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REGULAR ARTICLE

Identity of plant, lichen and moss species connects with microbial abundance and soil functioning in maritime Antarctica

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Abstract

Background and aims We lack studies evaluating how the identity of plant, lichen and moss species relates to microbial abundance and soil functioning on Antarctica. If species identity is associated with soil functioning, distributional changes of key species, linked to climate change, could significantly affect Antarctic soil functioning.

Methods We evaluated how the identity of six Antarctic plant, lichen and moss species relate to a range of soil attributes (C, N and P cycling), microbial abundance and structure in Livingston Island, Maritime Antarctica. We used an effect size metric to predict the association between species (vs. bare soil) and the measured soil attributes.

Results We observed species-specific effects of the plant and biocrust species on soil attributes and microbial abundance. Phenols, phosphatase and β-D-cellobiosidase activities were the most important attributes characterizing the observed patterns. We found that the evaluated species positively correlated with soil nutrient availability and microbial abundance vs. bare soil.

Conclusions We provide evidence, from a comparative study, that plant and biocrust identity is associated with different levels of soil functioning and microbial abundance in Maritime Antarctica. Our results suggest that changes in the spatial distribution of these species linked to climate change could potentially entail changes in the functioning of Antarctic terrestrial ecosystems.

Keywords Antarctic vegetation · Bacteria · Fungi · qPCR · Soil enzyme activities

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Introduction

Current exposed lands in Antarctica, mainly located at coastal regions or rock ridges, are the habitat for Antarctic plants and cryptogamic species –including

the Antarctic flowering plants *Deschampsia antarctica* and *Colobanthus quitensis*, and multiple bryophyte and lichen species, some of them forming biocrust communities. In these areas, Antarctic vegetation shows a spatial patchy distribution as a consequence of multiple ecological conditions (Kappen et al. 1985; Melick and Seppelt 1997). The establishment and distribution of Antarctic vegetation is primarily conditioned by ice and snow melt at some point during the year, and thus is ultimately determined by microclimatic factors (Kennedy 1993; Hughes et al. 2006; Vieira et al. 2014). These factors (e.g. moisture or texture micro-gradients) also affect soil properties and may compromise successful propagule colonization (Bergstrom et al. 2006), but the irruption of vegetation can have direct consequences on soil functioning. For instance, we know that the presence of cryptogams is positively associated with fertility islands (sensu Schlesinger et al. 1996) leading to higher N and C concentration underneath them in continental Antarctic soils (Cannone et al. 2008) and elsewhere (Delgado-Baquerizo et al. 2016). However, the species-specific association of plant, lichen and moss species identity with multiple soil attributes, nutrient cycling and microbial abundance (Cornelissen et al. 2007; Mallen-Cooper and Eldridge 2016) remains largely unexplored in Antarctica.

The role of plant, lichen and moss species identity (at both functional and taxonomic levels) as a potential environmental predictor of soil functioning is well-known in terrestrial ecosystems (Hooper and Vitousek 1997; Chen and Stark 2000; Chapman et al. 2005; Fan et al. 2011). Primary productivity, nitrogen (N) fixation capacity or thallus/stem structure are known to be involved in litter quality and quantity production or dust capture, important factors involved in the formation of the so called fertility islands in patchy vegetated ecosystems (e.g. arid ecosystems; de Graaff et al. 2014; Ochoa-Hueso et al. 2018). Similarly, recent studies have stated that the identity of biocrusts has important implications for both microbial communities and soil functioning in drylands (Concostrina-Zubiri et al. 2013; Delgado-Baquerizo et al. 2015; Liu et al. 2016, 2017). Therefore, not only the presence but also the identity of plant and biocrust (i.e. lichens and bryophytes) species may differentially influence both microbial communities and soil functioning. However, studies providing evidence for a link between species identity and soil attributes are largely lacking, limiting our capacity to predict how ongoing changes in the coverage, relative abundance, and metabolic activity of these plant and biocrust species with climate change (e.g. Torres-Mellado et al. 2011; Cannone et al. 2016; Amesbury et al. 2017) may potentially impact the functioning of Antarctic terrestrial ecosystems.

Using a comparative approach, we evaluated how four lichen species (*Leptogium puberulum, Stereocaulon alpinum, Sphaerophorus globosus*, and *Cladonia* sp.), one moss (*Sanionia uncinata*), and the most common Antarctic flowering-plant (*Deschampsia antarctica*) (Sancho et al. 1999; Søchting et al. 2004) are associated with multiple soil attributes related to carbon, nitrogen and phosphorus cycling and the abundance of soil fungi and bacteria at Livingston Island (Antarctic Peninsula). The expected changes in the relative abundance of these species due to, for example climate change, could alter soil functioning in this continent (Kardol et al. 2010; van der Putten et al. 2016; Liu et al. 2017). Alternatively, if vegetation patterns do not relate to soil functioning, changes in their relative abundance in response to changing climatic conditions may not entail differentiated changes in soil functioning in the region. We hypothesized that the identity of plant and biocrust species will largely relate to different levels of multiple soil attributes (i.e. concentration and cycling of soil nutrients) and the abundance of soil fungi and bacteria. To test this, we first evaluated whether soil functioning and microbial abundance differed under monospecific patches of the plant and biocrust species evaluated. We then characterized which variations associated with the observed differences. Additionally, we determined which soil attributes were more sensitive to species identity. Finally, we evaluated the differences in soil functioning between the different species evaluated and areas devoid of vegetation. Our study is among the first exploring the species-specific connections of Antarctic vegetation (i.e. lichens, bryophyte and vascular species) with below-ground soil functioning. Advancing our knowledge on the relationships between the identity of vegetation components and soil biochemistry and microbial communities in Antarctica is critical to understand this ecosystem and to accurately predict

potential impacts of changes in the relative abundance of these micro-habitats because of global change.

Materials and methods

Site description

The study was carried out in the vicinity of the Juan Carlos I Spanish Antarctic Base (62°39′46″S 60°23′20″W), which is located on Livingston Island (Fig. 1), 120 km north of the Antarctic Peninsula. Geology is primarily composed of acidic sedimentary, metamorphic, plutonic and volcanic rocks. The climate of Livingston Island is cold maritime, with mean summer temperature above freezing and minimum absolute temperature in winter not lower than −20 °C (Sancho et al. 2017). Annual precipitation is circa 445 mm, mainly concentrated in summer and autumn seasons (Bañón et al. 2013). Around 10% of the surface of Livingston Island is free of ice during the summer season (Fig. 1) – mainly coastal strips and rocky ridges– allowing the development of plant and cryptogamic species. Vegetation in these areas is dominated by terricolous or saxicolous lichens (species of the genera *Buellia*, *Caloplaca*, *Cladonia*, *Leptogium*, *Pertusaria*, *Placopsis*, *Rhizocarpon, Stereocaulon* and *Usnea*, among others), and bryophytes (species of the genera *Andreaea*, *Brachythecium*, *Bryum*, *Polytrichum* and *Sanionia*, among others), in combination with the native flowering plants *Deschampsia antarctica* and *Colobanthus quitensis* (Sancho et al. 1999; Søchting et al. 2004).

Sampling design

Soil sampling was conducted at the end of the Antarctic summer of 2015. We selected six of the most common species of vegetation growing on Livingston Island (Sancho et al. 1999; Søchting et al. 2004), including a flowering plant (*Deschampsia antarctica*,), four lichens (*Stereocaulon alpinum, Sphaerophorus globosus, Leptogium puberulum,* and *Cladonia* sp.), and one moss (*Sanionia uncinata*). We acknowledge that some selected species (i.e. *S. alpinum* and *S. globosus*) are not biocrusts per se but they grow forming dense and complex cryptogamic covers in combination with other biocrust forming species (e.g. *Ceratodon purpureus*, *Cladonia chlorophaea*, *Psoroma hypnorum*, *Placopsis contortuplicata*, *Ochrolechia frigida*). For simplicity, we use the term biocrust (sensu *lato*) throughout the manuscript to refer to these communities. *Leptogium puberulum* and *S. alpinum* are nitrogen fixing lichens

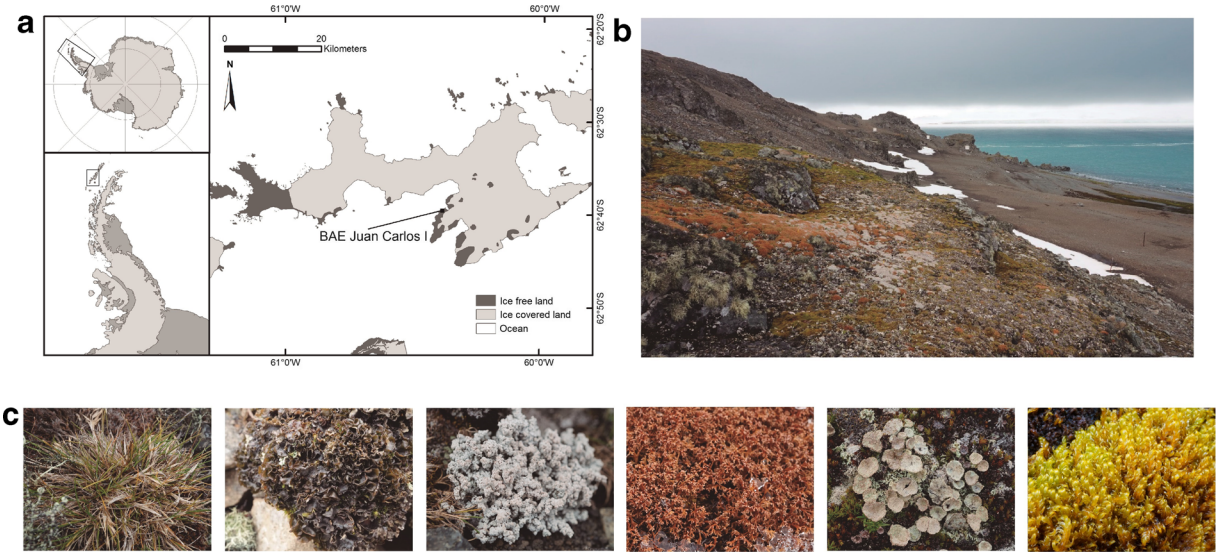


Fig. 1 Study site information. **a** Map of the sampling area in Livingston Island, South Shetland Islands, Antarctica; **b** Raised beaches in the vicinity of Juan Carlos I Spanish Antarctic Base showing the vegetation communities sampled; **c** Selected species, from left to right: *Deschampsia antarctica*, *Leptogium puberulum*, *Stereocaulon alpinum*, *Sphaerophorus globosus*, *Cladonia* sp., and *Sanionia uncinata*

including cyanobacteria (genus *Nostoc*) as a principal photobiont (*L. puberulum*) or as a secondary symbiont in cephalodia (*S. alpinum*). *Sphaerophorus globosus* and *Cladonia* sp. lack N-fixation capacity. The moss *S. uncinata* presents epiphytic cyanobacteria with lower fixation rates than that observed in abovementioned lichens (data not shown). *Deschampsia antarctica* was also included in our study because it has a significant presence in the studied area and coexists with the abovementioned biocrust species. From a total sampling area of 0.9 ha, we randomly selected single-species patches (having at least 10 cm diameter) for our soil sampling. A distance of at least 2 m was kept between patches to ensure spatial independency between samples (Delgado-Baquerizo et al. 2013). For each species, ten replicated soil samples from the top 5 cm mineral soil profile were collected with a 5 × 5 cm core, with the exception of *Cladonia* sp., which was more frequent on rocky substrates. This prevented us from obtaining more than six samples with soil profiles deeper than 5 cm for this species. Areas with no vegetation cover (bare soil) were used as controls (10 replicates). Thus, a total of 66 soil samples were collected, sieved with a 2 mm sieve and divided in two fractions. A fraction of soil was immediately frozen at −20 °C for molecular analysis. The other fraction was air dried for biogeochemical analyses. Both fractions were transported to the laboratory of Rey Juan Carlos University in Móstoles (Spain) for analyses.

Measurement of C, N and P variables in soil

We measured in the laboratory a total of 16 soil variables linked to the stocks and cycling of C, N and P: dissolved organic C (Corg), phenols, α-Glucosidase (AG, starch degradation), β-Glucosidase (BG, starch degradation), β-D-Cellobiosidase (CB, cellulose degradation), total N, available nitrogen (AN), proteins, potential net mineralization and nitrification rates, microbial biomass N, Xylosidase (XYL, hemicellulose degradation), L-Leucine-amidomethylcoumarin (LAP, protein degradation), N-acetyl-β-glucoasminidase (NAG, chitin degradation), dissolved inorganic P (DIP), and Phosphatase (PHOS, P mineralization). All these variables, referred as soil attributes hereafter (both including soil functions and properties), are either measurements of specific ecosystem processes (e.g. N mineralization rate) or key properties (e.g. organic C, total N, inorganic P and soil enzymes), which together constitute a good proxy of nutrient cycling, biological productivity and the build-up of nutrient pools (Reiss et al. 2009; Jax 2010; Maestre et al. 2012a, b).

The N of microbial biomass (MB-N) was determined using the fumigation-extraction method of Brookes et al. (1985). Soil pH was measured for all of the soil samples with a pH-meter in a 1:2.5 mass/volume soil and water suspension. Sand, clay, and silt contents were determined according to Kettler et al. (2001). Electrical conductivity was determined using a conductivity meter in the laboratory. Soil moisture content was measured by oven-drying the samples at 105 °C for 24 h, and soil water holding capacity was measured by gravimetry. Soil N was measured with a CN analyzer (Leco CHN628 Series; Leco Corporation, St Joseph, MI, USA). Organic C was determined following Anderson and Ingram (1993). Total available N (sum of ammonium, nitrate, and dissolved organic N) was colorimetrically analyzed from K_2SO_4 0.5 M soil extracts using a 1: 5 soil/extract ratio as described by Delgado-Baquerizo et al. (2011). Phosphate was determined by colorimetry from a 0.5 M $NaHCO_3$ extraction (Bray and Kurtz 1945).

We measured the potential activity of seven hydrolytic soil enzymes involved in the degradation of common organic matter constituents: α-Glucosidase (starch degradation; AG), β-Glucosidase (starch degradation; BG), β-D-Cellobiosidase (cellulose degradation; CB), leucine aminopeptidase (protein degradation; LAP), N-acetyl-β-Glucosaminidase (chitin degradation; NAG), Phosphatase (P mineralization; PHOS) and β-Xylosidase (hemicellulose degradation; XYL). All the enzyme assays were set up in 96-well microplates following Bell et al. (2013). Fluorescence was measured using a microplate fluorometer (Synergy™ HTX Multi-Mode Microplate Reader, BioTek Instruments, Inc., USA). The activities were expressed as nmol h^{-1} g^{-1}dry soil.

Quantification of fungi and bacteria

DNA was extracted from 0.5 g of defrosted soil fractions using the MoBio® PowerSoil DNA isolation kit (MoBio Laboratories, Carlsbad, CA) following manufacturer instructions. The quantity and quality of extracted DNA was checked using a NanoDrop® ND-2000c UV–Vis spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA). The abundances of the bacterial (16 s rRNA) and fungal (ITS) genes were analyzed using quantitative PCR (qPCR) on a CFX-96

thermocycler (Biorad, USA). Total bacterial 16S and fungal 18 s rRNA genes were quantified using primer pairs Eub 338-Eub 518 and ITS1F-5.8 s respectively, following Evans and Wallenstein (2012). Efficiencies for all quantification reactions were higher than 90%, with R^2 values above 0.90. The fungal: bacterial ratio was calculated using qPCR data. Results from qPCR were log-transformed for subsequent data analysis.

Statistical analyses

We first tested for significant differences in the 16 soil attributes measured across different plant and biocrust species by conducting a semiparametric MANOVA (PERMANOVA, Anderson 2001), with species as a fixed factor. Note that PERMANOVA allows unbalanced designs (i.e., different number of replicates), hence it is suitable for analyzing the data collected given our sampling design. Moreover, PERMANOVA do not require MANOVA assumptions (normality and homogeneity of variances), which were not met by our variables. We also conducted independent one-way PERMANOVA analyses for each soil and microbial variables evaluated, and tested for differences among plant and biocrust species for these variables using pairwise post hoc tests (Anderson 2001). To help visualize the differences among species, and to aid in the interpretation of PERMANOVA results, we conducted a principal component analysis (PCA) with the 16 soil attributes analyzed. We tested for differences in the soil variables analyzed including abundance of bacteria and fungi across different species by using one-way PERMANOVA. Before carrying out PERMANOVA and PCA analyses, the different variables measured were standardized by using the Z-score (Kreyszig 1978). PERMANOVA analyses were developed using 9999 permutations (permutation of raw data) and the Euclidean distance with the PERMANOVA+ for PRIMER statistical package (PRIMER-E Ltd., Plymouth Marine Laboratory, Ivybridge, UK). PCA analyses were also carried out using PRIMER.

We then assessed which soil variables, among the 16 measured related to C, N, and P cycling and storage, were the most important predictors of species identity (i.e. which variables differed the most across species). To do this, we conducted a classification random forests analysis (Breiman 2001) as described in Delgado-Baquerizo et al. (2015). The accuracy importance measure was computed for each tree, and was averaged over the forest (999 trees). These analyses were conducted using the rfpermute package (Archer 2013) of the R v3.3.2 software (http://cran.r-project.org/).

Finally, we evaluated the "fertility effect" of selected species on soil attributes using the relative interaction index (RII) of Armas et al. (2004). By "fertility effect" we mean the increase or decrease of a soil attribute under a given plant/lichen/moss species regarding the value of this attribute obtained in bare ground areas. RII was calculated as (Sli − Sbg)/(Sli + Sbg), where Sli and Sbg are the values of a given soil attribute under the lichen thalli/plant canopy and in bare ground areas, respectively (Armas et al. 2004). The RII index was calculated separately for each attribute and species studied, using as replicates for Sli the values obtained under each species sampled ($n = 10$, except for *Cladonia* sp. with $n = 6$), which were compared in all cases with the average of the ten replicates obtained from bare ground areas. Values of RII range from −1 to +1, with positive values indicating increases in the variable studied under the canopy of species compared to bare ground areas and negative values the opposite. To test whether RII values differed significantly from zero, we assessed their 95% bootstrap confidence interval by using the bootes R package (Kirby and Gerlanc 2013). Differences among species in the RII values were also evaluated by using one-way PERMANOVA, with species as a fixed factor. These analyses were carried out using 9999 permutations (permutation of raw data) and the Euclidean distance with the PERMANOVA+ for PRIMER statistical package.

Results

Soil functioning and microbial abundance levels under different plant and biocrust species

We found significant differences in soil functioning across different species (PERMANOVA $P < 0.001$; Pseudo-F = 3.97; d.f. = 6). In addition, we found the strongest differences in soil attribute for biocrusts vs. bare soil; and for *Leptogium puberulum* vs. all other studied species ($P < 0.001$; Table 1; Fig. 2). Similarly, *Sanionia uncinata* significantly differed to all other studied species except *Cladonia* sp. These observed differences were driven by species-associated variations of particular soil attributes and microbial abundances.

Table 1 Results of PERMANOVA pairwise post-hoc comparisons between studied species and bare ground areas including in the analysis all the C, N, P variables evaluated. *Leptogium puberulum* (LP), *Stereocaulon alpinum* (SA), *Spherophorus globosus* (SG), *Cladonia sp.* (CL), *Sanionia uncinata* (SU), *Deschampsia Antarctica* (DA) and bare soil (BS). *P*-values below 0.05 are in bold. (n = 10, except *Cladonia* sp. with n = 6)

Species	t	*P*
LP, SA	2.1015	**<0.001**
LP, SG	2.9407	**<0.001**
LP, CL	2.0644	**<0.001**
LP, DA	2.8037	**<0.001**
LP, SU	2.4886	**<0.001**
LP, BS	1.7098	**<0.001**
SA, SG	1.0383	0.3395
SA, CL	1.0649	0.3348
SA, DA	1.0495	0.3203
SA, SU	1.4698	**0.0379**
SA, BS	2.288	**<0.001**
SG, CL	1.2458	0.1621
SG, DA	1.3281	0.1077
SG, SU	1.6947	**0.0119**
SG, BS	3.4187	**<0.001**
CL, DA	1.0963	0.3008
CL, SU	1.0294	0.4001
CL, BS	2.1376	**<0.001**
DA, SU	1.7071	**0.003**
DA, BS	3.2669	**<0.001**
SU, BS	2.9817	**<0.001**

However, we did not detect differences for *Cladonia* sp., *D. Antarctica*, *Stereocaulon alpinum*, and *Sphaerophorus globosus* when analyzed together (Fig. 2, Table 1).

The values of the soil functioning variables measured differed under each studied species. The differences between *L. puberulum* and the rest of studied species were driven mostly by the lowest values of soil nutrients (organic C, total N and phenols; $P < 0.05$; Table 2), the highest potential nitrification rate, and the values of soil enzyme activities (highest AG activity, lowest BG and CB, and lowest PHOS) found under this species ($P < 0.05$; Table 2). In the case of *S. uncinata*, its differences with the rest of species were related to the highest PHOS activity and bacterial abundance (see below), and to the intermediate values of total N and organic C found under this species (Table 2).

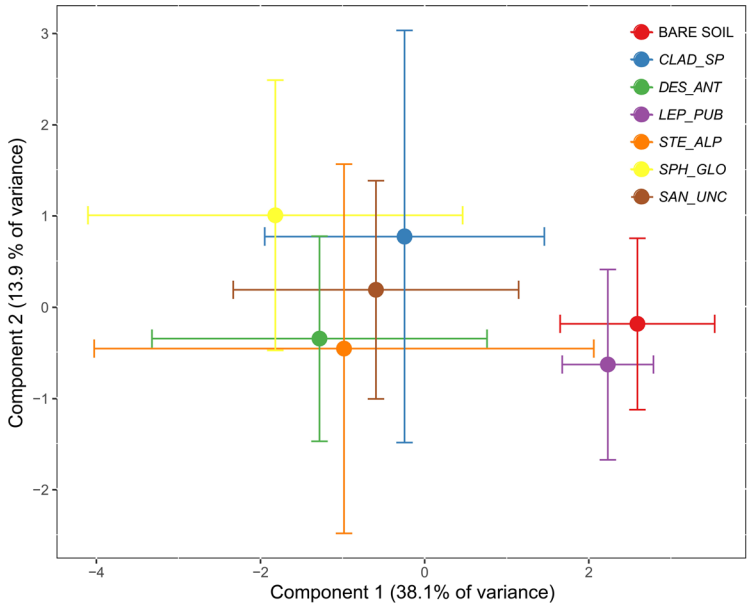
We found large differences in the abundance and structure (fungal:bacterial ratio) of soil bacteria and fungi across the studied species. Soils under most plant and biocrust species studied showed higher microbial abundance compared to bare ground areas, with the exception of *S. globosus* and *S. alpinum*, which had the lowest fungal and bacterial abundances, respectively (Fig. 3ab). In the case of *S. globosus*, soil fungal abundance was even lower than in soils devoid of vegetation. Soil fungal abundance under *S. alpinum, S. uncinata*, and *D. antarctica* was ~10 fold higher compared to bare ground areas. The highest soil bacterial abundances were reported under *S. uncinata* and *L. puberulum*, while soils under *S. alpinum* showed similar bacterial abundance than soils devoid of vegetation. The highest value of the fungal:bacterial ratio was observed under *D. antarctica* ($P < 0.05$, Fig. 3c). Soils under *L. puberulum* and *S. alpinum* showed intermediate values, which were different to those observed under *D. antarctica* and *S. globosus* ($P < 0.05$, Fig. 3c). *Sphaerophorus globosus* also showed similar fungal:bacterial ratio compared to soils devoid of vegetation.

Soil attributes and microbial abundance predicting observed differences across species

Our Random Forest analysis revealed that phosphatase activity, phenols, and β-D-cellobiosidase activity were the most important variables characterizing observed differences across soils under the studied species (Fig. 4), followed by other soil attributes related to nutrient availability, enzyme activities and abundance of soil microbes. However, some of the studied variables (e.g. NAG, proteins, available nitrogen, NIP, and phosphate) did not predict the differences observed across the plant and biocrust studied species.

RII index results

We observed differences in the "fertility effect" (as calculated by the RII index) of the plant, moss and lichen species studied (Fig. 5). Most of the RII values obtained were positive, i.e. the concentration and rates of the analyzed soil attributes were higher under plant and biocrust species when compared to soils devoid of vegetation. The fruticose lichen *S. globosus* had the highest positive RII value for soil total N and organic C content, potential mineralization rate and microbial



	Component 1	Component 2
TN	-0.797 (**<0.001**)	0.361 (**0.008**)
AN	-0.498 (**<0.001**)	-0.006 (0.960)
MB-N	-0.546 (**<0.001**)	0.331 (**0.001**)
NIP	0.054 (0.669)	-0.667 (**<0.001**)
MIN	-0.751 (**<0.001**)	0.356 (**0.003**)
Corg	-0.762 (**<0.001**)	0.412 (**0.001**)
Phenols	-0.823 (**<0.001**)	0.272 (**0.027**)
Proteins	0.132 (0.292)	0.507 (**<0.001**)
DIP	-0.207 (0.095)	-0.393 (**0.001**)
AG	-0.445 (**<0.001**)	-0.356 (**0.003**)
BG	-0.928 (**<0.001**)	-0.020 (0.871)
CB	-0.877 (**<0.001**)	-0.047 (0.705)
LAP	-0.488 (**<0.001**)	0.053 (0.670)
NAG	-0.840 (**<0.001**)	-0.196 (0.116)
PHOS	-0.682 (**<0.001**)	0.045 (0.720)
XYL	-0.757 (**<0.001**)	-0.264 (**0.032**)

Fig. 2 Results of a principal component analysis showing the differences between the plant and biocrust species studied according to the different soil C, N, and P attributes measured. The table on the right side shows the Spearman correlations between the PCA ordination components (PC1 and PC2) and the studied soil attributes (*P*-values <0.05 are in bold). Values in the PCA represent means ± SD ($n = 10$, except for *Cladonia* sp. with $n = 6$). CLAD_SP: *Cladonia* sp.; DES_ANT: *Deschampsia antarctica*; LEP_PUB: *Leptogium puberulum*; STE_ALP: *Stereocaulon alpinum*; SPH_GLO: *Sphaerophorus globosus*; SAN_UNC: *Sanionia uncinata*; TN: total nitrogen; AN: available nitrogen; MB-N: microbial biomass nitrogen; NIP: potential nitrification rate; MIN: potential mineralization rate; Corg: dissolved organic C; DIP: dissolved inorganic phosphorus; AG: α-Glucosidase; BG: β-Glucosidase; CB: β-D-Cellobiosidase; LAP: Leucine aminopeptidase; NAG: N-acetyl-β-Glucosaminidase; PHOS: Phosphatase; XYL: β-Xylosidase

biomass N. *Deschampsia antarctica* showed the highest RII value for all the soil nutrients evaluated, being the only species that had positive RII value for inorganic P. Similar results were observed under the moss *S. uncinata*, except for inorganic P, which decreased under this species compared to bare ground soils. Soil nutrient content under *S. uncinata* remained at intermediate levels. However, we also detected some negative relationships between RII and particular species (e.g., *L. puberulum* and *Cladonia* sp.). *Leptogium puberulum* showed the lowest RII values for soil total N, organic C, inorganic P, phenols and potential mineralization rates. However, this species showed the highest RII values for potential nitrification. Species-specific fertility effects were also observed when evaluating the RII values of soil enzymes (Fig. 3b). *Deschampsia antarctica* and *S. uncinata* had positive RII values for soil enzymatic activities, while enzymes such as BG, CB and PHOS showed very low RII values under *L. puberulum*. Similarly, we found very low levels of RII for AG and XYL under *Cladonia* sp.

Discussion

We provide solid evidence from a comparative study that the identity of plant, moss and lichen species is associated with different levels of soil functioning and microbial abundance in maritime Antarctica. More specifically, we observed that selected plant and biocrust species were related to very different values for soil variables linked to C, N and P cycling and storage (nutrient availability and enzyme activities) and microbial abundance (total fungi, bacteria and their ratio). Our observations are supported by previous observational and experimental studies conducted in drylands (Delgado-Baquerizo et al. 2015; Liu et al. 2016, 2017). Among measured soil attributes, the activity of phosphatase and β-D-cellobiosidase, and the concentration of phenols, were the most important variables characterizing the differences in soil functioning across the studied plant and cryptogamic species. Different concentrations of soil phenols and surrogates of soil P cycling (phosphatase and dissolved inorganic P) have been previously reported to be associated with different

Table 2 Soil variables measured in soils devoid of vegetation (bare soil) and in soils under six selected species. Data are means ± SE (n = 10, except for *Cladonia* sp. with n = 6). Different letters represent statistical differences among species ($P < 0.05$, PERMANOVA) for a given variable. EC: electrical conductivity; WHC: soil water holding capacity; DOC, dissolved organic carbon; TN: total nitrogen; MBN, microbial biomass nitrogen; AN: available nitrogen; PMR, potential mineralization rate; PNR, potential nitrification rate; DIP: dissolved inorganic phosphorus; AG: α-Glucosidase; BG: β-Glucosidase; CB: β-D-Cellobiosidase; LAP: Leucine aminopeptidase; NAG: N-acetyl-β-Glucosaminidase; PHOS: Phosphatase; XYL: β-Xylosidase

Variable	Units	Bare soil	*Leptogium puberulum*	*Stereocaulon alpinum*	*Sphaerophorus globosus*	*Cladonia* sp.	*Sanionia uncinata*	*Deschampsia antarctica*
pH		5.6 ± 0.09^{a}	5.5 ± 0.05^{ac}	5.3 ± 0.05^{b}	5.3 ± 0.06^{c}	5.2 ± 0.13^{b}	5.3 ± 0.10^{bc}	5.0 ± 0.13^{b}
EC	($\mu S\ cm^{-1}$)	47.12 ± 6.53^{ac}	44.81 ± 2.16^{a}	71.78 ± 7.10^{bd}	87.54 ± 9.23^{b}	64.22 ± 2.82^{cd}	37.37 ± 3.03^{a}	98.53 ± 13.53^{bd}
WHC	(%)	24.03 ± 1.16^{a}	27.65 ± 0.58^{b}	33.73 ± 1.37^{cd}	35.93 ± 1.22^{c}	31.57 ± 1.84^{cd}	30.34 ± 1.71^{bd}	33.56 ± 1.11^{cd}
DOC	($g\ C\ kg^{-1}$soil)	11.92 ± 2.05^{ab}	7.72 ± 0.87^{a}	23.11 ± 3.15^{c}	27.18 ± 2.35^{c}	19.83 ± 2.54^{c}	16.86 ± 2.45^{b}	23.11 ± 2.55^{c}
Phenols	($mg\ C_7H_6O_3\ kg^{-1}$soil)	2.68 ± 0.50^{a}	3.21 ± 0.34^{a}	7.97 ± 1.09^{bc}	9.19 ± 0.44^{b}	9.05 ± 0.91^{bc}	7.50 ± 0.67^{c}	10.78 ± 1.13^{b}
TN	(%)	0.13 ± 0.02^{ab}	0.08 ± 0.01^{a}	0.24 ± 0.04^{cd}	0.28 ± 0.02^{c}	0.26 ± 0.04^{c}	0.18 ± 0.02^{bd}	0.23 ± 0.02^{cd}
MBN	($mg\ kg^{-1}$)	1.23 ± 0.48^{a}	3.6 ± 0.86^{b}	7.68 ± 2.17^{bc}	9.99 ± 1.93^{c}	3.44 ± 1.22^{b}	9.36 ± 2.62^{bc}	5.39 ± 1.25^{b}
AN	($mg\ kg^{-1}$)	17.31 ± 1.10^{c}	16.99 ± 0.40^{ac}	20.03 ± 0.71^{bc}	20.12 ± 0.65^{b}	18.28 ± 1.65^{ac}	19.63 ± 0.77^{abc}	21.98 ± 0.88^{b}
Proteins	($mg\ BSA\ kg^{-1}$soil)	16.90 ± 2.44^{ab}	24.45 ± 4.52^{ab}	17.22 ± 4.86^{a}	24.80 ± 4.63^{b}	19.98 ± 4.48^{ab}	21.12 ± 3.92^{ab}	20.26 ± 5.41^{ab}
PMR	($mg\ N\ kg^{-1}$ soil day^{-1})	0.36 ± 0.12^{a}	0.93 ± 0.16^{b}	1.90 ± 0.57^{bcd}	2.73 ± 0.37^{c}	1.71 ± 0.20^{cd}	1.50 ± 0.22^{d}	2.23 ± 0.39^{cd}
PNR	($mg\ N\ kg^{-1}$ soil day^{-1})	0.50 ± 0.04^{ab}	0.67 ± 0.11^{a}	0.45 ± 0.09^{ab}	0.36 ± 0.08^{b}	0.55 ± 0.15^{ab}	0.49 ± 0.06^{ab}	0.66 ± 0.11^{a}
DIP	($mg\ kg^{-1}$)	0.0213 ± 0.002^{ab}	0.0172 ± 0.001^{a}	0.0206 ± 0.001^{ab}	0.0201 ± 0.002^{ab}	0.0189 ± 0.002^{ab}	0.0186 ± 0.001^{a}	0.0222 ± 0.001^{b}
AG	($nmol\ h\ g^{-1}$soil)	23.64 ± 1.23^{a}	29.96 ± 1.09^{b}	29.15 ± 1.28^{bc}	27.85 ± 1.61^{ab}	22.40 ± 5.28^{ac}	26.78 ± 1.35^{ac}	28.19 ± 0.84^{bc}
BG	($nmol\ h\ g^{-1}$soil)	38.65 ± 3.83^{a}	34.74 ± 3.25^{a}	81.32 ± 13.71^{b}	108.28 ± 19.43^{b}	90.42 ± 22.75^{b}	89.76 ± 14.52^{b}	112.14 ± 20.00^{b}
CB	($nmol\ h\ g^{-1}$soil)	31.79 ± 2.42^{a}	23.15 ± 1.49^{b}	75.43 ± 27.61^{c}	55.94 ± 6.64^{c}	43.17 ± 8.43^{ac}	46.43 ± 5.82^{c}	49.73 ± 4.68^{c}
LAP	($nmol\ h\ g^{-1}$soil)	20.03 ± 0.73^{a}	22.14 ± 0.43^{ab}	22.25 ± 1.99^{abc}	23.62 ± 1.37^{bc}	21.62 ± 0.94^{abc}	25.34 ± 1.21^{c}	20.56 ± 0.85^{ab}
NAG	($nmol\ h\ g^{-1}$soil)	26.34 ± 1.86^{a}	30.24 ± 1.40^{a}	44.80 ± 5.93^{b}	43.13 ± 6.42^{b}	36.87 ± 6.20^{ab}	44.24 ± 4.75^{b}	42.87 ± 3.19^{b}
PHOS	($nmol\ h\ g^{-1}$soil)	342.42 ± 35.03^{ab}	311.48 ± 15.22^{a}	400.44 ± 35.25^{bc}	513.86 ± 57.16^{c}	609.74 ± 12.57^{de}	746.73 ± 49.31^{e}	563.86 ± 29.80^{d}
XYL	($nmol\ h\ g^{-1}$soil)	18.93 ± 1.14^{a}	24.30 ± 0.78^{b}	34.76 ± 4.74^{cd}	31.85 ± 3.35^{cd}	22.32 ± 6.73^{abcd}	24.91 ± 2.22^{bc}	34.97 ± 4.05^{d}

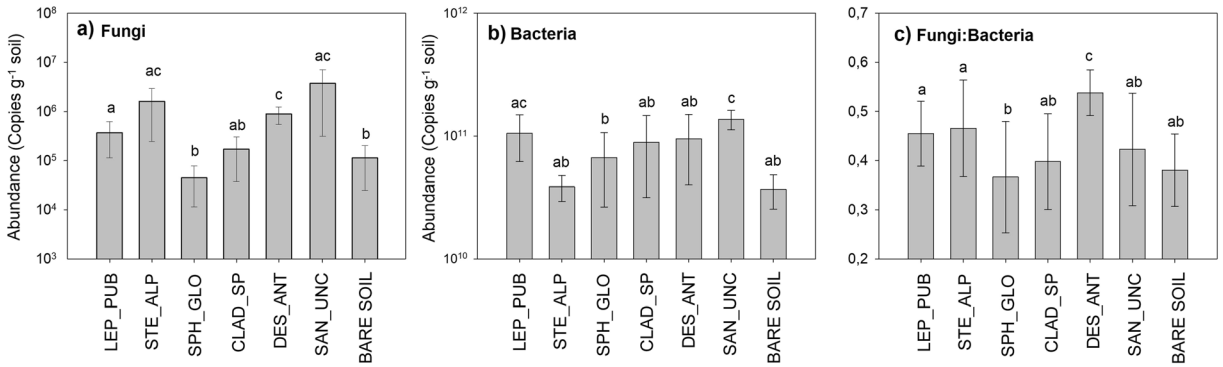


Fig. 3 Abundance, quantified using qPCR, of total fungi **a** and bacteria **b** and the fungi:bacteria ratio **c**. Note that different scales were employed on the y-axis of the graphs. Different letters indicate significant differences among the species studied ($P < 0.05$, post hoc test after PERMANOVA analyses). Values represent means ± SD (n = 10, except *Cladonia* sp. with n = 6). CLAD_SP: *Cladonia* sp.; DES_ANT: *Deschampsia antarctica*; LEP_PUB: *Leptogium puberulum*; STE_ALP: *Stereocaulon alpinum*; SPH_GLO: *Sphaerophorus globosus*; SAN_UNC: *Sanionia uncinata*

biocrust species (Delgado-Baquerizo et al. 2015), suggesting that these variables may consistently characterize soil-biocrust identity associations across the globe.

Soil functioning and microbial abundance levels under different plant and biocrust species

Most of the studied species were positively, but differentially, associated with soil attributes and microbial abundances when compared to bare ground areas devoid of vegetation. This positive association of vegetation patches with greater soil nutrient availability and cycling is similar to patterns previously observed in other regions (e.g. fertility islands in drylands or alpine tundra; Schlesinger et al. 1996; Cross and Schlesinger 1999; Escudero et al. 2004; Allington and Valone 2014). Here, we found that soils under particular species such as *L. puberulum* showed lower values of total and available N, organic C and inorganic P availability, which was also reduced under *Cladonia* sp. Although

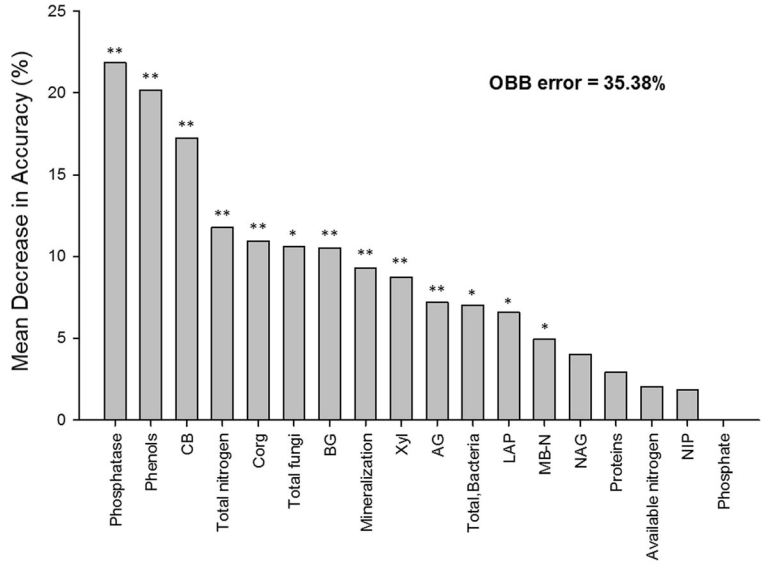


Fig. 4 Random forest mean predictor importance (Mean decrease in accuracy) of soil variables studied as drivers of the observed differences in the soil variables evaluated under the canopy/thalli of the plant and biocrust species studied. Predictor importance was computed for each tree and averaged over the forest (999 trees). Significance levels are as follows: *$P < 0.05$ and **$P < 0.01$. CB: β-D-Cellobiosidase; Corg: dissolved organic C; BG: β-Glucosidase; XYL: β-Xylosidase; AG: α-Glucosidase; LAP: L-Leucine-7-Amidomethylcoumarin; MB-N: microbial biomass nitrogen; NAG: N-acetyl-β-Glucoasminidase; NIP: potential nitrification rate

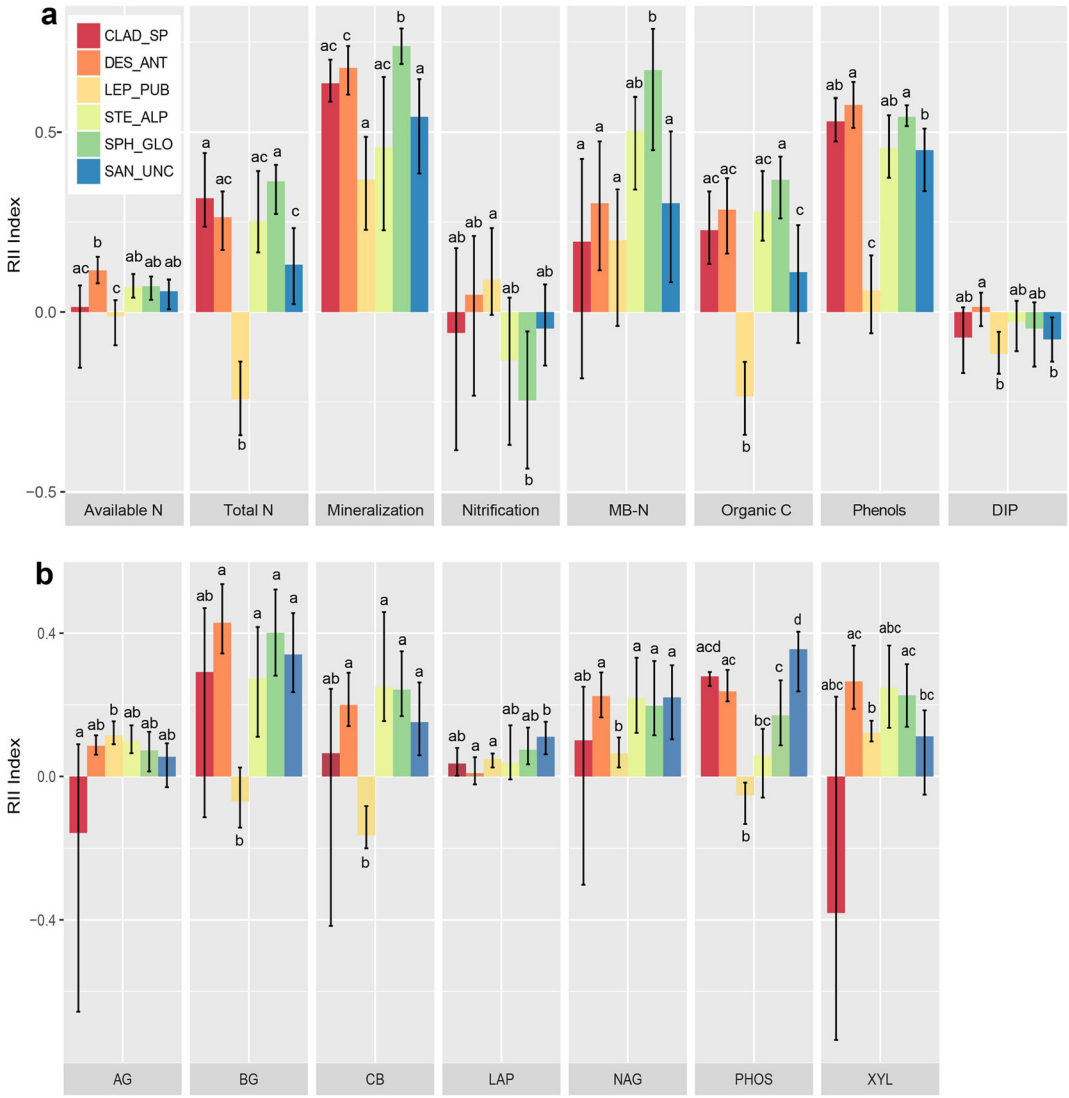


Fig. 5 "Fertility effects", as measured with the relative interaction index (RII), of the species studied (vs. bare ground areas) on soil C, N and P variables **a** and soil enzymatic activities **b** evaluated. Different letters indicate significant differences between the lichen species studied ($P < 0.05$, post hoc test after PERMANOVA analyses). Values represent means ±95% bootstrap confidence intervals (n = 10, except *Cladonia* sp. with n = 6). Data for the studied soil attributes that did not show significant differences between species ($P > 0.05$) are available in Fig. S1. CLAD_SP: *Cladonia* sp.; DES_ANT: *Deschampsia antarctica*; LEP_PUB: *Leptogium puberulum*; STE_ALP: *Stereocaulon alpinum*; SPH_GLO: *Sphaerophorus globosus*; SAN_UNC: *Sanionia uncinata*; N-BM: microbial biomass nitrogen; DIP: dissolved inorganic phosphorus

an explicit link with climate change is always difficult to establish using observational data, our results could provide some insights to help predict the responses of soil functioning and microbial abundance to climate change in Antarctica. Such predictions are linked to the expected changes in the community composition of plant and biocrust communities in response to warming in this region (e.g., Amesbury et al. 2017; Lee et al. 2017; Sancho et al. 2017). For example, *D. antarctica* has experienced an expansion in some regions of the Antarctic Peninsula and associated archipelagoes (Torres-Mellado et al. 2011; Cannone et al. 2016). According to our results, the expansion of this species due to warmer conditions and increased growing season length, could promote an increase in the availability of N and inorganic P in Antarctic soils, positively impacting local primary productivity (Wasley et al. 2006). Furthermore, it could promote an increment in

soil phenolics, which may directly impact on soil microbial community composition (Qu and Wang 2008). On the contrary, an opposite situation migth be expected with the expansion of the Antarctic endemic cyanolichen *L. puberulum.* This species predominantly occurs on temporarily wet snow beds and melt water channels (Sancho et al. 1999). Thus, increased ice melt and runoff due to warming may promote its expansion, negatively influencing soil fertility (lower soil N, organic C and inorganic P concentration). However, the absence of species-specific studies dealing with species acclimation to altered climatic conditions makes it impossible to accurately predict which trend (expansion or recession) is expected for the studied species (Colesie et al. 2017), which is an important topic for future research.

Soil attributes and microbial abundance drive observed differences across species

We found that phosphatase activity was the most important attribute distinguishing soil functioning across the studied species. For example, soils under *S. uncinata*, *Cladonia* sp. and *D. antarctica* had the highest phosphatase activities, while the opposite occurred under *L. puberulum* and *S. alpinum*. The capacity to obtain P is an essential functional trait for biocrust species. While C and N can be directly or indirectly obtained from the atmosphere (via collaboration with microbes; Barger et al. 2016; Sancho et al. 2016), P is mainly obtained from the bedrock (Belnap 2011; Jones and Oburger 2011), and therefore, the ability to obtain P will be an advantageous functional trait in these environments (i.e. bare rock left after ice retreat). Plants and biocrusts are known to influence soil P availability (Belnap et al. 2003; Delgado-Baquerizo et al. 2015; Mihoč et al. 2016). They secrete a wide range of organic acids and powerful metal chelators, and produce phosphatases in their cell walls and mucilaginous sheaths (Jones and Wilson 1985; Belnap 2011). These chemical or enzymatic compounds, which are highly genus-specific in many cases, promote rock weathering and increase the concentration of available P in the soil (Whitton et al. 2005; Belnap 2011; Jones and Oburger 2011). Thus, differences in P acquisition traits may explain the observed differences in both P concentration and phosphatase activities in soil under selected species, reinforcing the idea that species identity has a large influence on P availability.

After phosphatase activity, the concentration of phenols was the second most important variable characterizing the observed differences in soil functioning under the studied species. Thus, we found species promoting high (e.g., *D. antarctica*) and low (e.g. *L. puberulum*) levels of phenols underneath them. We would like to highlight the case of *L. puberulum*, as soils under its thalli had low levels of soil phenols. Interestingly, this genus is known to lack typical lichen secondary metabolites (Otálora et al. 2014). Similarly, the concentration of soil phenols was also a major factor charactering the differences observed among the lichen species studied by Delgado-Baquerizo et al. (2015) in a dryland ecosystem from central Spain. Phenolic substances are common UV protection compounds (Dixon and Paiva 1995; Agati and Tattini 2010), and are highly important for photosynthetic organisms in stratospheric ozone depleted territories such as Antarctica (Solomon 1999, 2004). The two native Antarctic vascular plants (*D. antarctica* and *C. quitensis*) are known to synthesize and store phenolic-type molecules against UV radiation (Xiong and Day 2001; Köhler et al. 2017). For example, Ruhland et al. (2005) observed the influence of ultraviolet-B radiation on the phenylpropanoid concentrations of *D. antarctica* during the springtime ozone depletion season, observing up to 60% increase in the concentration of some phenolic substances. We observed that soils under *D. antarctica* showed the highest concentration of phenols, which may be explained by the accumulation of phenolic substances in the soil released by decaying plant material. Furthermore, phenolic compounds are also common plant root exudates with different functions (e.g. micronutrient mobility; Cesco et al. 2010), which can also act as microbial allelopathic substances. Conversely, despite its high phenolic content, soils under *D. antarctica* showed high fungal and bacterial abundances, suggesting a lack of allelopathic effects from the phenolic substances produced by this species on soil microorganisms. Similarly, phenolic derivatives are an important feature of the biochemistry of lichens, which show a great diversity of compounds that are also highly species-specific (Crittenden 1999). Contrary to *D. antarctica*, soils under *S. globosus* thalli showed low microbial abundance (lowest fungal abundance and second lowest values for bacteria). Interestingly, soils under *S. globosus* showed the second highest

concentration of phenols. This suggests that synthesized phenolic substances by *S. globosus* may be involved, among other functions, in the chemical defense of this species against fungal activity (i.e. antimicrobial action; Lawrey 1986, 1989).

β-D-Cellobiosidase was the third most important variable characterizing the observed differences in soil functioning across the species studied. This enzyme, a cellulase, catalyzes the degradation of polysaccharides such as cellulose. This polymer is synthesized by higher plants, but also by bryophytes and, to a lesser extent, by algae and fungi (both constituents of lichen symbiosis; Haigler and Weimer 1991). Exoglucanases such as β-D-cellobiosidase are known to hydrolyze other polysaccharides (e.g. Lichenin, a storage polysaccharide found in lichens; Kanda et al. 1989; Iakiviak et al. 2011). Thus, the registered differences in soil CB activity may reflect different species-specific functional traits related to the polysaccharide content of their tissues and on their decomposability.

Microbial abundance, and fungi in particular, played a secondary but still important role in distinguishing soil functioning across species. In general, the studied species increased fungal and bacterial abundances and the fungi:bacteria ratio, in the soils under them. In addition, here we observed that plant and biocrust species patterns were related to spatial differences in soil microbial abundance. Similar results have been reported from other ecosystems (Delgado-Baquerizo et al. 2016). This is not surprising, as soil microbes are predominantly involved in soil nutrient cycling (Heritage et al. 1999), and vegetation traits (e.g. SLA in plants) indirectly condition soil microbial abundance and community composition by quantity and quality of litter production (Cleveland et al. 2014; Ochoa-Hueso et al. 2018). Thus, differences in vegetation traits may differentially condition the observed soil microbial abundance in vegetation patches in Livingston Island. Moreover, our results match with generally reported bacterial dominance over fungi under biocrusts (Bates et al. 2010; Delgado-Baquerizo et al. 2015). The fungi:bacteria ratio was generally higher under studied species compared to bare soil, indicating an enhanced soil capacity to sequester C (Malik et al. 2016). Interestingly, *S. globosus* was related to a lower fungal abundance, even lower than bare soil and differing up to two orders of magnitude with values registered under *S. uncinata*. As previously mentioned, this lower fungal abundance under *S. globosus* may reflect an antimicrobial effect of some synthetized phenolic substances (e.g. the depside sphaerophorin and the depsidone pannarin; Celenza et al. 2012, 2013).

Soil functioning under plant and biocrust species compared to bare ground areas

The values of the soil attributes evaluated were, in most cases, higher under the canopy of the studied species compared to bare ground areas. The positive relation between vegetation, including cryptogamic organisms, and soil nutrient availability compared to non-vegetated areas is largely referred to in literature (Schlesinger et al. 1990, 1996; Cross and Schlesinger 1999; Perroni-Ventura et al. 2010; Concostrina-Zubiri et al. 2013; Delgado-Baquerizo et al. 2015). Such connection has also been reported in Antarctica for single soil attributes. For example, Beyer et al. (2000) found that soil colonization by mosses in this region coincided with higher soil organic C and N. Here we have observed similar associations, but their magnitude varied with the species and soil variable considered.

All the species except the lichen *L. puberulum* were associated with greater soil nitrogen availability. As a cyanolichen with *Nostoc* as a unique photobiont, *L. puberulum* was expected to promote higher soil N concentrations due to its N fixation capacity. Lichens (both N-fixers and non-N fixers) are susceptible to N leaching during rewetting processes (Millbank 1978, 1982), but specifically N fixers have been proposed as important N sources in areas with low N availability (Vitousek et al. 2002). Thus, the low N concentration found under *L. puberulum* may respond to biotic or abiotic factors. For instance, habitat preference (wet snow beds and melt water channels; Sancho et al. 1999) may deplete soil N availability by washing soluble compounds leached from *L. puberulum*. Conversely, lower N availability may indicate the presence of a higher rate of N transformation and cycling under this species. Supporting this idea, soils under this species showed also the highest potential nitrification rate, lowest ammonium concentration, highest nitrate concentration and highest abundance of ammonia oxidizing bacteria (unpublished data). Conversely, soils under *S. alpinum* –also a N-fixing species– did not follow the same pattern (i.e. higher values of total and available N and lower nitrification rate than *L. puberulum*). This

may be a consequence of its lower N-fixation rate (compared to *L. puberulum*, data not shown) or better retention capacity of fixed N in its cephalodia (Rai 2002). Although our study was not designed to specifically assess the influence of functional traits on soil attributes, the relationship between both N-fixing lichens and soil N attributes strengthens the statement that species-specific functional traits may play an important role influencing soil biogeochemical cycles.

Phosphorus availability was mostly negatively associated with biocrust presence, as all cryptogamic species studied had lower *P* values in soils under their thalli (compared to bare ground areas), while the opposite occurred under the vascular plant *D. antarctica*. This may result from a high input of organic matter deposited around this species due to sea bird nesting preferences. Some studies have reported that Antarctic sea birds (*Catharacta* spp. and *Larus dominicanus*) use *D. antarctica* communities for breeding (Albuquerque et al. 2012; Parnikoza et al. 2012). However, this should increase N availability as well by guano addition, and the highest levels of N were not found under this species. Although always negative, the magnitude of changes in P availability under biocrusts compared to bare ground areas differed across species. Delgado-Baquerizo et al. (2015) also observed that variables related to soil P availability showed the highest contrast among different biocrust-forming lichens in a dryland ecosystem from Spain. This again supports the idea that species identity may potentially exert a large influence on the P availability in the soil surface.

Finally, we found that the occurrence of most of the studied species was associated with greater enzyme activities under their canopy/thalli. However, differences were also observed depending on the enzyme considered. Similar species-specific associations of plant (Bell et al. 2014a) and biocrust (Liu et al. 2014) species with soil enzymes have been previously reported. Soil enzymes are fundamental drivers of organic matter degradation (Bell et al. 2014b), and the presence of vegetation is considered a factor enhancing enzyme activity in comparison with bare ground areas (Gianfreda 2015). Some studies conducted in drylands (Miralles et al. 2012; Zhang et al. 2012; Liu et al. 2014) have found that the activity of several enzymes is positively associated with biocrust-forming species (when compared to bare ground areas), a relationship that depend on the species considered. Enzyme activities are highly dependent on soil temperature and moisture (Burns et al. 2013; Arnosti et al. 2014; Baker and Allison 2017), and both factors are directly associated with vegetation traits. The functional diversity of cryptogams is known to influence these soil properties by, for instance, increasing substrate temperature because of dark pigment concentration and increasing soil aggregation via the exudation of carbon compounds (Belnap et al. 2003; Belnap 2006; Almeida et al. 2014). The thalli of *Sphaerophorus globosus* (unpublished data) and the lichen *Umbilicaria aprina* (Schroeter et al. 2011) are known to reach temperatures above 10 °C compared to air temperature in Antarctica. Similarly, Schlensog et al. (2013) observed differences in the temperature of thalli among Antarctic moss and lichen species. This increased temperature may enhance soil nutrient cycling under lichen thalli, naturally constrained by low soil temperature in Antarctica. Besides temperature, there are multiple other pathways for biocrust control on soil enzymes (i.e. soil pH, nutrient release or microbial activity conditioned by secondary metabolites synthesis; Hauck et al. 2009; Bowker et al. 2011). Similarly, other microhabitat features associated with spatial patterns of species distribution may also influence enzymatic activity in soil (e.g. liquid water availability or debris accumulation by cryoturbation; Cannone et al. 2008; Cannone and Guglielmin 2010). Our data highlight the enzymes phosphatase and β-D-cellobiosidase as being greatly associated with species identity. As mentioned above, the enzyme phosphatase has previously been found highly connected to biocrust identity (Delgado-Baquerizo et al. 2015) and may be a crucial variable to characterize biocrust identity effects globally. However, more efforts are needed to clarify the magnitude and pathways and explain the mechanisms by which biocrust identity regulates soil attributes such as nutrient mineralization and, consequently, to accurately predict consequences of changing species distribution for soil and ecosystem functioning in Antarctica.

Conclusions

Using a comparative approach, we provide evidence that the identity of plant, lichen and moss species was largely associated with different concentrations of soil C, N and P cycling variables and the abundance and structure (fungal:bacterial ratio) of soil microbes in maritime Antarctica. Soil phenolic content and enzymatic

activity (phosphatase and β-D-cellobiosidase) were the most important variables predicting the observed differences in soil functioning across the studied species. Most evaluated species were positively associated (as measured using the RII index) to higher availability of C, N and P in soil compared to bare ground areas, which may be explained by higher soil enzymatic activities and microbial abundance. However, the magnitude of these differences was species-specific, and negative associations with some soil attributes were also observed. Our results suggest that any changes in the distribution and composition of plant and cryptogamic communities, linked to ongoing climate change or seasonal patterns, might lead to changes in the functioning and microbial abundances of Antarctic soils. They also highlight that the links between Antarctic vegetation and soil functioning are species-specific; consequently black-box approaches –considering vegetation or biocrusts as a unique entity– must be avoided to accurately characterize the role of plant and biocrust species in the functioning of Antarctic ecosystems.

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