



The largest moss carpet transplant in Antarctica and its bryosphere cryptic biodiversity

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Received: 21 January 2021 / Accepted: 1 June 2021 / Published online: 11 June 2021
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Abstract

As part of the reconstruction of the Brazilian Antarctic Station on King George Island, three areas of moss carpet were transplanted to minimize the impact of the new facilities on the local biodiversity. A total of 650 m² of moss carpet was transplanted to neighboring but previously uncolonized locations and has subsequently survived for the last 3 years. Antarctic moss carpets typically comprise low moss species diversity and are often monospecific. We investigated the cryptic biodiversity that was transplanted along with the carpets using a metabarcoding approach through high throughput sequencing. We targeted 16S rRNA for Bacteria and Archaea, ITS for Fungi and Viridiplantae and Cox1 for Metazoa. We detected DNA representing 263 taxa from five Kingdoms (Chromista, Fungi, Metazoa, Protista and Viridiplantae), two Domains (Archaea and Bacteria) and 33 Phyla associated with the carpet. This diversity included one Archaea, 189 Bacteria, 24 Chromista, 19 Fungi, eight Metazoa, seven Protista and 16 Viridiplantae. Bacteria was the most abundant, rich and diverse group, with Chromista second in diversity and richness. Metazoa was less diverse but second highest in dominance. This is the first study to attempt transplanting a significant area of moss carpet to minimize anthropogenic environmental damage in Antarctica and to use metabarcoding as a proxy to assess diversity associated with Antarctic moss carpets, further highlighting the importance of such habitats for other organisms and their importance for conservation.

Keywords Antarctica · Moss carpet · *Sanionia* · Metabarcoding · Diversity · HTS

Communicated by I. Cann.

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Introduction

Antarctica is well known for its extreme environmental conditions. Its terrestrial vegetation comprises only two native angiosperms and about 116 species of Bryophyta (Ochyra et al. 2008; Ellis et al. 2013a, b, 2013a; Sollman et al. 2015; Câmara et al. 2019). However, Antarctic vegetation is still poorly characterized in terms of genetic diversity and few studies using molecular tools have yet been carried out (Biersma et al. 2018a, b, 2020; Câmara et al. 2018, 2019). In particular, although the dominant bryophyte vegetation of the maritime Antarctic provides the habitats occupied by multiple other groups of organisms (e.g. Block et al. 2009), molecular tools are yet to be widely applied in assessing the overall biodiversity potentially occupying and relying on the bryosphere.

Antarctica is governed under the Antarctic Treaty, an international treaty that was negotiated in 1959 and came into force in 1961. Antarctic Treaty governance applies to

all areas south of the 60° latitude parallel. The Treaty is dedicated to peace and science, with a primary purpose of protecting the Antarctic environment. Brazil became a Consultative Party to the Antarctic Treaty in 1984 and, promoting its interests in scientific research in Antarctica, its research station “Comandante Ferraz” was built in 1983 on the Keller Peninsula in Admiralty Bay on King George Island (South Shetland Islands). Tragically, in February 2012, the station was destroyed by fire. Subsequently, Brazil set the goal of rebuilding the station at the original location, considerably modernizing its facilities and increasing the area of its footprint. As is the required procedure under the Protocol on Environmental Protection to the Antarctic Treaty (hereafter referred to as the Protocol), the rebuild plans underwent detailed international scrutiny through the Protocol’s Environmental Impact Assessment (EIA) process. The expanded ground area where the new station and its associated facilities were to be built was partially occupied by established moss carpets that would inevitably have been destroyed during the construction of new structures such as fuel tanks and the new helipad. Therefore, to minimize the environmental impact of the rebuild and attempt to actively preserve these moss carpets, the Brazilian Ministry of Environmental Affairs and its Environmental Agency (MMA/IBAMA) made the decision to relocate the moss carpets to a geomorphologically similar but uncolonised location close to the station, the first such translocation attempt anywhere in Antarctica. Globally, there have been very few significant transplant attempts for bryophytes, especially when compared with other groups of plants (Brooker et al. 2011; Flagmeier et al. 2016), and particularly in remote and extreme regions, with most conservation actions being in a context of habitat restoration rather than the preservation of existing bryophyte habitat. The use of transplant approaches, either locally as we describe here or at a larger scale, has been highly debated as a conservation tool (Brooker et al. 2011; Hewitt et al. 2011).

Moss carpets are a typical feature in the maritime Antarctic (Smith 1984; Ochyra et al. 2008), although it is important also to recognize that the overall area of vegetation development is itself only a small fraction of the already very small area of ice-free ground (Hughes et al. 2016). The most commonly encountered wet moss carpets typically consist of extensive and almost completely monospecific stands of mosses of the genus *Sanionia*. Pleurocarpous mosses such as *Sanionia* are characterised by their low genetic diversity (Shaw et al. 2003), as has been reported in other pleurocarps in Antarctica (Biersma et al. 2017). Studies of Antarctic *Sanionia* populations have also confirmed low levels of genetic diversity (Hedenas 2012; Hebel et al. 2018), further promoted by the lack of sexual reproduction in this genus in Antarctica (Smith and Convey 2002; Ochyra et al. 2008; Hebel et al. 2018).

Moss carpets also harbor a potentially diverse community of organisms including various microbial groups (prokaryotes, algae, fungi, protists), micro-invertebrates (nematodes, rotifers, tardigrades) and micro-arthropods (mites, spring-tails and the native fly *Belgica antarctica* where it occurs) that depend on the habitats provided by the moss. However, while these groups are reasonably well known at a regional scale, detailed community characterization studies have been carried out at very few specific locations (e.g., Usher and Booth 1986; Richard et al. 1994; Convey and Quintana 1997; Convey and Smith 1997). Recent and rapid advances in molecular biology, such as DNA metabarcoding through high throughput sequencing (HTS), have provided important new tools for the detection of species by their DNA, with particular value in identifying rare elements of the biodiversity present (Rippin et al. 2018; Ruppert et al. 2019). For instance, in a study on Livingston Island (South Shetland Islands; Rippin et al. 2018) a molecular approach yielded richness estimates 11 times higher than did traditional morphological approaches. A range of recent metabarcoding studies of microbial groups in different habitats in the South Shetland Islands and northern Antarctic Peninsula have detected the presence of DNA representing a much higher number of taxa than those previously reported using traditional methods (e.g. Câmara et al. 2020; Garrido-Benavent et al. 2020; Rosa et al. 2020a,b; Ogaki et al. 2021), although it should also be noted that metabarcoding approaches alone do not confirm the presence of living organisms or viable propagules. In this study, we describe what we believe to be the largest moss transplant attempted in Antarctica and investigate the cryptic and previously uncharacterized biodiversity associated with the transplanted moss carpet with the use of metabarcoding.

Methods

Moss carpet transplantation

Three distinct areas of moss carpet required transplanting to avoid destruction as a result of the station rebuild. The three transplanted patches were documented using ImageJ software (Schneider et al. 2012), and are located as follows: Area 1: located between the station helipad and meteorology laboratory (62.086986°S 58.394754°W); with an area of 530 m², this is the largest patch and contains moss carpet originally located at the new helipad site; area 2, located near the new fuel tanks (62.086964°S 58.394197°W), with an area of 100 m², contains moss carpet originally located at the site of the new fuel tanks; area 3, located near to the station’s wind generators (62.083501°S 58.392200°W), with an area of 20 m², contains moss carpet originally located on the sites now occupied by the wind turbines. The transplanted

carpets comprised mainly the moss *Sanionia uncinata* (Hedw.) Loeske, with small proportions of *Schistidium antarctici* (Cardot) L.I. Savicz and Smirnova, *Polytrichastrum alpinum* (Hedw.) G.L.Sm. and a few clumps of Antarctic hairgrass (*Deschampsia antarctica* E. Desv.). The following methodology was applied to transport the transplants: the moss carpets were divided into manageable units (about 400 cm²) and, with the help of a knife or chisel, were manually lifted from the underlying surface and immediately relocated to a previously selected area on slightly higher ground, a few meters from their original location. The new area was selected to be as similar as possible to the original location in terms of its slope and orientation, water availability and type of underlying substrate, but free of vegetation. The surface layer of soil was also translocated to attempt to maintain possibly vital fungal connections and to minimize the change in nutrient availability and pH relative to the original site and thereby assist in the moss re-establishment (Glime 2017a, b). According to Glime (2017a, b), signs of death can occur rapidly in moss transplants, but they become stabilized within a few weeks. The transplants were carried out in February 2017. The site was visited again after one year and the condition of the transplanted patches assessed. The patches were then photographed two seasons later using a UAV (Phantom5® drone) during the austral summer of 2019/20.

Metabarcoding analysis

A single sample from the largest moss carpet was collected in the austral summer of 2019/20. One single shoot of *Sanionia uncinata* was removed using gloves and previously sterilized forceps and placed in a sterilized WhirlPak bag (Sigma-Aldric, USA). The sample was taken immediately to the microbiology laboratory at Comandante Ferraz Station where DNA extraction was completed in a laminar flow cabinet. Extraction used the QIAGEN Power Soil Kit (QIAGEN, Carlsbad, USA), following the manufacturer's instructions. DNA quality was analyzed by agarose gel electrophoresis (1% agarose in 1 × Trisborate-EDTA) and then quantified using Quanti-iT™ Pico Green dsDNA Assay (Invitrogen). We aimed to target DNA from six groups of organisms: Bacteria, Chromista, Fungi, Metazoa, Protista and Viridiplantae.

The internal transcribed spacer 2 (ITS2) of the nuclear ribosomal DNA was used as a DNA barcode for molecular species identification of Chromista, Protista, Viridiplantae and Fungi (Chen et al. 2010) using the universal primers ITS3 and ITS4 (White et al. 1990). For Bacteria and Archaea, we used the 16S rRNA gene V3-V4 region (Herlemann et al. 2001; Klindworth et al. 2013) and for Metazoa, Cox1 (Folmer et al. 1994). Library construction and DNA amplification were performed using the Library kit Herculese II Fusion DNA Polymerase

Nextera XT Index Kit V2, following Illumina 16S Metagenomic Sequencing Library Preparation Part #15,044,223 Rev. B protocol. Paired-end sequencing (2 × 300 bp) was performed on a MiSeq System (Illumina) by Macrogen Inc. (South Korea).

Raw fastq files were filtered using BBDuk version 38.34 (BBMap – Bushnell B. –sourceforge.net/projects/bbmap/) to remove Illumina adapters, known Illumina artefacts, and the PhiX Control v3 Library. Quality read filtering was carried out using Sickle version 1.33 -q 30 -l 50 (Joshi et al. 2011), to trim 3' or 5' ends with low Phred quality score, and sequences shorter than 50 bp were discarded. The remaining sequences were imported to QIIME2 version 2019.10 (<https://qiime2.org/>) for bioinformatics analyses (Bolyen et al. 2019). The qiime2-dada2 plugin is a complete pipeline that was used for filtering, dereplication, turn paired-end fastq files into merged, and remove chimeras (Callahan et al. 2016). Taxonomic assignments were determined for amplicon sequence variants (ASVs) using the qiime2-feature-classifier (Bokulich et al. 2018) classify-sklearn against SILVA 138 Ref NR 99 (Quast et al. 2013) for the 16S rRNA gene, UNITE Eukaryotes ITS database version 8.2 (Abarenkov et al. 2020) for Eukaryota, and MIDORI (Leray et al. 2018) for COX1, trained with Naïve Bayes classifier. We aimed to maximize resolution by obtaining data from specific and curated databases for the specific target groups.

Rarefaction calculations were carried out using the rarefaction analysis command in the platform MOTHUR (Schloss 2009), where we clustered sequences into OTUs by setting a 0.03 distance limit. Many factors, including extraction, PCR and primer bias, can affect the number of reads obtained (Medinger et al. 2010), and thus lead to misinterpretation of absolute abundance (Weber and Pawlowski 2013). However, Giner et al. (2016) concluded that such biases did not affect the proportionality between reads and cell abundance, implying that more reads are linked with higher abundance (Deiner et al. 2017; Hering, 2018). Therefore, for comparative purposes, we used the number of reads as a proxy for relative abundance. Ecological indices were calculated using PAST 1.90 (Hammer et al. 2001).

Sequences from the Phyla Ochrophyta and Oomycota were obtained from Cox1 and the Midori database while Ciliophora used ITS and the UNITE database.

The classification systems used were: Garrity et al. (2012) and Yilmaz et al. (2014) for Bacteria; Leliaert et al. (2012) for Viridiplantae; Cavalier-Smith (2007) for Chromista, Protista and Metazoa; Kirk, (2011), Tedersoo et al. (2011), MycoBank (<http://www.mycobank.org>) and the Index Fungorum (<http://www.indexfungorum.org>) for Fungi.

Results

Moss carpet transplantation

The first assessment of the transplanted moss carpet condition, a year after the transplant, confirmed that the plants not only survived the transplant but were thriving, based on direct observation and comparison with non-transplanted areas. Pictures, obtained three years after the transplant, using the UAV (Figs. 1, 2, 3) showed no differences in color or gross morphology.

Metabarcoding analysis

The calculated rarefaction curves for all taxa investigated approached a plateau, indicating that the reads gave an accurate representation of the local sequence diversity (Suppl. Figs. 1, 2). For 16S, a total of 275,658 DNA reads was generated and 20,111 reads remained after quality filtering. For ITS a total of 160,430 reads was generated and 29,454 reads remained after quality filtering and for Cox1 a total of 423,264 reads was generated and 48,543 reads remained after quality filtering. Sequences from two prokaryotic Domains (Bacteria and Archaea) were detected, representing 263 taxa in 18 Phyla. Sequences of representatives of five Eukaryota Kingdoms were detected: 24 representing three Phyla of Chromista, 19 representing four Phyla of Fungi, eight representing four Phyla of Metazoa, seven representing

two Phyla of Protista and 16 representing two Phyla of Viridiplantae (Fig. 4). Krona charts (Suppl. Figs. 3–5) illustrate the relative abundances of the different groups.

A large number of sequences that could not be assigned to any rank was also found (47% for 16S; 62% for COX1 and 10% for ITS), suggesting that they represent taxa that are absent from the consulted databases, or new and as yet undescribed taxa (or both).

Domain bacteria

A total of 20,111 sequences were obtained representing this domain, distributed in 189 ASVs. Chloroplast DNA was the source of 8,551 of these sequences, and mitochondrial DNA contributed a further 1,515 sequences; both were removed from the analysis. The remaining sequences represented 18 bacterial phyla, and no archaeal 16S rRNA gene sequence was detected (Suppl. Table 1). The largest proportion of sequences represented the phylum Actinobacteria (25%), followed by Proteobacteria (20%) and Bacteroidetes (18%). The detected sequences represented 141 bacterial families, but only 23 families contributed > 1% of relative abundance. Intrasporangiaceae (Actinobacteria) and Chitinophagaceae (Bacteroidetes) were the most abundant families, contributing 9.2% and 6.7%, respectively (Fig. 5). The highest relative abundance at the generic level was 5% for “B1rii41” (Myxococcota), *Kineosporia* (Actinobacteria) and *Ferruginibacter* (Bacteroidetes).

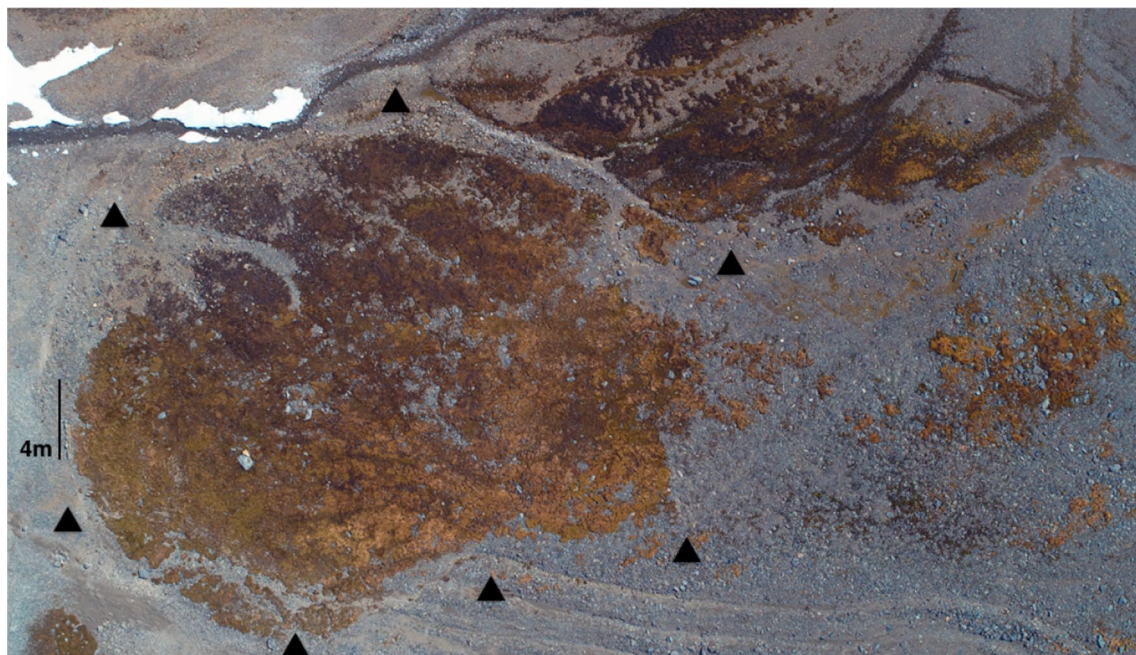


Fig. 1 Transplanted Area 1, the largest transplanted patch with an area of 530 m², photographed using a UAV three years after the transplant. Triangles delimit the transplanted area. Moss carpets beyond the transplanted area were already present. Photo: L.H. Rosa

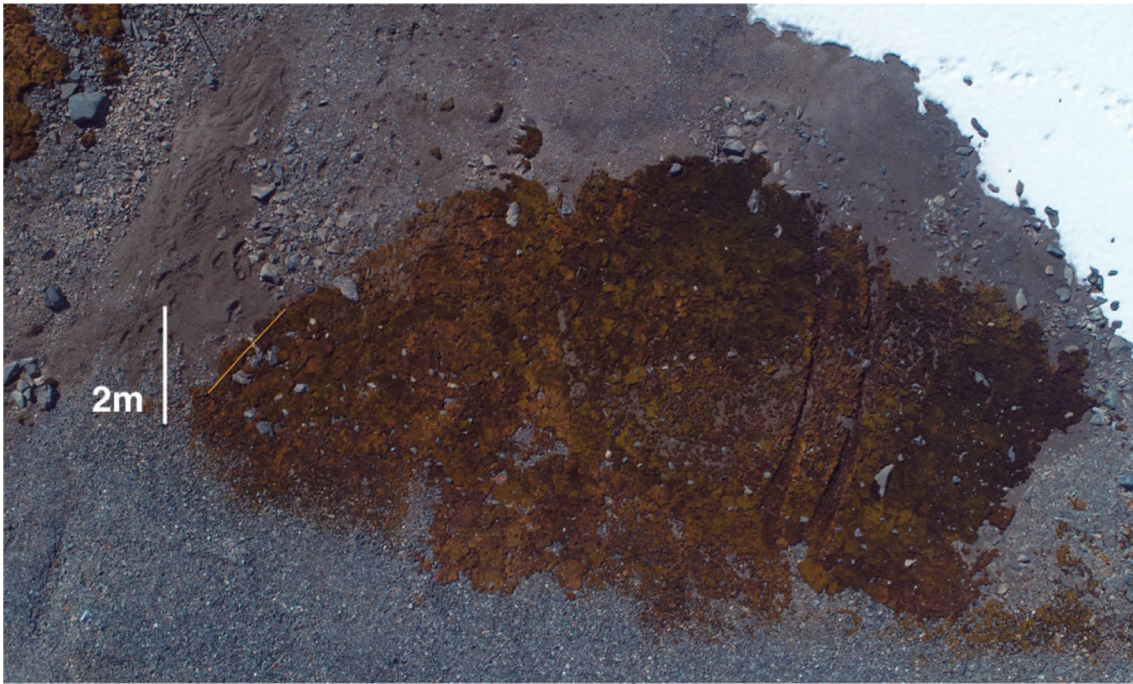


Fig. 2 Transplanted Area 2, with a total area of 100 m². Photo: L.H. Rosa

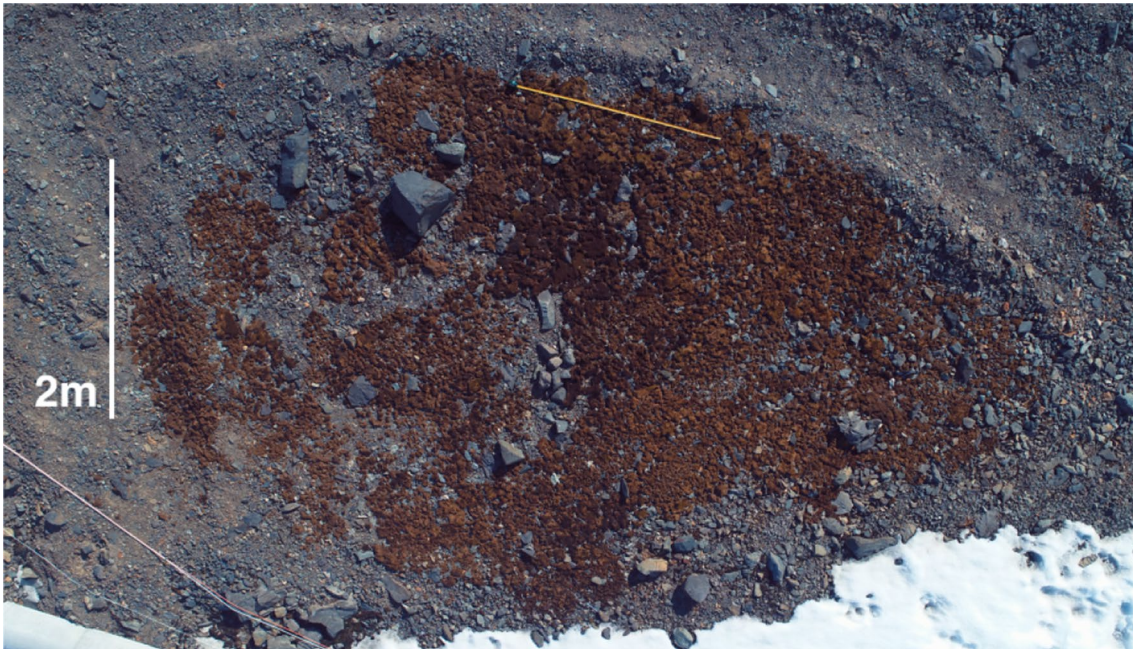


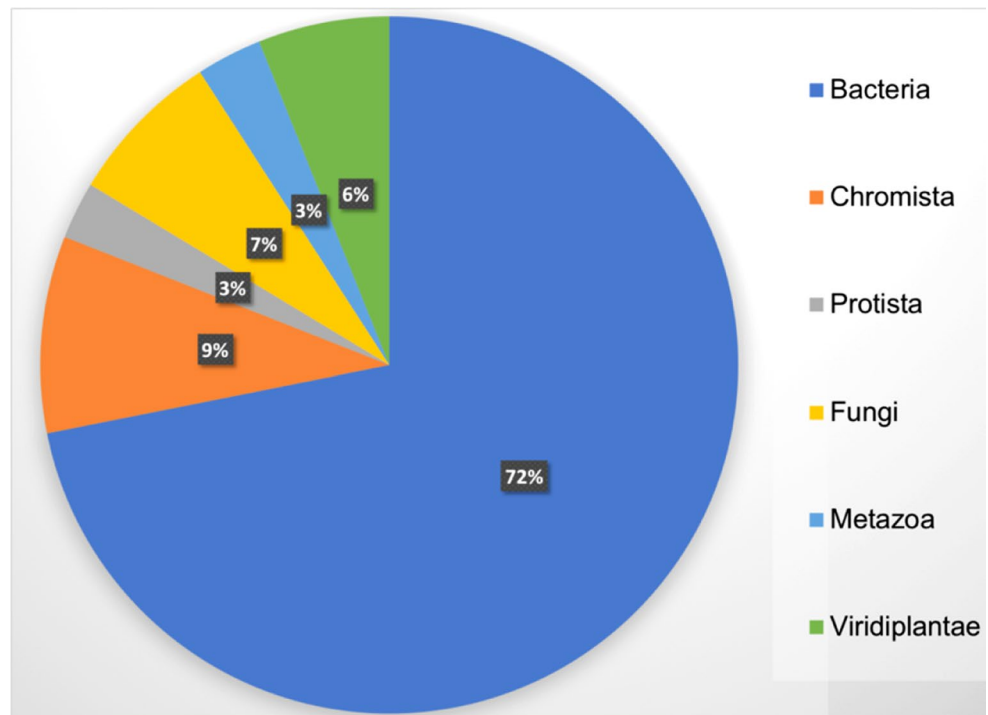
Fig. 3 Transplanted Area 3, with a total area of 20 m². Photo: L.H. Rosa

Kingdom Chromista

A total of 8,682 sequences were assigned to Chromista, distributed in 24 ASVs (Suppl. Table 2). Taxa were

divided in three Phyla, Ciliophora, Ochrophyta and Oomycota, with the Oomycota being the most diverse and abundant phylum (Fig. 6).

Fig. 4 Overall diversity of taxa found



Kingdom Fungi

A total of 7,984 reads were assigned to 19 fungal ASVs. These represented 11 genera from the phyla *Ascomycota*, *Basidiomycota*, *Chytridiomycota* and *Monoblepharomycota*, in rank order of abundance (Suppl. Table 3). However, 20,492 (71.9%) of the total of 28,474 fungal reads detected could only be classified as Fungal sp., again likely to represent as yet undescribed taxa or taxa not included in the UNITE database. Relative abundances of fungal phyla are presented in Fig. 7

Kingdom Metazoa

A total of 39,439 metazoan sequences was obtained, representing eight ASVs (Suppl. Table 4). These were divided across four phyla: Arthropoda, Nematoda, Rotifera and Tardigrada (Fig. 8). Arthropoda had by far the greatest relative abundance while Arthropoda and Rotifera had the greatest diversity, although absolute taxon numbers in each phylum were low.

Kingdom Protista

A total of 880 sequences were assigned to Protista, representing seven ASVs (Suppl. Table 5) in two phyla, Discosea and Excavata (Fig. 9). Sequences representing

Discosea were the most diverse and had the greatest relative abundance.

Kingdom Viridiplantae

A total of 29,244 Viridiplantae sequences were obtained, representing 16 ASVs (Suppl. Table 6) from two Phyla: Chlorophyta (green algae) and Bryophyta (mosses). Sequences representing Bryophyta had the greatest relative abundance while Chlorophyta contained the greatest sequence diversity (Fig. 10).

Molecular Sequence Diversity and Ecological Indices

The overall sequence diversity of each of the targeted groups and the calculated ecological indices are shown in Table 1. Bacteria were the most diverse, rich and abundant group present in terms of sequence (ASV) diversity detected. Chromista was the second most diverse and rich group found. Metazoa sequences, while indicating low diversity and richness, were present at very high abundance when compared with all other groups except Bacteria.

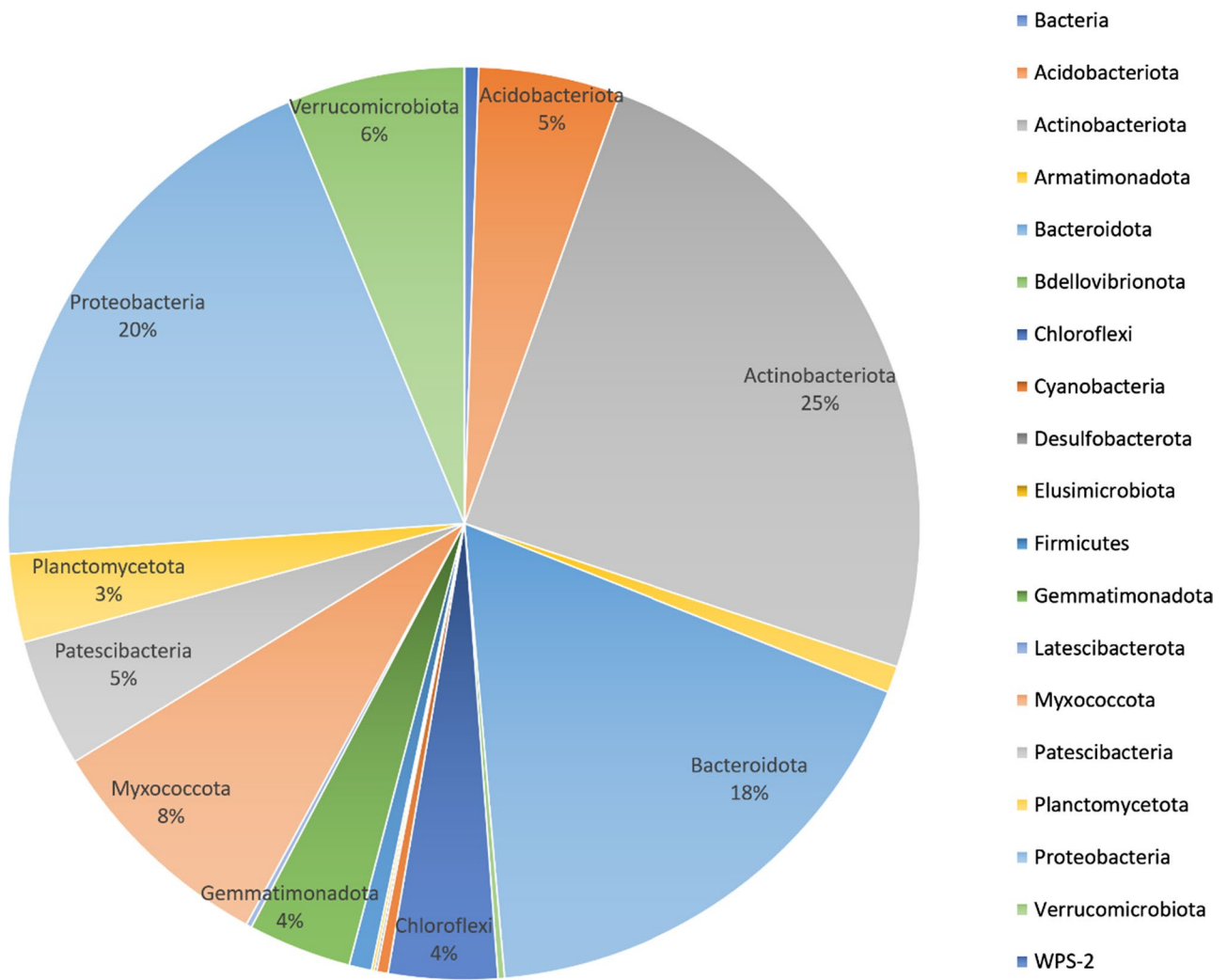


Fig. 5 Bacterial phyla diversity found in the metabarcoding analysis

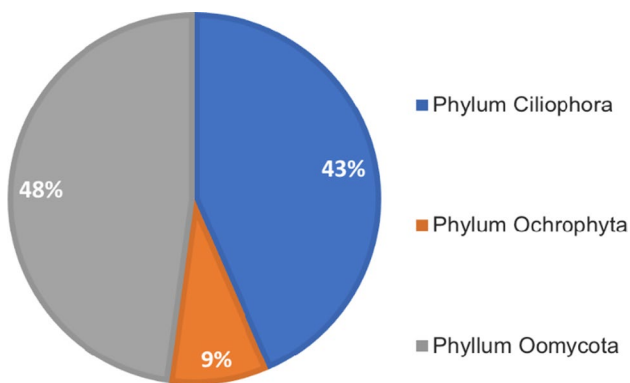


Fig. 6 Chromista diversity found in the metabarcoding analysis

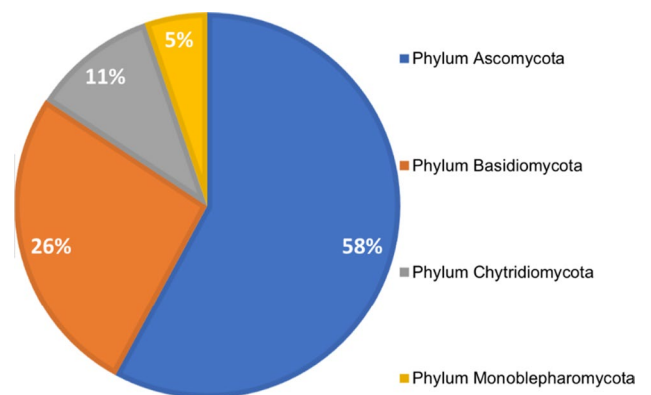


Fig. 7 Fungal diversity found in the metabarcoding analysis

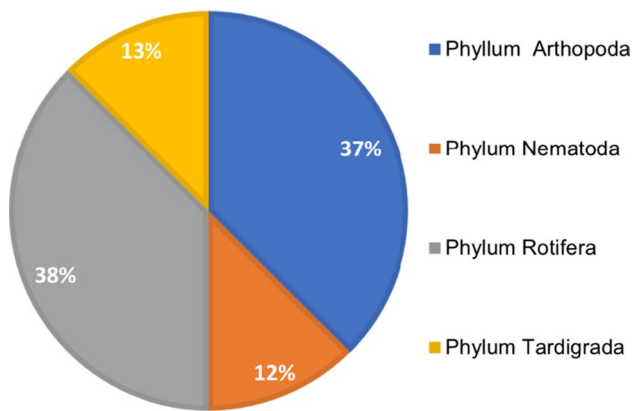


Fig. 8 Metazoa diversity found in the metabarcoding analysis

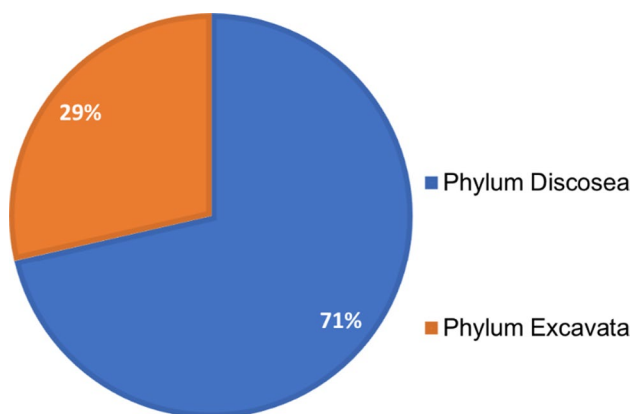


Fig. 9 Protista diversity found in the metabarcoding analysis

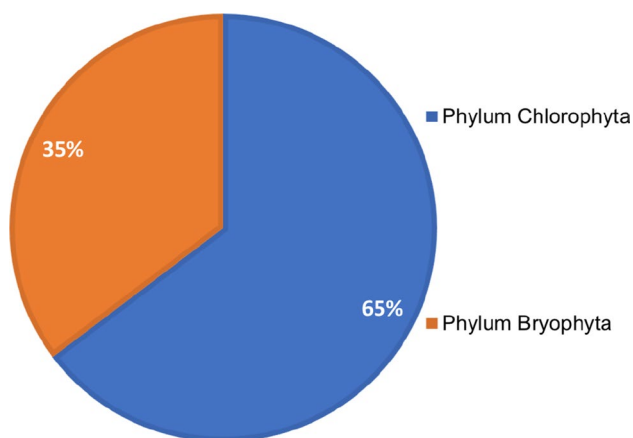


Fig.10 Viridiplantae diversity found in the metabarcoding analysis

Discussion

Environmental sensitivity and protection in Antarctica

Antarctic terrestrial ecosystems are fragile and vulnerable to physical damage. The dominant bryophyte vegetation, lacking the roots of higher plants and with weak or no connection to the underlying substrate, is vulnerable to being damaged or dislodged. This fragility has become a conservation issue and challenge in Antarctica, owing to the combination of the small overall amount of ice-free ground available, the small proportion of that area actually colonized by vegetation, and the inevitable competition this leads to with the demand for locations where human activity is concentrated (Tin et al. 2009; Terauds et al. 2012; Hughes et al. 2016; Brookes et al. 2019). Guidelines prepared by the Antarctic Treaty System's Committee for Environmental Protection and the Scientific Committee on Antarctic Research clearly enunciate the vulnerability of these ecosystems and the need for careful management of human behavior to avoid damage. Nevertheless, multiple and continuing instances of such damage, which can remain apparent for many decades after the event, have been reported and many more are not formally reported (Tin et al. 2009; Braun et al. 2012, 2018; Convey 2020). The 'footprint' of human activities is particularly great in the South Shetland Islands, where multiple nations operate research stations and field facilities and tourism operators use regular visitor sites, to the extent that virtually all ice-free areas or significant headlands in the archipelago host research stations, campsites, field instrumentation or sampling sites, refuges or other visitor sites.

Despite the scale of human interaction with and damage to terrestrial ecosystems, other than the guidelines mentioned above and the need for preparation of environmental impact assessments, one of whose roles is to minimize environmental impacts of activities such as station construction, we are not aware of any instances of pre-emptive conservation measures, such as transplantation, taken to avoid loss of vegetation that inevitably lies within construction footprints. Similarly, no restoration approaches have been applied aiming to assist the recovery of areas of vegetation known to have been damaged. Further, no monitoring effort has been applied to known damaged areas to assess the possibility or speed of natural recovery. We are aware of a single study that assessed vegetation recovery after the removal of a small refuge hut in the South Shetland Islands (Putzke et al. 2019), concluding certain elements of moss vegetation could potentially recover quite rapidly. However, Smith (2003) concluded that vehicle damage to wet moss carpets (including *Sanionia*) on the

Table 1 Ecological indexes calculated

Index	Bacteria	Chromista	Fungi	Metazoa	Protista	Viridiplantae	TOTAL
No. of ASVs	189	24	19	8	7	16	263
Simpson	0.97	0.56	0.49	0.77	0.55	0.05	0.9
Shannon	4.24	1.49	1.14	1.74	1.05	0.17	3.12
Evenness	0.37	0.18	0.16	0.71	0.41	0.07	0.08
Margalef	20.33	2.53	2.00	0.66	0.88	1.56	23.16
Fisher's α	32.81	3.01	2.33	0.73	1.03	1.77	33.74

Fildes Peninsula remained apparent after several decades and may never fully recover (Tin et al. 2009).

With this background, to our knowledge no pre-emptive moss transplants aiming to conserve extensive moss carpets and their contained biota that would otherwise inevitably be lost have been proposed or attempted previously in Antarctica. Moss transplant studies have been reported elsewhere, generally involving only small areas and often in a domestic and gardening-oriented context (Glime 2017a, b). In Northern Hemisphere temperate forests, Parker et al. (1997) used small-scale transplants to investigate the role of hair-cap mosses in the regeneration of spruce forests, Cobb et al. (2001) investigated moss recolonization processes on maple branches and Frego (1996) investigated the regeneration of boreal bryophytes.

Elsewhere, moss transplants appear to be relatively successful (Lewis and Smith 1977; Longton 1981; Kallio and Saarnio 1986). In the Mojave Desert, up to 50% of transplanted small patches of *Syntrichia caninervis* Mitt. survived for 27 months (Cole et al. 2008). There are a number of instances of transplants being used as a conservation tool (e.g. Flagmeier et al. 2016). Gunnarsson and Söderström (2007) successfully transplanted *Sphagnum angermanicum* Melin to new sites in Sweden and Kooijman et al. (1994) re-introduced *Scorpidium scorpioides* (Hedw.) Limpr. from Ireland into the Netherlands, from where it had become extinct. Gauthier et al. (2018) and Hugron et al. (2013) have successfully demonstrated the potential for transplants to be used in the restoration of both mining-related and glacially-influenced habitats. Graf and Rochefort (2010) and Aradottir (2012) also successfully used moss transplants in restoration experiments. Transplants have also been used in studies focused on microenvironmental or ecophysiological aspects of moss success or distribution (e.g. Merinero et al. 2020; Dahlberg, 2014; Graf and Rochefort 2010; Frego 1996)). However, such studies are not directly comparable with the current conservation-oriented study and all involved much smaller transplanted areas.

Taxonomic Diversity

The relatively high number of DNA reads obtained from a single moss gametophyte shoot revealed a cryptic (hidden)

diversity inhabiting moss carpets that is usually ignored, as is the ecological role of such carpets and their contained diversity, as we discuss below.

Bacteria

Bacterial communities associated with mosses are commonly dominated by the phyla Proteobacteria and Bacteroides (Wang et al. 2018; Holland-Moritz et al. 2018). This was the case for the transplanted *Sanionia uncinata* in the present study. However, in contrast with a study of boreal *S. uncinata* (Holland-Moritz 2018), the transplanted sample analyzed here generated the highest relative proportion of sequences belonging to the phylum Actinobacteria, as also reported in another study on Antarctic *S. uncinata* (Park et al. 2013). Other bacterial families commonly present in boreal *S. uncinata*, such as the Proteobacteria families Comamonadaceae and Sphingomonadaceae, as well as the Nostocaceae (Cyanobacteria) and Chitinophagageae (Bacteroidetes), were detected in the bacterial community associated with the transplanted samples, but they were not dominant. Park et al.'s (2013) study of Antarctic *S. uncinata* reported the presence of 56 identified bacterial genera, considerably fewer than the 196 genera identified here. This difference could represent a true difference between the two samples, or be a result of differences in the experimental design. For instance, Park et al. (2013) analyzed endophytic bacteria from multiple samples and used pyrosequencing to obtain the data. In the present study, both epiphytic and endophytic bacterial DNA were analyzed by Illumina MiSeq platform, and the database was considerably updated since 2013 with many sequences previously considered unclassified now having a taxonomic assignment.

Chromista

The Oomycota, a group formerly considered to be fungi, was the most diverse group found with 12 taxa. Most members of this group are obligate parasites and cause plant and animal diseases. Among the Peronosporales sequences assigned, *Peronospora* is an obligate parasite of angiosperms (Göker et al. 2009), causing severe diseases such as downy mildew, and *Phytophthora* (meaning 'plant destroyer') with ca. 313

species described worldwide (www.mycobank.org) is also responsible for multiple plant diseases (Cavalier-Smith and Chao 2006). However, while the genera are well-known worldwide, it is not clear how many representatives are present in Antarctica. Among the Pythiales, *Pythium* with ca. 355 described species (www.mycobank.org) is one of the few oomycete genera that has been widely reported in Antarctica (Bridge et al. 2008), and is also known to cause plant disease. The species *P. tenue* has been reported in continental Antarctica (Knox and Paterson 1973), and *Pythium* sp. have been reported from several sites in both continental and maritime Antarctica (e.g. Paterson and Knox 1971; Ellis-Evans 1985; Hughes et al. 2003; Fell et al. 2006; Bridge and Denton 2007). Bridge et al. (2008) isolated representatives of this genus from visibly unhealthy liverworts from Signy Island (South Orkney Islands) and confirmed their potential pathogenicity to local vascular plants. The genus *Aphanomyces* (known as ‘water moulds’) includes about 30 species (Johnson et al. 2002) mostly known from Europe and North America, some of which are plant or animal pathogens (Grünwald et al. 2003). Among the Order Lagenidiales, *Lagenidium giganteum* Couch ex Redhead is associated with infections in dogs, cats and humans (Grooters et al. 2004; Mendoza and Vilela 2013; Reinprayoon et al. 2013) and has been reported from the South Orkney Islands (Willoughby 1969). At present, there is no means of assessing whether these pathogens are native to Antarctica or have been introduced in association with human activity. It is perhaps appropriate to note that in the early decades of operation of research stations (generally late 1940s onwards in the South Orkney and South Shetland Islands) and the preceding whaling industry (1930s), exploring expeditions (1930s) and sealing industry (Nineteenth Century) the presence of cats and other domestic animals on stations and ships and, subsequently, sledge dogs (until the mid-1990s) was commonplace, which may be consistent with the detection of some animal parasites not known to be associated with native marine mammals and birds.

Ciliophora

Known for feeding on bacteria, the sequences assigned to some ciliates reported here represent taxa that are often common and widespread and may well have been previously overlooked. Some of the taxa identified are predominantly marine (e.g. *Anteholosticha*, *Cyrtohymena*) but the study site is very close to the shore and subject to marine spray. Species of *Cyrtohymena* have been found in soil and/or moss/litter in tropical areas, such as *C. australis* in the Amazonian rain forest (Foissner 1995) and *C. candens*, *C. citrine* and *C. quadrinucleata* in Kenya (Foissner 1999). Two species of *Anteholosticha* (*A. rectangular* and *A. sigmoidea*) and two species of *Cyrtohymena* (*C. candens* and *C. citrina*) have

been reported from Antarctica (Thompson et al. 2019). The genus *Halteria*, whose members are known as ‘jumping oligothichs’, is widely distributed globally and *H. grandinella* has been reported from Antarctica (Thompson et al. 2019). The genus *Hemicycliostyla* is poorly known, and consists of only four species (Paiva et al. 2012), none of which has previously been reported from Antarctica. The genus *Homalogastra* has one species record (*H. setosa*) from Antarctica, while the genus *Kahliella* has not previously been recorded in Antarctica.

Some taxa were only identified at higher rank (Class Oligohymenophorea, Order Urostylida and family Oxytrichidae), making it more difficult to access their geographical range. According to the Register of Antarctic Marine Species (De Broyer et al. 2020), ciliates in the classes Spirotrichea and Oligohymenophorea can occur in both marine and terrestrial environments in Antarctica. Ciliate communities present in marine, freshwater and soil ecosystems are known to be important bacterial consumers and nutrient cyclers (Foissner 1999; Grossmann et al. 2015). In Antarctica, they may play an important role making scarce resources available to plants.

Ochrophyta

Five species of *Spumella* are known worldwide (Europe, South America and New Zealand; Guiry and Guiry 2020), all from freshwater habitats. The only species recorded from Antarctica is *S. vulgaris* (Findenig et al. 2010). Boenigk et al. (2006) isolated several cold-tolerant strains of *Spumella*-like ciliates from samples of fresh water and soil from both maritime and continental Antarctic sites (Signy Island, Alexander Island and Davis Valley). These strains, although morphologically similar to already reported Antarctic morphotypes, are clearly distinct in molecular analyses (Tong et al. 1997; Butler 1999), and may represent an interesting case of microbial geographic isolation (cf. Vyverman et al. 2010; Verleyen et al. 2021). According to Guiry and Guiry (2020), the genus *Segregastopumella* only includes a single species (*S. dracosaxi*) considered to be endemic to Europe, which would make this the first report for Antarctica.

Fungi

Our data indicated the presence of 18 fungal ASVs representing 11 genera from the phyla *Ascomycota*, *Basidiomycota*, *Chytridiomycota* and *Monoblepharomycota*. The most common fungal taxa reported in Antarctic studies are generally representatives of *Ascomycota*, followed by *Basidiomycota* (Rosa et al. 2019). In the current study, we also detected representatives of *Chytridiomycota* and *Monoblepharomycota*, which are less frequently reported in Antarctic studies. Notably, the majority of DNA sequences detected could

only be as assigned at the level of Fungal sp., most likely highlighting that currently available databases covering this group are very incomplete and also suggesting that moss carpets may contain currently unknown fungal taxa.

Metazoa

Being a very diverse group, we consider each phylum in this kingdom separately here.

Arthropoda: The high number of reads associated with Insecta is perhaps surprising as there are only two species of native insect in Antarctica, the midges *Belgica antarctica* and *Parochlus steinenii*. There is also some possibility that Collembola DNA could match as insects sensu lato in databases as it is only relatively recently that studies (e.g. Gao et al. 2008) removed Collembola from the Insecta sensu stricto and placed them basally in the Hexapoda.

A possible confounding factor is the potential presence of exotic insects or, more likely, their remains. According to Chwedorzewska, (2013), 359 invertebrates and their remains were found in cargo transported to the Polish Arctowski Station (also in Admiralty Bay), the majority of which were insects (23 families of insects including food pests, wood – destroying pests and domestic insects). The close proximity to the Brazilian Ferraz station combined with seven years of construction activity may increase the likelihood that insect remains could have been transported with the large quantities of cargo involved. The assigned sequence with a species-level match in the database consulted was a Collembola, *Cryptopygus antarcticus* Willem. This collembolan is a very common native species throughout the Antarctic Peninsula region that reaches some of its highest population densities in *Sanionia* moss carpets (e.g. Convey and Smith 1997). Vegetation cover mitigates a number of the environmental challenges faced by insects and other organisms in Antarctica, making it a crucial environment for the survival of these groups (Grantz et al. 2018). According to Hogg and Stevens (2002), 14 Collembola and 28 Acari species are known from the South Shetland Islands.

Nematoda: approximately 68 nematode species are currently reported from Antarctica (Andrássy 1998; Kagoshima et al. 2019). Our sequence data identified only one species, *Plectus frigophilus*, which is a freshwater species endemic to Antarctica and one of the few that has been provisionally reported from both continental and maritime Antarctica (Yeates 1979; Maslen and Convey 2006; Kagoshima et al. 2019). However, traditional morphological taxonomy remains inadequate to confirm these identifications (Maslen and Convey 2006) and molecular studies of Antarctic nematodes are in their infancy (Kagoshima et al. 2019), although it is clear that virtually no species occur across both maritime and continental Antarctica. It is important to note that our collection did not include soil samples where most

species (habitat specialized or not) are expected to occur (Tomasel et al. 2013). Free-living nematodes are among the groups of invertebrates that are commonly found in bryophytes (Glime 2017a, b).

Rotifera: These microscopic animals have had a long evolutionary relationship with bryophytes (Waggoner and Poinar 1993). Rotifers have very well-developed cryptobiotic adaptations, especially in the Bdelloidea, and are able to withstand long periods of drought or freezing. They are easily dispersed along with fragments of the moss they inhabit (Glime 2017a). Representatives of both genera whose sequences were identified in this study are common in maritime Antarctica. Members of *Macrotrachela* are found in terrestrial and freshwater habitats, with 16 species known in Antarctica. Members of *Philodina* are found in marine, freshwater and terrestrial habitats, with eight species reported from Antarctica (RAS 2020). In general, the most abundant and dominant rotifers in mosses are bdelloids, with the typically damp carpets of *Sanionia* providing an ideal habitat (Glime 2017a; Linhart et al. 2002; Vlčková et al. 2002). A much wider diversity of bdelloid rotifers is known from classical morphological studies in Antarctica than were detected in our study (cf. Priddle and Dartnall 1978; Dartnall 1980). Using an integrated phylogenetic approach, Iakovenko et al. (2015) reported 66 bdelloid morphospecies from various locations around the continent and 83–91 putative species were identified, with very high levels of Antarctic endemism (see also Cakil et al. 2021).

Tardigrada: Tardigrades are another important group of Antarctic terrestrial and freshwater meiofauna (Convey and McInnes 2005; Tsujimoto et al. 2014). Around 60 tardigrade species are currently recorded from Antarctica, with the greatest diversity being present in the maritime Antarctic (Guidetti et al. 2019). Molecular phylogenetic studies of Antarctic tardigrades are in their infancy, but it is already clear that considerable species-level cryptic diversity is present in the few species examined to date (Kihm et al. 2020; Guidetti et al. 2014). The single genus identified in this sequencing study, *Dactylobiotus*, is globally distributed in freshwater habitats. According to Kihm et al. (2020), until very recently only one species was reported from Antarctica (*D. ambiguous*), until a new species from King George Island was described (*D. ovimutans*).

Protista

Discosea: Members of the genus *Cochliopodium*, with about 23 described species worldwide, are amoeboid eukaryotes that inhabit mostly freshwater but also brackish and marine habitats (Tekle et al. 2013). Of the species assigned from sequences obtained here, *C. pentatrifurcatum* was described in 2013 as endemic to the United Kingdom and *C. marri* as endemic to Alabama, USA (Melton et al. 2019). The

presence of the genus in Antarctica is noted in the SCAR Antarctic terrestrial biodiversity database (https://data.aad.gov.au/aadc/biodiversity/taxon_profile.cfm?taxon_id=114665). Only *C. tentaculatus* has been reported from Antarctica but as an incomplete record (Thompson et al. 2019). All the specific assignments obtained in the current study are new to Antarctica, suggesting that the diversity of the genus in the continent may be much higher than previously reported, but species identities cannot be confirmed in the absence of specimens. *Vannella simplex* is one of the best-documented and relatively easily recognizable species of amoebae. Representatives are known from both freshwater and brackish habitats globally (Smirnov et al. 2002), with three species including *V. simplex* reported from Antarctica (Thompson et al. 2019).

Excavata: *Reclinomonas americana* is the only described species in this genus. It has been reported from freshwater environments in New Zealand and North America (Flavin and Nerad 1993) but not from Antarctica. However, members of the Heterolobosea appear to have very wide distributions, including in extreme environments (Park and Simpson 2011) and are likely to have been overlooked in Antarctica.

Viridiplantae

The algal community identified by sequences obtained here is similar to that described by Câmara et al. (2020) from Deception island, including common snow algal taxa such as *Chlamydomonas* and some terrestrial taxa such as *Chlorococcum*. The presence of *Chlorothrix*, a marine genus is plausible as the study site is close to the coastline. Some taxa only assigned to higher ranks may again represent taxa not present in the consulted databases or new undescribed taxa. Among the mosses, the taxa assigned are most widely distributed in this region (Ochyra et al. 2008). Although *Pohlia crudoides* is not recorded from Antarctica other members of the genus are present, and this is likely to indicate a lack of resolution in the available sequence databases. The presence of multiple moss sequences may reflect the presence of either spores or propagules transported either by wind or water to the study site. The high number of reads of *Bryum pseudotriquetrum* is notable, being one of the most common moss species in Antarctica (including close to this study site) and one that is also commonly found with sporophytes.

Conclusions

In this study, DNA sequences assigned to 253 taxa representing 31 phyla were obtained from a single shoot of the moss *Sanionia uncinata* from the transplanted moss carpet. Our data are indicative that an entire community associated with the moss carpet are also transplanted, further emphasizing

the Antarctic conservation importance of this transplant effort. This is the first study to use metabarcoding to assess diversity potentially associated with an Antarctic moss carpet, with the data obtained emphasizing that a moss carpet is far more than a monospecific group of shoots of a common moss species, but provides habitat for considerable and often overlooked, cryptic, biodiversity. We are aware that our sampling effort was low and that the detection and assignment of a DNA sequence do not confirm the presence or viability of a given organism. Further targeted studies are required to confirm the presence of a species. However, studies such as this provide important clues as to the diversity potentially present, particularly in ecosystems and taxonomic groups that have not been a focus of detailed research. Furthermore, Antarctic moss carpets and their associated diversity play important roles in nutrient cycling. They also have high aesthetic value bringing color and contrast to a white and grey continent and are a feature of many Antarctic protected areas.

Supplementary Information The online version of this article (<https://doi.org/10.1007/s00792-021-01235-y>) contains supplementary material, which is available to authorized users.

Acknowledgements We thank the Brazilian Navy, Brazilian Air Force and the staff at Ferraz station (GB Ferraz). This study received financial support from CNPq, PROANTAR, INCT Criosfera 2. P. Convey is supported by NERC core funding to the BAS ‘Biodiversity, Evolution and Adaptation’ Team. We also thank congresswoman Jô Moraes and the Biological Sciences Institute of the University of Brasilia.

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