+00	2.68E-05	*Usnea* - Moribund	-8.30E-02	1.92E-02
			Treatment x Community	9	1.05E+00	4.06E-01			
ANOVA	*Psammothidium*	square root	Whole Model	15, 83	4.80E+00	1.41E-06	Moribund - Healthy	-3.71E-02	1.00E-05
			Treatment	**3**	**6.02E+00**	**9.17E-04**	Crustose - Healthy	-4.19E-02	1.31E-05
			Community	**3**	**1.47E+01**	**9.53E-08**	*Usnea* - Healthy	-3.23E-02	6.92E-05
			Treatment x Community	9	9.07E-01	5.23E-01	(Water+Nutrient) - Water	-3.42E-02	1.55E-03

Statistical Test	Variable	Transformation	Test	DF (model, error)	*F* Ratio	P Value	Post Hoc Comparison	diff	P Value
ANOVA	*Humidophila*	square root	Whole Model	15, 83	4.27E+00	8.44E-06	Moribund - Healthy	-2.78E-01	6.70E-06
			Treatment	3	5.65E-01	6.40E-01	Crustose - Healthy	-2.72E-01	1.42E-04
			Community	**3**	**1.86E+01**	**2.53E-09**	Crustone - *Usnea*	-3.84E-01	1.00E-07
			Treatment x Community	9	8.24E-01	5.96E-01			

Statistical Test	Variable	Comparisons	Test	DF (model, error)	*F* Model	P Value	R^2
PERMANOVA	Full Diatom Dataset	Treatment*Community	Treatment	3	8.76E-01	5.00E-01	
			Community	**3**	**1.29E+01**	**1.00E-04**	**0.29**
			Treatment*Community	9	1.01E+00	4.30E-01	
PERMANOVA	Full Diatom Dataset	Water*Nutrient	Water	1	5.34E-01	6.30E-01	
			Nutrient	1	5.68E-01	6.08E-01	
			Water*Nutrient	1	8.10E-01	4.45E-01	

Moribund (Tukey's HSD, p<<0.01) and crustose (p<<0.01) vegetation types had greater relative abundances of *Luticola* than healthy bryophytes. Relative abundances of *Luticola* were also greater in crustose lichens than in *Usnea* (p<<0.01), but lower in *Usnea* than in moribund bryophytes (p<<0.01). Larger relative abundances of *Pinnularia* were observed upon crustose lichens than in both healthy bryophyte (p=0.04) and *Usnea* (p<<0.01) vegetation. *Pinnularia* relative abundances were lower on *Usnea* than moribund bryophyte vegetation (p=0.02). Lastly, *Humidophila* showed lower relative abundances on moribund bryophytes than for healthy bryophytes (p<<0.01) and *Usnea* (p<<0.01) vegetation, while relative abundances on moribund bryophytes were lower than healthy bryophytes (p<<0.01).

Community analyses

Overall, the most conspicuous differences in diatom species between vegetation types were for two species of *Luticola*. Specifically, both *Luticola muticopsis* and *L. austroatlantica* were primarily associated with moribund bryophytes and crustose lichens (Fig. 2). Permutational analysis of variance (PERMANOVA) showed that diatom communities were significantly different among the different vegetation types (p<<0.01, R^2=0.29, Table III). To investigate differences between these vegetation types as a function of nutrient/water treatment, separate redundancy analyses (RDA) were performed for each vegetation type, where diatom relative abundance data were constrained against treatments (Fig. 5). However, no apparent “groupings” of samples or species by treatment were present, and the total variance explained for each RDA was between 3% for *Usnea* and 23% for moribund vegetation types. Furthermore, when tested with PERMANOVA, diatom communities were not statistically different between treatments or when explained with the combined effect of treatment and vegetation type (Table III).

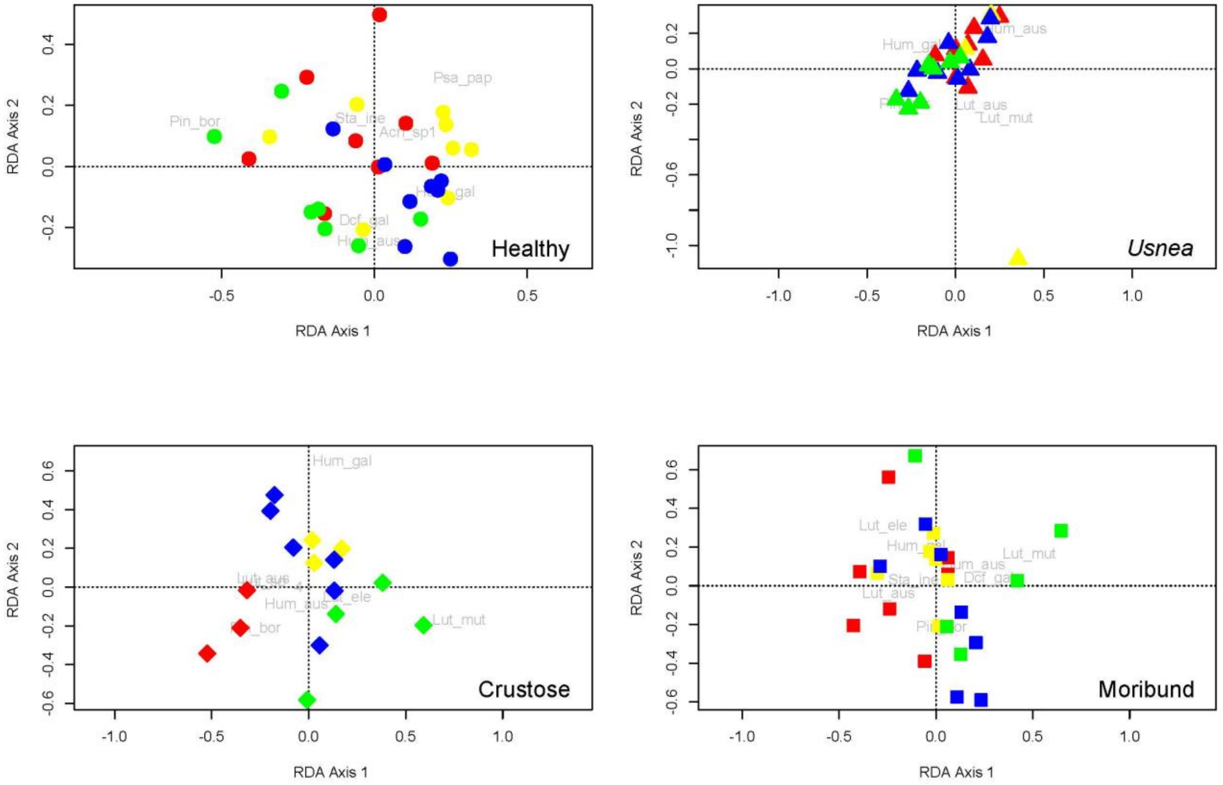

Fig. 5. Results of RDA grouped by vegetation type, displaying diatom taxa (codes defined in Table II) aligned against treatment. Individual vegetation types are labeled within the corner of each RDA. Vegetation type is coded by shape: "Circle" (healthy bryophyte), "Square" (moribund bryophyte), "Diamond" (crustose lichen), and "Triangle" (*Usnea* lichen). Treatments are color coded within each plot, Control (Red), Water (Yellow), Nutrients (Blue), and Water + Nutrients (Green).

The results of the PCA (Fig. 6) comparing vegetation physiological characteristics and diatom diversity variables showed a number of important relationships, and the primary and secondary axes accounted for 24 % and 20% of the total variation explained, respectively. In general, bryophyte communities (square and circle shapes) were arranged more towards the bottom-left of the figure, while lichens (triangles and diamonds) appeared more toward the top-right. Thus, %P was positively associated with lichen communities, with *Usnea* in particular, while δ^{13}C was positively related to healthy bryophytes. Furthermore, moribund bryophytes and crustose lichens showed positive associations with %N, while healthy bryophytes were negatively associated. Diversity indices were overall inversely correlated with the nutrient content of the host vegetation, with Shannon's diversity and Evenness were both negatively correlated to %P (and thus positively related to δ^{13}C and bryophyte vegetations), and both species and genera richness were negatively correlated with %N. Overall, chlorophyll *a* and total water content explained very little of the overall variability.

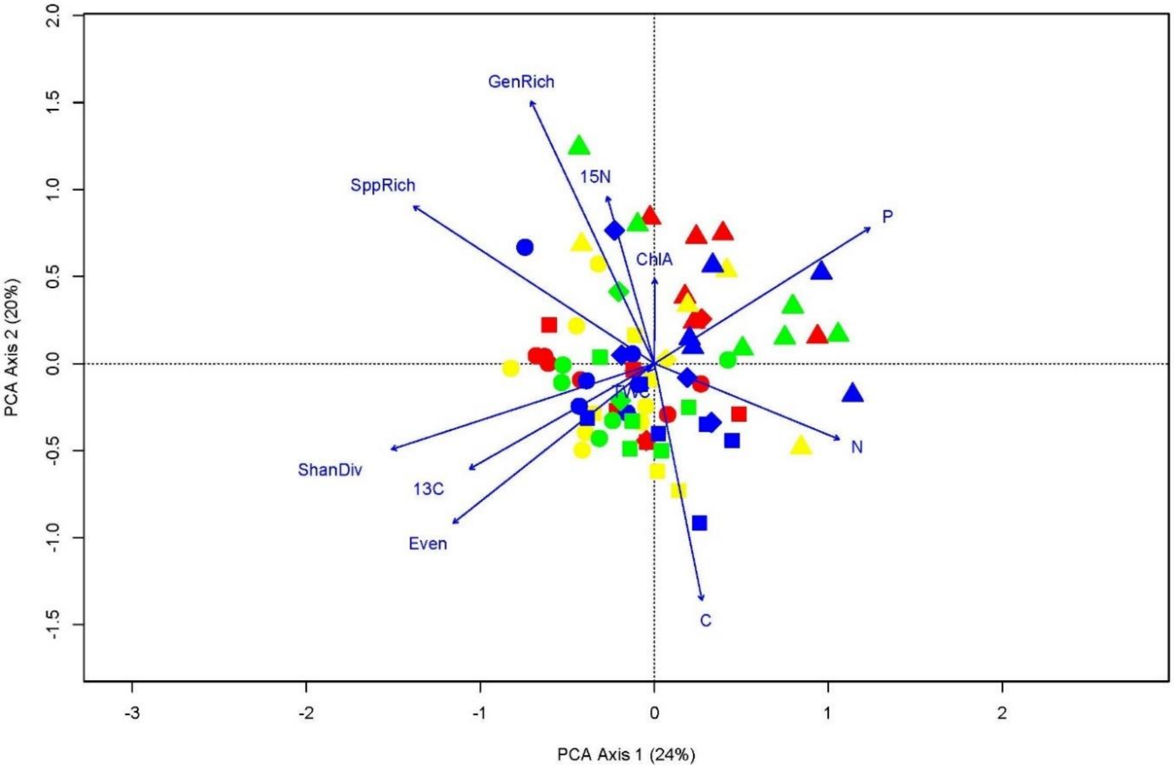

Fig. 6. The results of a PCA comparing bryophyte and lichen physiological variables (%P [P], %,N [N], %C [C], Chlorophyll a content [ChlA], Total Water Content [TWC], and stable δ^{13}C[13C] and δ^{15}N[15N]), and diatom diversity data (Shannon's Diversity [ShanDiv], Evenness[Even], Species Richness [SppRich] and Genera Richness [GenRich]). Vegetation type is coded by shape: "Circle" (healthy bryophyte), "Square" (moribund bryophyte), "Diamond" (crustose lichen), and "Triangle" (*Usnea* lichen). Treatments are color coded within the plot: Control (Red), Water (Yellow), Nutrients (Blue), and Water + Nutrients (Green).

Diatom species relative abundance data were also compared with vegetation characteristics using a db-RDA, which explained a total of 53% of the variability in the dataset (Fig. 7). Overall, the primary and secondary axes explained 41% and 12% of the variation, respectively. ANOVA revealed that only two terms, %N (p=0.003) and %P (p=0.024), were individually significant within the model. The most prominent relationship was between the %N content of vegetation and *L. muticopsis* (Lut_mut) on the primary axis of the ordination (Fig. 7), and perhaps to a lesser extent *L. austroatlantica*. Other diatom species, such as *H. australis* and *Psammothidium* species, such as *Ps. stauroneioides* (Psa_sta) and *Ps. papilio* (Psa_pap), were negatively correlated with %N, and *H.* cf. *gallica* (Dcf_gal) was positively associated with vegetation %P. Lastly, *Ps. stauroneioides* and *Ps. papilio* were both positively associated with δ^{13}C and δ^{15}N.

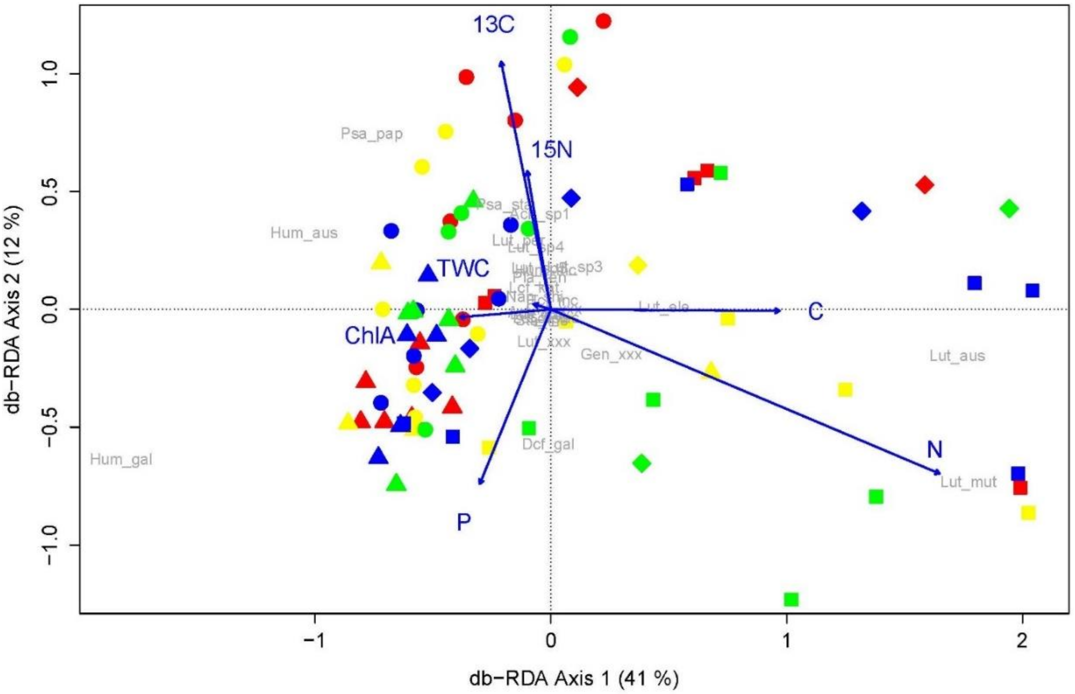

Fig. 7. The results of a db-RDA using Hellinger-transformed relative abundances constrained against moss physiological variables (%P [P], %N [N], %C [C], Chlorophyll a content [ChlA], Total Water Content [TWC], and stable isotopes δ^{13}C[13C] and δ^{15}N[15N]). Vegetation type is coded by shape: "Circle" (healthy bryophyte), "Square" (moribund bryophyte), "Diamond" (crustose lichen), and "Triangle" (*Usnea* lichen). Treatments are color coded within the plot: Control (Red), Water (Yellow), Nutrients (Blue), and Water + Nutrients (Green). Diatom species codes are defined in Table II.

Discussion

In this study, we examined the epiphytic diatom communities of four terrestrial vegetation types (healthy and moribund bryophytes as well as crustose and *Usnea* lichens) that received four different treatments (Control, Water, Nutrients, and Water + Nutrients). We found vegetation type to be a highly influential factor for both diatom diversity metrics and community structure, but did not observe a significant effect from the different treatments. However, relationships between diatom community structure and vegetation physiological characteristics suggest that the long-term availability of water and nutrients is still important, if only indirectly by favoring different vegetation types. These results suggest that conditions favoring diatom habitat loss, or gain, via bryophyte and lichen vegetation contraction/expansion may have widespread implications for terrestrial diatom diversity and distributions in Antarctica.

Terrestrial diatom communities within the Antarctic realm

The current study provides some of the first observations of diatoms associated with bryophyte and lichen vegetations from the Windmill Islands of East Antarctica. Previous studies throughout the Windmill Islands have examined benthic diatoms within marine bays (Cunningham & McMinn 2004) and lake and pond sediments (Roberts et al. 2001), though the current study differs from these in both its ecological setting and the observed flora. In the present work, the predominant taxa belong to the genera *Luticola*, *Psammothidium*, *Pinnularia*, and *Humidophila*, and the flora is markedly different than that reported from moss diatom communities from both the Maritime and Sub-Antarctic biogeographical regions, as well as other East Antarctic localities.

For example, the McMurdo Dry Valleys Long Term Ecological Research (LTER) Project has maintained a database of diatom counts from throughout the McMurdo Dry Valleys (MDV) spanning several decades (http://mcm.lternet.edu/). Here, the predominant moss-inhabiting genera include *Hantzschia* Grunow and *Nitzschia* Hassall, and common species include *Hantzschia amphioxys* (Ehrenberg) Grunow, known to be a species complex (Souffreau et al. 2013), and *Nitzschia australocommutata* Hamsher, Kopalová, Kociolek, Zidarova & Van de Vijver. These taxa are often present at ~30% and 40% relative abundance, respectively **(**Spaulding et al. 2020**)**, though they were effectively absent from our study, highlighting major biogeographical differences between Continental Antarctic localities**.** However, similar to the present study, sites within the MDV still contain overall species richness values of 10 – 20 species per site.

Observed species richness is much greater from the Maritime Antarctic Region, including Livingston and James Ross islands, observed species richness was much greater, with 123 and 57 moss diatom species reported, respectively (Kopalová et al. 2014). Although the Maritime and Continental Antarctic Regions share common genera, they are far more speciose in the former. On Livingston Island, *Humidophila* (reported as *Diadesmis* Kützing), *Muelleria* (Frenguelli) Frenguelli, *Navicula* Bory, and *Nitzschia* all contained 7 species each, whereas the dominant genera *Pinnularia*, *Luticola* and *Psammothidium* contained 16, 13, and 9 species, respectively. Upon James Ross Island, *Luticola*, *Diadesmis* and *Pinnularia* featured 11, 6, and 5 species respectively, with the species complex *Pinnularia borealis* (Pinseel et al. 2019), *Hantzschia amphioxys* and *Nitzschia perminuta* Grunow appearing at 24.6%, 10.7% and 8.9% relative abundance across sites (Kopalová et al. 2014). In contrast to the mosses, Chattová (2018) reported 56 diatom species from lichens on James Ross Island, with *Luticola*, *Hantzschia*, and *Pinnularia* being the most common genera, and richness ranging from 7 to 23 species per sample.

Diatom vegetation type preferences

Our findings that diatom community composition is largely determined by the underlying vegetation type is informative and has implications for potential habitat loss (or gain) as different moss and lichen species may shift in their abundance due to ongoing climate change. For example, the response of three bryophyte species (*Schistidium antarctici*, *Ceratodon purpureus* (Hedwig) Bridel and *Bryum pseudotriquetrum* (Hedwig) P.G.Gäertner, B.Meyer & Scherbius) to desiccation and submergence was examined in Wasley et al. (2006b), and of these, the endemic *S. antarctici*, was shown to be less tolerant to desiccation while being highly tolerant of submergence (Wasley et al. 2006b). Within the current study, *S. antarctici* is the major component of the healthy bryophyte vegetation type, and the dominant bryophyte across the remainder of the experimental gradient. Within close proximity to the current study site, the dominant bryophyte *S. antarctici* occurred at over 90% relative abundance within the bryophyte communities and was present within the "transitional" (equivalent to the moribund community) and crustose lichen communities at approximately 40% and 20% relative abundance, respectively (Wasley et al. 2012).

Robinson et al. (2018) detailed a drying trend within recent years in the Windmill Islands and a concomitant reduction in the abundance of *S. antarctici*, whereas the abundance of the more desiccation tolerant (and submergence intolerant) cosmopolitan moss species *C. purpureus* and *B. pseudotriquetrum* increased. Within this adjacent study site, (ASPA 135 melt puddle) the proportion of moribund moss also increased. Given the observed differences in relative abundances of the four diatom genera among different vegetation types, an increase in moribund vegetation may preferentially favor *Luticola*, whereas healthy bryophyte vegetation (stands comprised predominantly of *S. antarctici*) may demonstrate higher abundances of *Humidophila* and *Psammothidium.* Given that the samples analyzed here date from nearly two decades ago, it is not unreasonable to suggest that the diatom communities have already undergone change since this field experiment took place.

The "turf morphology", or the degree of complexity and folding within vegetation, of *S. antarctici*, *C. purpureus* and *B. pseudotriquetrum* has been previously suggested to be an avenue of water retention, and thereby preventing vegetation desiccation (Wasley et al. 2006b). As both temperature and water levels have been shown to vary within the fine scale microclimate of mixed bryophyte vegetation types of *Ceratodon* Brisson and *Bryum* Hedwig (Lewis Smith 1999), the accessibility of this turf morphology may serve as a selective pressure acting upon diatoms, potentially influencing dispersion/colonization between patches, especially if *S. antarctici* is in decline. Our results suggest that *P. borealis* and *Humidophila* species (such as *H. gallica* and *H. australis*) may be particularly suited to inhabit a broad range of conditions (or be better competitors therein), including variable nutrient availability, site topology and bryophyte and lichen vegetation types, as these widely distributed taxa demonstrate a large range of environmental preferences and were ubiquitous in our counts.

Effects of water and nutrient availability

In this study, we analyzed diatoms from samples collected from an experiment examining the physiological responses of bryophyte and lichen communities to water and nutrient additions (Wasley et al. 2006a). Although these treatments were not targeted at diatoms directly, it is reasonable to assume that any experimental additions affecting the physiological characteristics of the host vegetation, and by extension its microclimate, will also bear influence on its resident epiphytes. Furthermore, given the previously reported importance of moisture in structuring moss diatom communities within the Maritime Antarctic (Kopalová et al. 2014) and the Sub-Antarctic

(Van de Vijver et al. 2002, 2008), we expected that the water additions alone should have produced noticeable effects. Yet, it is interesting to note in our analysis, water additions did not appear to influence diatom community structure. While we know that water is critical for diatoms, as well as for the maintenance of lichen and bryophyte vegetations and their capacity to form robust microclimates, it may be that after a certain threshold is met, water quantity provides only limited selection pressure for the aerophilic taxa observed here.

However, another possibility is that the ambient gradient in water availability, with or without our water additions, has already fundamentally structured these diatom communities, although perhaps in a more indirect way. As explained in Wasley et al. (2006a), the healthy bryophytes primarily occupied the area near the meltwater pond, in contrast to the lichen vegetation types, which were located with greater distance from the pond up the ridge. These differences in proximity to the pond are reflected in the more enriched δ^{13}C signatures of bryophytes, which is likely a result of more frequent submergence in water, which in turn produces a greater diffusion limitation of CO_2. In line with this, diversity and evenness, as well as small-bodied diatoms species from the genus *Psammothium*, were positively correlated with δ^{13}C in our work, and may reflect this long-term availability of liquid water. Whether the differences between diatom communities across vegetation types reflects this fundamental difference in the abundance of water or some other distinguishing factor between vegetation types remains an open question, and represents an interesting avenue for further study.

Similarly, epiphytic diatom communities did not respond to the experimental nutrient additions. This suggests that either nutrients at the soil-vegetation interface are not directly available to the epiphytic diatom community, or that these communities are not limited in their nutrient supply and therefore not responsive to fertilization. While both of these scenarios are possible, Wasley et al. (2006a) found large responses of healthy bryophytes and crustose lichens to nutrient treatments (which also exhibited the most enriched δ^{15}N signatures, indicating greater nutrient recycling), casting the generalization of the latter possibility into doubt. However, as previously discussed for water availability, a natural gradient in nutrient availability was also present at the experimental site, with concentrations increasing up the ridge toward the abandoned penguin rookery. As a result, nutrient availability is elevated for lichen vegetation and moribund bryophytes, and indeed Wasley et al. (2006) report greater %N for these vegetation types (and more depleted δ^{15}N signatures) than for healthy bryophytes.

Interestingly, we found that diatoms from the genus *Luticola*, especially *L. muticopsis*, to be highly correlated with vegetation %N. However, *L. muticopsis* was also the most common in moribund bryophytes and crustose lichens, which also contained the most N. Thus, it is not clear if this association is indeed due to the nutrient content or the vegetation type. *Luticola muticopsis* is often found at great abundances in close proximity to penguin rookeries (Sakaeva et al. 2016), which generally have elevated concentrations of N, and therefore it would make sense if N availability was driving the relative abundances of this diatom. However, *L. muticopsis* was also (in general) negatively associated with vegetation δ^{13}C, which may indicate an aversion to repeated or prolonged submergence for this aerophilic diatom (e.g. as for healthy bryophytes). If %N is responsible for explaining patterns in diatoms communities, it is also unclear how these stored nutrients are made available to diatom cells, though it is reasonable to expect that greater vegetation %N is likely accompanied by greater N recycling within the vegetation matrix. Future experimental work should be aimed towards disentangling the mechanisms behind these scenarios, such that we can improve our understanding of how microbial life will respond to climate change.

Conclusions

Within this study, we characterized diatom communities from four vegetation types that received added nutrients and water within the projected range expected due to climate change. Our hypothesis that these additions would directly influence diatom community structure was not supported. Instead, vegetation type best explained differences in diatom community composition, indicating that, at most, water and nutrient treatments may have indirectly influenced diatom community structure through favoring the establishment of these different vegetation types. These results inform larger trends within microbial and macroflora diversity within Antarctica, as future expansion and/or contraction of different vegetation types may therefore affect terrestrial diatom distributions and abundances. However, the effects of climate change upon microbial life in Antarctica are not well understood, especially when coupled with other concomitant threats such as invasive species. As such, this study represents an important dataset for the informing the management and preservation of Antarctic diatom communities.

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Author Contributions: JW, and SAR performed fieldwork and collected samples. KK subsampled the collections. JB processed bryophyte and lichen samples within the laboratory, prepared and counted slides. JB, KK, BVDV, TJK contributed equally to identify diatom taxa, statistical analyses and data interpretation. The manuscript was written with significant input and editing from all authors.

Supplemental Material:

Table S1. List of samples used within the analysis. Diversity indices calculated for each sample include species richness, Shannon Diversity, and Evenness.

Table S2. Diatom relative abundance data from each sample within the study. Diatom species codes are listed in Table II.

Table S3. Selected diatom samples alongside corresponding bryophyte and lichen physiological data.

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