



Diversity and species associations in cryptogam communities along a pedoenvironmental gradient on Elephant Island, Maritime Antarctica

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Received: 27 February 2020 / Revised: 30 July 2020 / Accepted: 12 September 2020 / Published online: 28 October 2020
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Abstract The Maritime Antarctica region has terrestrial ecosystems dominated by lichens and mosses, representing important ecological indicators of climate change. However, little is known about environmental factors that shape regional cryptogam communities at local scale. In this study we analyse changes in species richness, species composition and coverage of representative cryptogam communities across a pedoenvironmental gradient in Maritime Antarctica. We hypothesized that soil texture and chemical properties shape variations in species richness and composition. We selected fifteen different

pedoenvironments, where 20 plots (20 × 20 cm) were sampled for obtaining phytosociological parameters of cryptogamous communities, and in each plot a composite topsoil sample was collected to determine chemical and physical soil properties. We then evaluated the main effects of soil attributes on the richness and composition of cryptogam species using direct gradient analysis and linear models. The ecological value of species was determined, allowing to identify the type of plant community and species associations in each pedoenvironment. Differences in species composition, richness and coverage were detected along the pedoenvironmental gradient. The model analysis showed that soil fertility has significant effects on species composition, but not on species richness. Based on gradient analysis, variability on soil fertility and nutrient contents were important pedoenvironmental filters for cryptogam communities in Maritime Antarctica. This study reveals that small-scale heterogeneity contributes to specific associations along pedoenvironmental gradients. We conclude that soil attributes drive the composition pattern of cryptogam species and also the type of communities present.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s12224-020-09376-2>) contains supplementary material, which is available to authorized users.

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Keywords lichens · mosses · richness · soil texture · soil fertility · species composition

Introduction

There is continued interest in understanding how multiple factors control species distribution, abundance and diversity across environmental gradients at different

scales (Götzenberger et al. 2012). With particular regard to Maritime Antarctica, this interest has been growing in recent decades due to its importance for climate change monitoring (Thomazini et al. 2018) and its impacts on high-latitude plant diversity (Amesbury et al. 2017). However, few studies have focused on the factors shaping the assembly of plant communities along gradients in this region (e.g. Leishman and Wild 2001).

At landscape scale, the availability of ice-free areas determines the distribution of terrestrial vegetation in Antarctica (Leishman and Wild 2001). These areas are restricted to coastal regions, rocky slopes, or nunataks and soils at different stages of development (Campbell and Claridge 1987; Bokhorst et al. 2007). The vegetation is mostly composed of bryophytes and lichens, with only two native angiosperms species *Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunth) Bartl. (Putzke and Pereira 2001; Victoria et al. 2013). Differences in species composition can be found within small areas (Victoria et al. 2009; Schmitz et al. 2018) due to high environmental heterogeneity (microtopography, geology, soil properties; Victoria et al. 2013; Benavent-González et al. 2018).

In this study we evaluated the relationship between richness and composition of cryptogamous communities and soil chemical and physical properties along a pedoenvironmental gradient on Elephant Island, Maritime Antarctica. Cryptogamous communities inventory data from 300 plots (20 × 20 cm), distributed among fifteen pedoenvironments, were used to evaluate the effect of soil texture and soil fertility on the species richness and composition. In this context, the following questions were addressed: (1) What is the richness, species composition and coverage pattern along a pedoenvironmental gradient in Maritime Antarctica? (2) Is there variation in species associations along the pedoenvironmental gradient? (3) What are the effects of soil chemical and physical properties on species richness and composition?

Material and methods

Study area

This study was conducted at Stinker Point (61°21' S, 55°20' W), located on Elephant Island (Fig. 1). Elephant Island is located north of the South Shetland archipelago, between the Drake Passage and the Weddell Sea

(Pereira and Putzke 1994) and has a cold climate with extreme fog and snowfall conditions. Mean annual temperature is −2°C, and mean summer temperature is 1°C (Štátná 2010; Putzke et al. 2020). Snow storms and fog are frequent at Stinker Point (Putzke et al. 2020).

Geologically, the island is composed of Paleozoic metamorphic rocks of the Skotia arc (O'Brien et al. 1979). Ice-free areas are found mainly in coastal areas, on raised marine deposits mixed with glacial drift, forming alternating cliffs with steep glaciers fronts or ice cliffs (Navas et al. 2018).

Stinker Point is one of the largest ice-free areas of Elephant Island (CGE-UAM-UFRJ 2005; Navas et al. 2018) and possesses a rich fauna and flora (Pereira and Putzke 1994). These authors recorded the occurrence of two native angiosperms for the Maritime Antarctic region, *Colobanthus quitensis* (Kunth.) Bartl. and *Deschampsia antarctica* Desv., 38 species of moss, seven liverworts, 68 lichens, two species of terrestrial algae and four macroscopic fungi.

Selection of pedoenvironments

We selected fifteen pedoenvironments (defined here as P1 to P15) on different landforms, following the types described by López-Martínez et al. (2012) and Navas et al. (2018), see Table 1, with contrasting soils (Fig. 2).

Cryptogamous communities survey

On each pedoenvironment 20 plots of 20 × 20 cm were sampled, following the Braun-Blanquet (1932) square methodology, adapted to Antarctic vegetation conditions, to assess the coverage of each species at each plot. In total, 300 plots were sampled in the austral summer of 2017/2018. Bryophytes were identified at species level in each plot using the taxonomic identification keys by Putzke and Pereira (2001), and Ochrya et al. (2008); Redon (1985), Øvstedal and Lewis-Smith (2001), and Olech (2004) were used to identify lichens. Lichens and mosses collected were deposited in the HCB Herbarium of the University of Santa Cruz.

Ecological significance index (ESI)

The importance of the species in each pedoenvironment, the plant community's classification and species

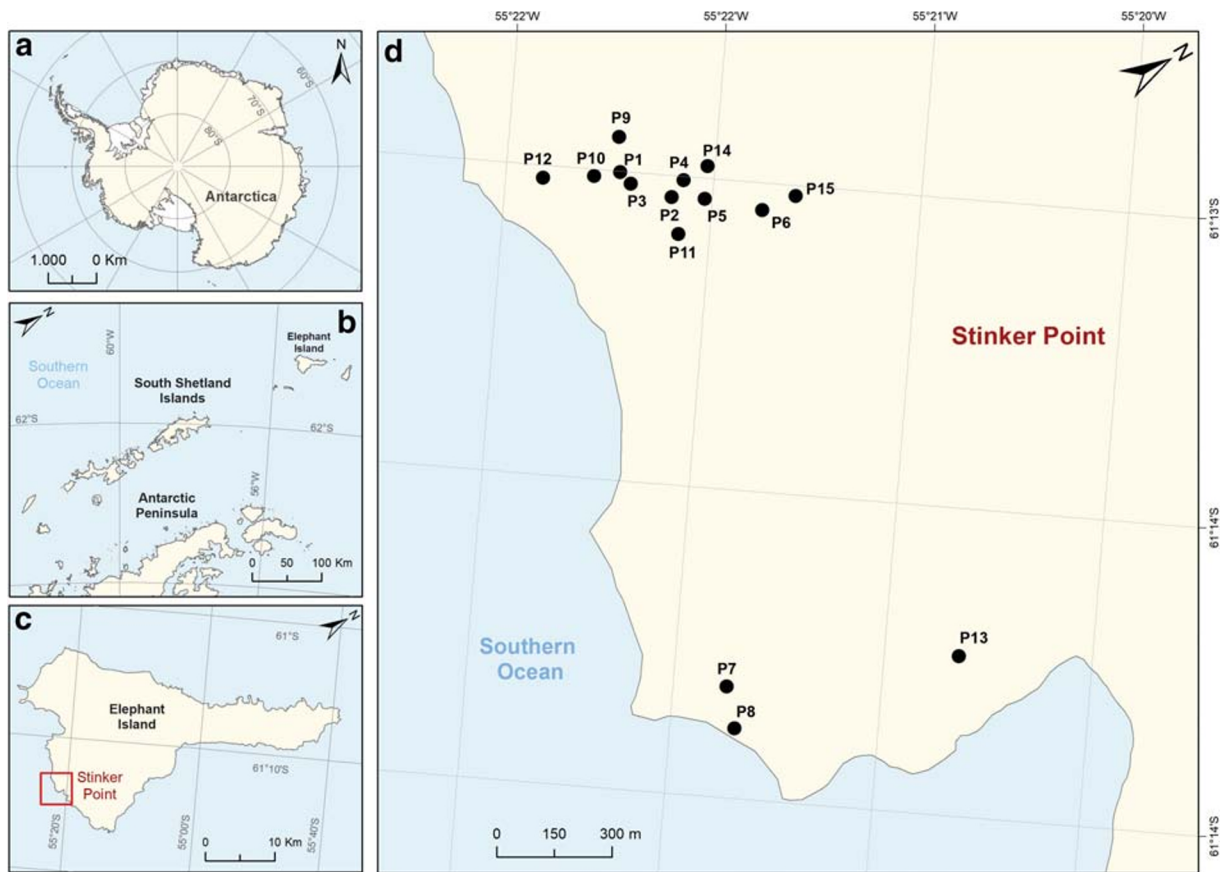


Fig. 1 Location of the study area: Antarctica (a), South Shetland Islands (b), Elephant Island (c), Stinker Point with fifteen sampled pedoenvironments (d)

association, were determined using the ecological significance index (ESI), which combines the frequency and coverage of each species in the plot (Lara and Mazimpaka 1998; Marques et al. 2005). These researchers defined the ecological significance index as:

$$ESI = F(1 + C) \quad (1)$$

$$F = 100x/n, \quad (2)$$

where F is the relative frequency of the species in the area or habitat and is generated by the number of occurrences (x) divided by the total number of samples considered (n), and C is the average coverage of the species in the samples, calculated as:

$$C = \sum(ci)/x, \quad (3)$$

where ci is the class of coverage and x is the number of samplings in which the species occurs (e.g. Schmitz

et al. 2018). This index determines the scale of importance of the species in the area, which ranges from 0 to 600, where values above 50 indicate ecological significance (Victoria and Pereira 2007). The species with the highest values and their form of growth define the name of the community, following the classification by Longton (1988). The associations are characterized by dominant species or by restricted occurrence in more specific habitats (Schmitz et al. 2020).

Soil collection

In order to measure the soil properties within each plot, a topsoil sample was taken (at 0–10 cm depth). Soil properties were measured following standard protocols (EMBRAPA 1997). The following parameters were assessed: Soil pH was determined in distilled water (pH H₂O), phosphorus available exchangeable (P), potassium (K⁺), sodium (Na), calcium (Ca²⁺), magnesium

Table 1 Description of the 15 sampling pedoenvironments (P). Where: R= Species Richness; Cover = percentage of vegetation cover in the pedoenvironment

P	Plots	R	Cover (%)	Drainage level	Landform /Geomorphology	Plant community
P1	20	2	92.6	Drained	Middle platform/ sheet gelifluction	Moss cushion community <i>Bryum-Sanionia</i> association
P2	20	10	100	Moderately drained	Middle platform/ sheet gelifluction	Moss turf community <i>Chorisodontium-Sanionia</i> association
P3	20	10	68.5	drained	Middle platform/ debris slope	Moss carpet community <i>Sanionia- Polytrichastrum</i> association
P4	20	6	99.8	little drained	Middle platform/ vertical clasts	Moss carpet community <i>Warnstorfia-Sanionia</i> association
P5	20	7	96.1	poorly drained	Middle platform/ Gelifluction lobes	Moss carpet community <i>Warnstorfia-Sanionia</i> association
P6	20	12	92.1	little drained	Middle platform/ Sheet gelifluction	Moss carpet community <i>Sanionia</i> spp.
P7	20	9	63.2	well drained	Moraine/holocene beaches	Moss cushion community <i>Bryum-Brachythecium</i> association
P8	20	8	54.9	well drained	Moraine/holocene beaches	Moss cushion community <i>Bryum-Brachythecium</i> association
P9	20	14	96.5	well drained	Middle platform/ Gelifluction lobes	Cryptogamic-phanerogamic community: association <i>Sanionia-Deschampsia</i>
P10	20	14	85.8	well drained	Platform edge/ sheet gelifluction	Fruticose lichens community associate with <i>Andreaea regularis</i>
P11	20	15	94.3	well drained	Platform edge/ sheet gelifluction	Moss turf community <i>Chorisodontium</i> -fruticose lichens association
P12	20	10	47.3	well drained	Platform edge/ sheet gelifluction	Musciculous-lichens community
P13	20	9	52.7	Moderately drained	Till/Moraine	Moss cushion community <i>Bryum-Henediella</i>
P14	20	7	98.6	poorly drained	Middle platform/ Gelifluction lobes	Moss carpet community <i>Sanionia-Brachythecium</i>
P15	20	19	93.8	drained	Moraine	Fruticose lichens community

(Mg²⁺), aluminium (Al³⁺), potential acidity (H + Al), sum of bases (SB), potential cation exchange capacity at pH 7.0 (T), percentage of bases saturation (V), aluminium saturation (m), sodium saturation index (ISNa), organic matter (OM), remaining phosphorus (P Rem), copper (Cu), manganese (Mn), iron (Fe), zinc (Zn), total nitrogen (N) and soil texture, classified as coarse sand (Sand_c), fine sand (Sand_t), clay and silt contents.

Data analysis

All analyses were carried out using the R Environment (R Core Team 2018). For soil variables we tested normal distribution with the Shapiro-Wilk test and by evaluating the Q-Q plot; The homogeneity of variances was

assessed with Bartlett's test using the 'dplyr' package (Crawley 2013). To compare soil properties (non-normally distributed data), between pedoenvironment sites, we used Kruskal-Wallis's test followed by a post hoc Dunn's test performed with the 'dunn.test' package (Dinno 2017).

We compared species richness patterns between pedoenvironments using sample-based data to estimate rarefaction and extrapolation curves based on the first Hill number (Chao et al. 2014). Extrapolations were made based on presence/absence of species in the plot data using Hill number order 0 (Colwell et al. 2012), with the purpose of evaluating the sampling sufficiency in each pedoenvironment. Estimates were obtained using the 'iNEXT' package (Hsieh et al. 2016). The Hill number was estimated as the mean of 100 replicate

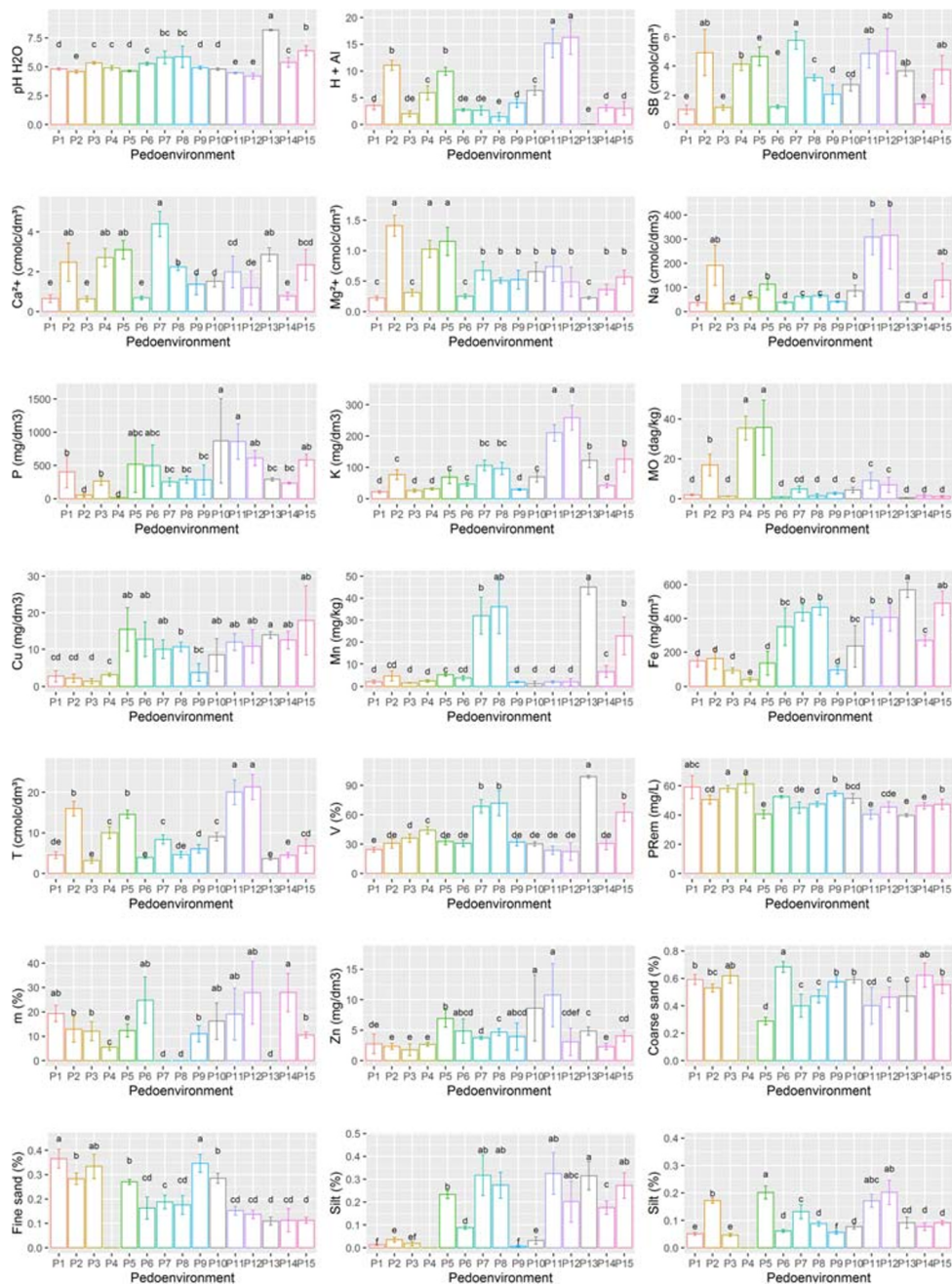


Fig. 2 Barplots soil properties. For analysis, available: pH (H₂O), exchangeable acidity (H + Al), sum of bases (SB), Ca²⁺, Mg²⁺, Na, P, K⁺, organic matter (MO), Cu, Mn, Fe, potential cation exchange capacity (T), percentage of bases saturation (V),

remaining phosphorus (P Rem), aluminium saturation (m), Zn, and soil texture as coarse sand, fine sand, clay and silt contents were included

bootstrap runs to estimate 95% confidence intervals (e.g. Schmitz et al. 2020). Whenever the 95% confidence intervals did not overlap among assemblages at each pedoenvironment, and species numbers differed

significantly at $P < 0.05$, we considered in the analysis (Colwell et al. 2012).

We performed non-metric multidimensional scaling (NMDS) to analyse differences between

pedoenvironments in terms of species composition using Euclidean dissimilarities (Clarke 1993). The NMDS was performed using the ‘metaMDS’ function of the ‘vegan’ package (Oksanen et al. 2018). Permutational multivariate analysis of variance (PERMANOVA, 9999 permutations) was used to determine differences in species composition using the ‘adonis’ routine available within the ‘vegan’ package (Oksanen et al. 2018).

Soil variables were summarized using principal component analysis (PCA) to identify a possible pedoenvironmental gradient and to reduce the number of redundant soil properties, following Qian et al. (2014) and Villa et al. (2018); all variables were centred and standardized. We also calculated Pearson correlations among soil properties and the PCA ordination axes. The PCA was performed using the ‘FactoMineR’ package (Husson et al. 2017). To investigate a possible relationship between soil properties and biotic (species) variables, canonical correspondence analysis (CCA) was used. CCA examined similarity or dissimilarity in the floristic composition of plots along the pedoenvironmental gradient. The significance of each soil variable in determining species compositional change was assessed by Monte Carlo randomizations (999 randomizations). The CCAs were performed using the ‘ggord’ and ‘ordiplot’ functions of the ‘vegan’ package (Oksanen et al. 2018). Species coverage distribution was evaluated using species-rank curves, for each study area, by ranking all species from the most to the least abundant (Magurran 2004).

We evaluated the effect of potential predictors on species richness and species composition (e.g. extracting the scores on frequency-weighted NMDS Axis 1; Oksanen et al. 2018; Villa et al. 2018) via linear mixed effect models (LMMs). We have used a nutrient-based PCA (i.e. P, K⁺, Na, Ca²⁺, Mg²⁺, Cu, Mn, Fe, Zn, N) to extract the scores of variability of nutrient-related soil fertility (PCA1f), and after we used a texture-based PCA (clay, silt, sand) to extract the scores of variability of physical properties-related soil texture (PCA1t). To reduce any strong correlations among local environmental conditions (Fig. S2 in the [Electronic supplementary material](#)), we used the two axes of the PCA for soil fertility (PCA1f) and texture (PCA1t) variables. Thus, the first PCA axis was considered as a proxy for soil fertility and soil texture gradient across all the tested models (Ali et al. 2016; Villa et al. 2018). We used generalized linear mixed effects models (GLMMs) with Poisson error distribution to investigate the effect of individual soil properties, soil fertility, and soil texture on species richness. Species composition was assessed using LMMs after checking the Shapiro-Wilk test

for normality and Q-Q graphs (Crawley 2013). Predictor variables (fixed effects) were plant coverage, soil fertility (PCA1f) and soil texture (PCA1t), defined as the first principal component from PCA, considering all eighteen parameters analysed (see above), as well as further soil parameters such as sand, silt, clay, SB, OM and pH. Plant coverage is defined as the proportion of plant community space occupied in each pedoenvironment (Ji et al. 2009); therefore, plant coverage is considered to be an important predictor with possible effects on plant diversity (Ji et al. 2009; Sanaei et al. 2018). Soil chemistry and texture were used, as well as individual soil parameters, as explanatory variables for modelling, because individual soil parameters may also show a direct effect on species richness and species composition (Villa et al. 2018; Schmitz et al. 2020). For predictor selection, we assessed collinearity between selected predictor variables using Spearman correlation analysis; when two variables were strongly correlated ($r \geq 0.6$) the most ecologically-relevant predictors were selected, which were included in separate models (Fig. S2). In all mixed models, pedoenvironments were included as a random factor and the first axis of the soil chemistry and texture PCA was used as a fixed factor (Villa et al. 2018, Schmitz et al. in press). All models were fitted using the package ‘lme4’ (Bates et al. 2014) from the R platform (R Core Team 2018); for illustration, we used the package ‘ggplot2’ (Hadley 2015).

To assess the best models (GLMMs and LMMs), a multi model inference approach was applied (Burnham and Anderson 2002) with the ‘dredge’ function from the ‘MuMIn’ package (Barton 2015), which returns all possible combinations of the explanatory variables included in the global model. To determine which of these variables were the most decisive in explaining changes in species richness and species composition, we used an information theory approach based on the Akaike information criterion (AIC) with a correction for finite sample sizes (AICc) and AIC weights (Burnham and Anderson 2002). The model with the lowest AICc was considered to be the best, but all models that differed by fewer than four units from the best model were considered as equally good models (Burnham et al. 2011).

Results

General soil attributes

The soil properties differed among all pedoenvironments studied, forming a marked edaphic gradient (Fig. 2). The

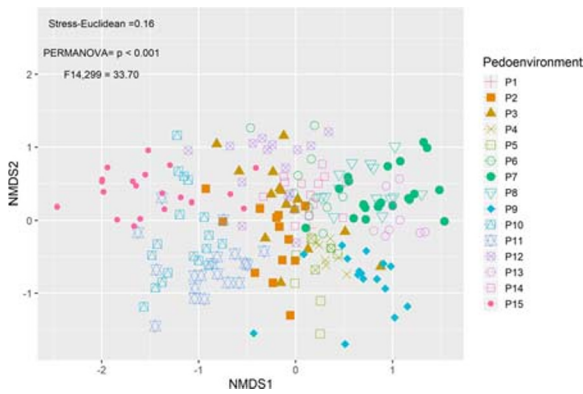


Fig. 3 Non-metric multidimensional scaling (NMSD) based on species composition from different pedoenvironment sites

soils ranged from highly acidic to alkaline (pH 4.19 to 8.18). Available phosphorus values ranged from 17.44 to 870.44 (mg/dm³), of which only P2 and P4 showed no omithogenic influence, with lower levels of P. The amounts of soil organic matter were low except for P2 (16.94 dag/kg), P4 (35.39 dag/kg), and P5 (35.39 dag/kg), while the total OM were high for Maritime Antarctica standards. The soil was dominated by the sand fraction, sandy loamy as a predominant textural class, but silt and clay levels were high in P5, P7, P10, P12, and P13 (Table S2 from *ESM*). The soil texture of P4 could not be measured due to the very high amount of organic matter.

Species composition and species richness pattern

We identified 39 species in the fifteen pedoenvironments studied; 21 bryophytes (19 mosses and two liverworts), fifteen lichen species, two angiosperms (*D. antarctica* and *C. quitensis*) and a macroscopic alga (*Prasiola crispa*, Table A.1 from *ESM*). The families with the highest species richness were the Bryaceae for the bryophytes and the Parmeliaceae for lichens, both with four species. A distinct richness pattern was observed among the pedoenvironments (Fig. S1 in the [Electronic supplementary material](#)), where P1 presented the smallest number, with only two species, and P15 had the highest richness, with nineteen species (Table 1). Coverage also varied significantly among pedoenvironments (Tab. 1, Fig. S1B).

The NMSD revealed that species composition varied significantly between pedoenvironments (PERMANOVA $F_{14,299} = 33.70, P < 0.001$), but with a marked overlap among most groups (Fig. 3). *Sanionia uncinata* was dominant, being present in 139 of the 300 sampled plots; other species present in a large number of plots were *Sanionia georgicouncinata* (82), *Cystocoleus niger* (72), and *Usnea antarctica* (71) (Table S1). On the other hand, the occurrence of some species was restricted to some pedoenvironments, as can be observed in the

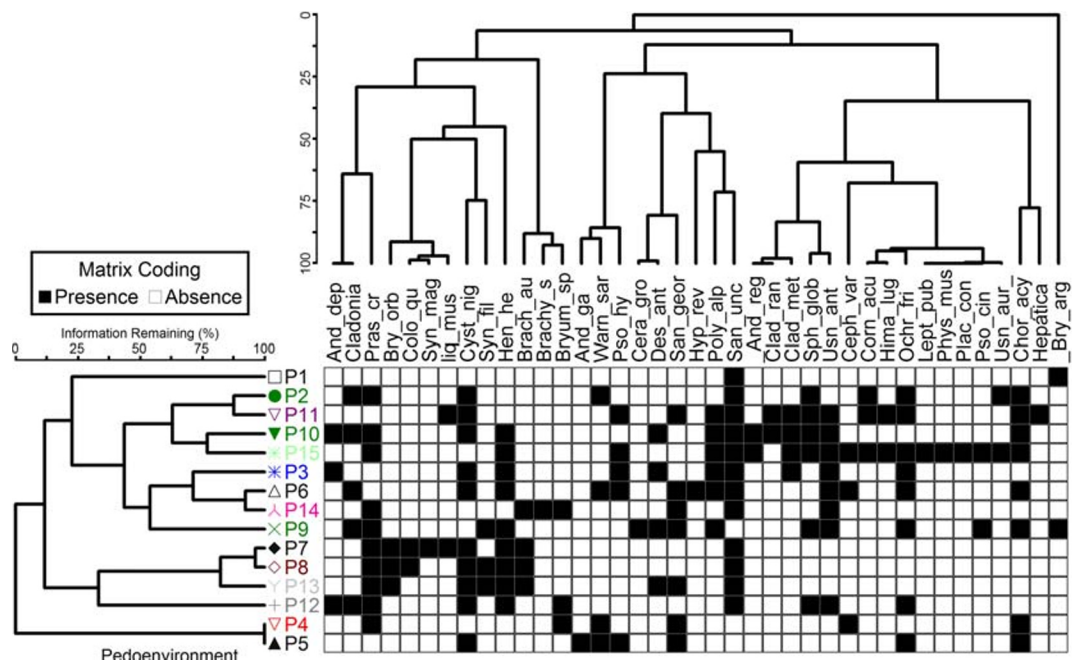


Fig. 4 Distribution of 39 species within 300 samples plots installed along a pedoenvironmental gradient by a two way cluster dendrogram based on Euclidian distance. See full names of the species in Table S1 in the [Electronic supplementary material](#)

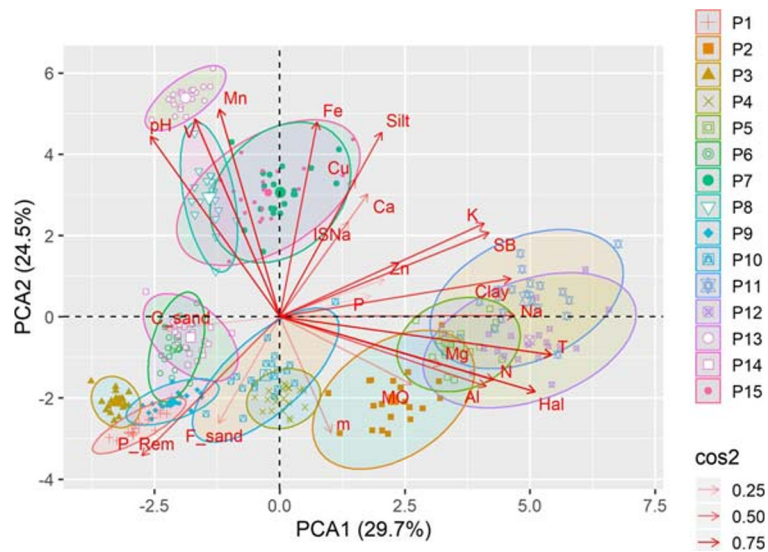


Fig. 5 Principal component analysis (PCA) for the soil parameters of different types of pedoenvironment sites. For analysis, available pH (H₂O), exchangeable acidity (Hal), sum of bases (SB), Al³⁺, Ca²⁺, Mg²⁺, Na, available P, K⁺, N, organic matter (MO), potential cation exchange capacity (T), percentage of bases

saturation (V), remaining phosphorus (P Rem), aluminium saturation (m), Zn, sodium saturation index (ISNa), Mn, Cu, Fe, Zn, and soil texture as coarse sand (C_Sand), fine sand (F_Sand), clay and silt contents were included. The level of Pearson correlation of each vector is indicated (cos2)

dendrogram cluster analysis (Fig. 4). For example, the moss species *Andreaea gainii* only occurred in P5, *Syntrichia magellanica* only occurred in P7, *Hypnum revolutum* was recorded only in P6, *Ceratodon grossiretis* in P9, *Brachythecium* sp. only in P14, and, finally, *Leptogium puberulum*, *Physconia muscigena* and *Placopsis contortuplicata* only occurred in P15.

Ecological significance index

Differences in the ecological significance of species (ESI) were observed among pedoenvironments. Based on the coverage of the dominant species, six plant communities with eleven distinct associations were identified: the moss cushion community, with three associations, *Bryum-Sanionia* (P1), *Bryum-Brachythecium* (P7 and P8), and *Bryum-Hennediella* (P13); the moss turf community, with two associations: *Chorisodontium-Sanionia* (P2) and *Chorisodontium-fruticose lichens* (P11); the moss carpet community with four associations: *Sanionia-Polytrichastrum* (P3), *Warnstorfia-Sanionia* (P4 and P5), *Sanionia* spp. (P6), *Sanionia-Brachythecium* (P14); the cryptogamic-phanerogamic community with a *Sanionia-Deschampsia* association (P9); the fruticose lichens community (P15) and

associated with *Andreaea regularis* (P10); and the musciculous-lichens community (P12) (Table 1).

Descriptors of soil fertility and texture

High variability in soil chemical properties was observed along the pedoenvironmental gradient (Fig. 5). However, some attributes formed clusters of pedoenvironments (Fig. 5), as can be observed for pH, V, Mn, Fe, and silt, which separated P7, P8, P13, and P15 from the other pedoenvironments. In general, most pedoenvironments presented high values of P Rem, coarse and fine sand (P1, P3, P4, P6, P9, P10 and P14). The first two axes of the PCA explained 54.2% of the variation in soil data (Fig. 5). The first axis explained 29.7% of the data variation and was positively correlated with T ($R=0.95$, $P<0.05$), exchangeable acidity (Hal, $R=0.89$, $P<0.05$), Na ($R=0.82$, $P<0.05$) and clay ($R=0.80$, $P<0.05$). The second axis of the PCA explained 24.5% of the soil data variation and was positively correlated with Mn ($R=0.89$, $P<0.05$), V ($R=0.85$, $P<0.05$), Fe ($R=0.83$, $P<0.05$) and silt ($R=0.79$, $P<0.05$), and negatively correlated with P Rem ($R=-0.59$, $P<0.05$) (Figs. S2 and S3).

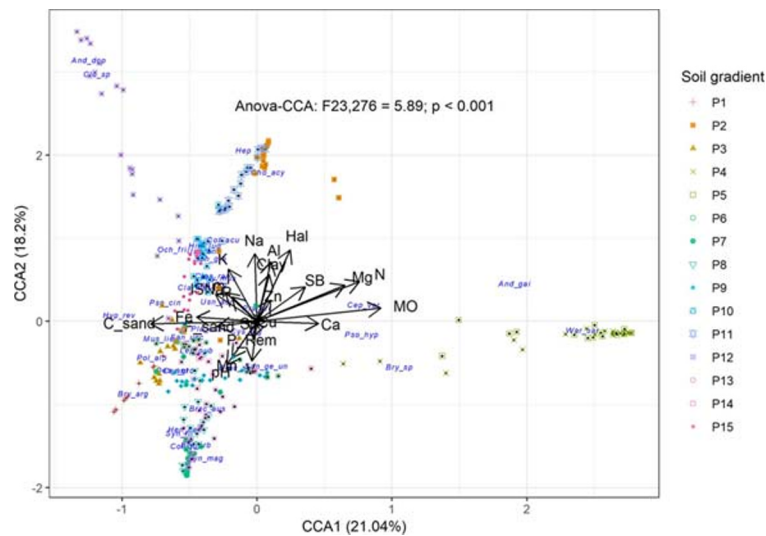


Fig. 6 Canonical correspondence analysis (CCA) showing species and plot scores in function of soil properties sampled within different types of pedoenvironments (a), and CCA only with texture properties (b). For analysis, available pH (H₂O), exchangeable acidity (Hal), sum of bases (SB), Al³⁺, Ca²⁺, Mg²⁺, Na, available P, K⁺, N, organic matter (MO), potential cation exchange

capacity (T), percentage of bases saturation (V), remaining phosphorus (P Rem), aluminium saturation (m), Zn, sodium saturation index (ISNa), Mn, Cu, Fe, Zn, and soil texture as coarse sand (C_Sand), fine sand (F_Sand), clay and silt contents were included.

Soil-cryptogamous communities relationship

The first axis of the CCA explained 21.04% of species composition based on differences in soil properties, while the second axis explained 18.2% (Fig. 6). According to the CCA, the moss species *Andreaea gainii* is closely related to organic matter contents (OM), which is in line with the high values found in P5, the only pedoenvironment in which this species was recorded in

this study. Similarly, *Warnstorfia sarmentosa*, which was the dominant species in P4 and P5, showed the highest OM values. *H. revolutum*, which occurred only in P6, showed a relationship with coarse sand (C_sand), which was at its highest level in this pedoenvironment. The CCA also showed a relationship between *Chorisodontium aciphyllum* and sodium (Na); although this species appears in several pedoenvironments with varying levels of Na, it was dominant in P2 and P11 (Table S3 from [ESM](#)), which showed high values for this attribute (Table S2). The fruticose lichen *Cladonia rangiferina* was related to the high levels of P found in P10 and P11. *Andreaea depressinervis* and *Cladonia* sp. were dominant in P12 and may be related to the high K levels found in this pedoenvironment.

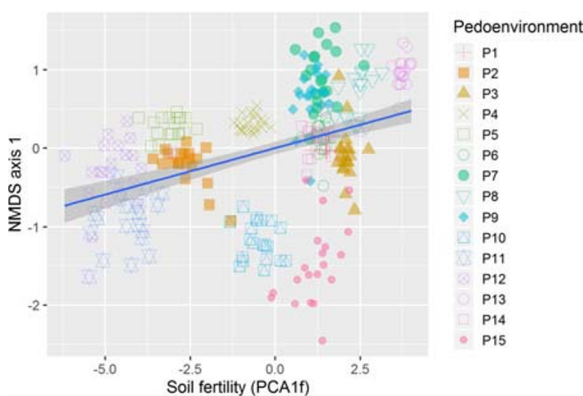


Fig. 7 NMDS axes 1 (Species composition variability) and the axis 1 of PCA of soil nutrients (PCA1f) relationship according with GLM approach. Colour-filled circles indicate data per treatments. The solid line represent the fitted value (prediction) of the model, and the shaded area the 95% confidence interval of the predicted value of the model

Effects of soil properties on species richness and species composition

From the comparison of models tested, we found that the predictors of soil fertility, soil texture, and individual soil properties (clay, sand, silt, T, OM and SB) had no significant effect on species richness, generally (Table S4 in the [Electronic supplementary material](#)). By contrast, according to our best model, significant effects of soil fertility variability on species composition

(LMM: $Z = 3.01$, $P < 0.001$) were observed (Fig. 7, Table S4).

Discussion

Our results demonstrate that richness, species composition and coverage of cryptogam communities change along the pedoenvironmental gradient on Elephant Island. In the models tested, we have demonstrated the main effects of different environmental predictors (soil texture and fertility), highlighting how soil fertility has a strong influence on species composition variation along the pedoenvironmental gradient, albeit without affecting species richness. To explain the possible processes that determine changes in species composition, we described the relationship between cryptogam communities and soil properties (mainly fertility) for each pedoenvironment. Also, we produced a detailed description of different types of mosses and lichens associations that determine different cryptogam communities along the pedoenvironmental gradient.

The species richness found in this study was considerably lower than that recorded by Alison and Lewis-Smith (1973) for Elephant Island (80 species, 24 of which were mosses) and also that one reported by Pereira and Putzke (1994) at Stinker Point (115 species, 38), because we selected representative and contrasting pedoenvironments that form the gradient, allowing to test our hypothesis. However, we identified previously unreported moss species (Putzke and Pereira 2001; Pereira and Putzke 2013) for the area: *Brachythecium* sp., *Bryum orbiculatifolium*, *Hypnum revolutum*, *Sanionia georgicounicinata* and *Syntrichia magellanica*. Recently-documented climate change in this part of the Maritime Antarctic and Antarctic Peninsula (Turner et al. 2016) has promoted increasing ice-free areas, offering favourable conditions for other species to colonize and develop (Amesbury et al. 2017). On the other hand, we assume that, despite the proximity of the pedoenvironments and the small elevational variation between them, this study showed differences in community diversity and cover, due to small scale differences between pedoenvironments.

We detected marked differences in soil chemical and physical properties among the pedoenvironments. Partially because they have varying degrees of ormithogenic influence, landforms, and histories of ice retreat

processes (Michel et al. 2014; Turner et al. 2016). Elephant Island's soils are been forming since the mid-Holocene glacial retreat under wetter, warmer climate condition, compared with continental Antarctica, which favours soil development (Bockheim 2015). Recent studies have investigated the local geomorphological features and mapped eight different types of periglacial landforms at Stinker Point, such as marine platforms (flat-floored valleys, laminated cracking on rock, patterned ground, gelifluction sheets and lobes, and vertical stone fields), till deposits (patterned ground, gelifluction lobes, and vertical stone fields), and slopes (debris talus and cones) (López-Martínez et al. 2006, 2012; Navas et al. 2018).

According to the map proposed by Lopez-Martínez et al. (2012) and Navas et al. (2018), most pedoenvironments correspond to platforms in Elephant Island. Conversely, the pedoenvironments P10, P11 and P12 are slopes at the edges of the platform, and P7, P8, P13 and P15 are located on unconsolidated newly-exposed glacial drift (moraines). This may explain the higher variation in soil pH found in these pedoenvironments, which is alkaline in moraines, and highly acid in the platforms (Navas et al. 2018). This striking difference corresponds to the more-recent exposure of the moraines, preserving most of the characteristics of the sedimentary material (Navas et al. 2018). Moraines are also closer to glaciers, while the pedoenvironments adjacent to the coast have much greater acidification due to bird nesting and guano mineralization (Tatur and Barczuk 1985; Simas et al. 2007), and phosphatization as a long-term soil formation process (Beyer et al. 2000; Navas et al. 2017, 2018). Similarly, higher soil organic matter on platforms is related to the proximity of the coast, and longer exposure time, combined with the presence of seabirds, responsible for soil nutrient input (Beyer et al. 2000), and vegetation development (Bockheim and Haus 2014). According to Navas et al. (2018), high P and K values present not only on the coast but also on the intermediate platforms of Elephant Island, are related to bird activity, especially recent and abandoned penguin colonies (Michel et al. 2006; Simas et al. 2007). We infer that this crucial nutrient input may be a key driver of community diversity, forming specific associations of lichens and mosses species.

The lowest fertility values (except P) were recorded in P1, which also had the lowest species richness in this study. The dominant *Bryum argenteum* (ESI = 540),

associated with *Sanionia uncinata* (ESI = 115), formed a dense carpet of mosses only seen at this location on Stinker Point. High P levels is explained by the presence of active giant petrel nests (*Macronectes giganteus*) on this area, with phosphatization and strong acidification by guano mineralization, as described by Simas et al. (2007). Conversely, P2 showed higher fertility, high OM, and higher Mg values, but lower levels of P. Located on the central platform, on rock fields, its phytophysiognomy is a dense community of peat bog mosses with a dominance of *Chorisodontium acyphillum* (ESI = 503.5) associated with *S. uncinata* (IES = 99), and the presence of the muscicolous lichen *Cystocoleus niger* (ESI = 195.5) growing on both. This pedoenvironment shows lower cover, higher richness (ten species) and a community of *S. uncinata*-dominated moss carpet (IES = 258.75) associated with *Polytrichastrum alpinum* (IES = 115.5) with occasional *Deschampsia antarctica* grass (IES = 75.25). P4 and P5 are both pedoenvironments located on opposite sides of the drainage line that cuts across Stinker Point, and often waterlogged and with high amounts of OM (~ 35.5 dag/kg). However, chemically, soil attributes of P4, and P5 are very dissimilar. The cover, richness, and species composition are similar, and both are dominated by *Warnstorfia sarmentosa* in the moss carpet community. In P4, *W. sarmentosa* is associated with *Prasiola crispa* algae whereas at P5 the moss *S. georgicouncinata* is the accompanying species. According to the CCA, *W. sarmentosa* showed a relationship with organic matter, consistently with Putzke and Pereira (2001), and Ochyra et al. (2008), who described this moss as a typically hydrophilic, growing in saturated wetlands.

The community at P6 was the only moss carpet with exclusive dominance of *Sanionia* spp. Although ten other species of mosses and lichens were identified at the site, only *S. uncinata* (ESI = 303.75) and *S. georgicouncinata* (ESI = 231) had ESI >50. The available P amounts varied widely among the plots, even within the pedoenvironment itself, but were high overall (498.13 ± 313.52 mg/dm³). Increasing values are attributed to the presence of abandoned bird nests at some points, as reported by Francelino et al. (2011) and Moura et al. (2012). Despite its low frequency, P6 was the only pedoenvironment where *H. revolutum* was present and related to coarse sand, with the highest value. Previous studies have described communities dominated by this moss near drainage lines, or areas of snow accumulation (Barták et al. 2005).

P7 and P8 are close to each another, located on an elevated marine terrace near the beach just above an active penguin rookery. These pedoenvironments have the lowest levels of cover, with similar species richness and composition (Fig A.1A and Fig. 4). Both are cushion moss communities, dominated by *Bryum orbiculatifolium* associated with *Brachythecium austrosalebrosus*, with occasional, low frequency presence of *Colobanthus quitensis* this high plant, according to with the CCA, is related to pH and Mn (ranging from 32 to 36 mg/dm), although Parnikoza et al. (2007) report that it inhabits a large ecological range of habitats. The moss *Syntrichia magellanica* only appeared in the P7 pedoenvironment (Fig. 4), and maybe related to high levels of Ca²⁺ and SB, the only edaphic attribute that differed significantly from P8. According to Ochyra et al. (2008), this moss grows in a range of habitats, including acidic or base-rich substrates, in either sandy or silty soils, and on moraines, or close to bird colonies.

P9 supported a phanerogamic community of *D. antarctica* (IES = 369) associated with *S. uncinata*, with occasional *P. crispa* algae. This area was located on a slope near the lake, which is often visited by skuas (*Stercorarius antarcticus*) for settling and nesting in dry lakes (Quintana and Travaini 2000), thereby promoting the of nutrient's input. The P10 was near the slope edge of the platform, with a strong omithogenic influence in the past, and currently located near a giant petrel nests, with the highest P level recorded (870.44 ± 635.89 mg/dm³) and high fertility, creating favourable conditions for vegetation (Tatur and Myrcha 1993). This pedoenvironment showed high variability in species composition, representing a fruticose lichen community, dominated by *Sphaerophorus globosus* and *Usnea aurantiacoatra*, associated with the moss *Andreaea depressinervis*. Other species such as *Cladonia rangiferina*, THE seaweed *P. crispa*, *S. uncinata*, and *Chorisodontium acyphillum* also had high ESI values, and are commonly reported with association with *S. globosus* (Øvstedal and Lewis-Smith 2001; Olech 2004).

In P12, less than 60% of the cover was recorded, due to the rockiness stoniness of the area. A muscicolous lichen community (*Cladonia* sp., *C. niger* and *Ochrolechia frigida*) grows on *A. depressinervis* (ESI = 300) and *S. uncinata* (ESI = 165) mosses. This pedoenvironment (P12) is the most acidic, and the highest Al³⁺, exchangeable acidity (H + Al), and cation exchange capacity at pH 7 (T) values. This

pedoenvironment is located adjacent to a current penguin colony and is probably an abandoned penguin rookery at the platform slope. The high Na values are caused by the saline sprays carried by winds (Michel et al. 2006). Conversely, P13 was a recently exposed area close to meltwater lakes following glacier retreat. These lakes are often used by wandering skuas, in the vicinity (Quintana and Travaini 2000), representing initial spots for plant colonization, on rich-nutrient soils. The P14 has a dense moss carpet community (*S. uncinata*–*B. austrosalebrosus* association) located in a seasonal waterlogged area, with high coverage by the hydrophilic moss *B. austrosalebrosus* that grows well on sandy soils along the borders of meltwater channels (Ochyra et al. 2008).

Finally, P15 was the pedoenvironment that show the highest species richness, being located at a small elevation above a moraine, and having pH 6.4, high fertility, and high levels of P (suggesting ornithogenic influence) but no current bird nesting. Although *S. uncinata* was dominant (IES = 360), this formation was classified as a fruticose lichen community, by the widespread presence of *S. globosus*, *U. antarctica*, *O. frigida*, *Psoroma cinnamomeum*, *C. aculeata* and *H. lugrubis*, as well as other moss and lichen with low frequencies (ESI > 50). The Antarctic endemic *H. lugrubis* was only found in P11 and P15, and the CCA suggested a relationship with high K⁺ in both pedo-environments. Regarding Choi et al. (2015) this species, showed that the main factors that influence its distribution and development were substrate and soil moisture.

Conclusion

(1) Cryptogamic communities have differences in diversity and cover of cryptogam communities along a pedoenvironmental gradient on Elephant Island. (2) The models employed showed that only soil fertility had significant effects on species composition, but not on richness; Soil nutrient status is therefore the main significant predictor of species composition of cryptogamic communities in Maritime Antarctica. However, differences in species composition were not as pronounced as expected, showing high sharing between different pedoenvironments. (3) Pedoenvironmental filtering determined differences in the composition of species on Elephant Island (Maritime Antarctica), and small-scale heterogeneity contributed to the formation

of typical cryptogamic species associations along the pedoenvironmental gradient. (4) Soil attributes not only drive the patterns of diversity, but also the types of cryptogam communities.

Acknowledgements We acknowledge the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brazil, for concession the scholarship of the first author, and PDJ (CNPq) scholarship for the second author; and for the CNPq, Brazil for financial support of this project (Conselho Nacional de Desenvolvimento Científico e Tecnológico) (project # 406793/2013-1). This work is a contribution of the INCT-Criosfera TERRANTAR group.

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