How does the pedoenvironmental gradient shape non-vascular species assemblages and community structures in Maritime Antarctica?

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Pedoenvironmental filtering
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Mosses
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A B S T R A C T
The main terrestrial ecosystems dominated by lichens and mosses, which represent important ecological indicators of climatic changes in high polar latitudes, are found in the Antarctic continent. However, little is known about how environmental filtering shapes cryptogamic communities’ assemblages at fine-scale. In this study, we analysed changes in non-vascular species richness, species composition and plant coverage along a pedoenvironmental gradient in Maritime Antarctica. We hypothesized that pedoenvironmental filters (i.e. soil texture and chemistry properties) drive the non-vascular assembly community. We classified soils according to the World Reference Base for Soil Resources, selecting ten different pedoenvironments at fine-scale. The plant inventory data from 206 plots across these pedoenvironments was used to evaluate the main effect of plant coverage, soil texture and soil chemistry on non-vascular species richness and composition. The ecological value of the species was determined and the type of community it occurred in was characterized, then the associations of the species were classified in each pedoenvironment. Differences in species richness, species composition and plant coverage were detected along the pedoenvironmental gradient. However, plant coverage, soil chemistry, soil texture and soil variables did not affect species richness and species composition, with the exception of clay content that was particularly an important predictor of species composition. High pedoenvironmental filtering apparently has no effect on species richness but determined differences in species composition. Therefore, we assumed that pedoenvironmental filtering determined high beta diversity in this island from maritime Antarctica. This study reveals that fine scale heterogeneity contributes to specific species associations along a pedoenvironmental gradient; thus, pedoenvironmental filtering not only determines diversity pattern in non-vascular plants, but also type of communities.

1. Introduction
Predicting how multiple drivers shape plant community assembly along environmental gradients is one of the most important issues in ecology and conservation biology (Götzenberger et al., 2012). Community assembly may be driven by different processes at different spatial scales, selecting species from a regional species pool into a local habitat, i.e. by environmental filtering (Kraft and Ackerly, 2010). Environmental constraints can be the main drivers of community assembly, resulting in the establishment of functionally similar species under the influence of habitat filtering (Götzenberger et al., 2012; Kraft et al., 2015). For instance, soil properties can be an important environmental filter at small spatial scales (Laliberté et al., 2014; Conti et al., 2017; Scherrer et al., 2018). Thus, even at small scale, the same community patterns might be the result of different processes and only by testing the dependence on within-community abiotic heterogeneity can we tease them apart (Kraft et al., 2015). In consequence, in community assembly studies greater attention must be paid to the role of within-community abiotic heterogeneity in promoting diversity.

Studies have revealed the existence of a close positive relationship between environmental heterogeneity and plant diversity (Tilman, 1982; Yang et al., 2015), where increasing heterogeneity is associated with an increase in the number of species coexisting along environmental gradients, it being a determinant factor for community assembly.
Environmental heterogeneity may affect abiotic resources such as soil nutrients, which in turn strongly affect species diversity and community structure (Clarke, 1993; García-Palacios et al., 2011; Poelking et al., 2015). Furthermore, pedological variability causes fine-scale heterogeneity of nutrient availability, meaning that species can differentially explore patchily distributed resources (Carmo and Jacobi, 2016; Carmo et al., 2016; Conti et al., 2017), which can lead to higher species richness and species composition variability (Questad and Foster, 2008; Conti et al., 2017).

Several studies have shown how pedological variability causes fine-scale heterogeneity in resource availability, i.e. nutrients (e.g. Carmo et al., 2016; Conti et al., 2017), and determines the assembly of plant communities (Kraft and Ackerly, 2010; Götzenberger et al., 2012; Kraft et al., 2015), especially in vascular plant communities. However, there are still few studies on the ecological drivers of the community assembly of non-vascular plants, such as bryophytes, mainly analysing effects of environmental filters (Amorim et al., 2017; Silva et al., 2017). Bryophytes have a wider distribution and larger latitudinal and altitudinal gradient than vascular plants and thus marked changes in species diversity and compositions along environmental gradients (Andrew et al., 2003). For this reason, there are studies based on the premise that the species composition and richness of non-vascular plants are strongly related to environmental filtering with deterministic distribution (e.g. Sun et al., 2013; Amorim et al., 2017).

In this context, the Antarctic is special in being the main terrestrial ecosystem characterized by being dominated almost exclusively by non-vascular plants, such as lichens and mosses (Øvstedal and Lewis-Smith, 2001; Poelking et al., 2015; Rodriguez et al., 2018). The Antarctic vegetation is restricted to ice free areas, which occur mainly in coastal regions, rocky slopes or in nunataks (Campbell and Claridge, 1987; Bokhorst et al., 2007). Maritime Antarctic vegetation is largely composed of bryophytes (mosses and liverworts) and lichens, with only two species of flowering plants, Deschampsia antarctica Desv. and Colobanthus quitensis (Kunth) Bartl, and some macroscopic algae (Purzke and Pereira, 2001). In these areas, the vegetation shows a patchy spatial distribution as a consequence of multiple ecological conditions (Kappen, 1985; Benavent-González et al., 2018). However, the effects of environmental filtering on changes in non-vascular plant diversity and community structure remain poorly understood. This is important in the face of ongoing climate change, which may affect non-vascular...
plants in their response to increasing global temperatures (e.g. Robinson et al., 2018).

In this study we analysed changes in non-vascular species richness, species composition and plant coverage along a pedoenvironmental gradient in Maritime Antarctica. We used plant inventory data from 206 plots across ten pedoenvironments, allowing us to evaluate the effect of plant coverage, soil texture and soil fertility on non-vascular species richness and composition. So, to evaluate the ecological patterns of non-vascular species diversity at fine scale, we asked the following four research questions. 1) How does species richness, species composition and plant coverage change along the pedoenvironmental gradient? 2) What are the main effects and relative importance of coverage, soil chemistry and texture on species richness and species composition? 3) How does fine scale within-pedoenvironment heterogeneity contribute to species association and beta diversity along a pedoenvironmental gradient?

Based on the premise that non-vascular plant communities have distributions shaped by environmental filters (e.g. Sun et al., 2013; Amorim et al., 2017; Peñaloza-Bojacá et al., 2018); we hypothesized that soil properties (e.g. soil texture, soil chemistry) drive the species assemblage. We expected that pedoenvironmental heterogeneity promotes high species composition variability at fine-scale, with low similarity between different pedoenvironments. On the other hand, we expected that pedoenvironmental conditions further drove the community structure, e.g. plant coverage (Sanai et al., 2018a,b); therefore, we expected to detect a relation between high plant coverage and high species richness. Also, we expected that pedoenvironmental heterogeneity promoted different species associations (species-level) and beta diversity that determined the type of different communities.

2. Materials and methods

2.1. Study area

This study was performed on the Stansbury Peninsula, located on Nelson Island (61° 18’ S and 59° 03’ W), one of the largest islands of the South Shetland Archipelago, maritime Antarctica, being isolated by a small channel from King George Island (Fig. 1). The peninsula is approximately 3 km² in area and is the second largest ice-free area of Nelson Island (Putzke et al., 1998). The local climate is a maritime climate (Ferron et al., 2004) with small variations in temperature during the year, high relative humidity and constant cloud cover (Jiahong et al., 1994). The climate is polar type tundra (after Köppen’s climatic classification, 1948) with average annual atmospheric temperature of -2.8 °C, with variations in the summer period of -1.3 to 2.7 °C and in the winter of -15.5 to -1.0 °C (Ferron et al., 2004; Poelking et al., 2014). The region represents a typical coastal zone periglacial environment, in which ice melting during summer leads to abundant drainage and water supply to the lakes (Poelking et al., 2014).

2.2. Selection of different pedoenvironments

We selected ten pedoenvironments based on a geological approach (Figs. A.1-A.10 Appendix/from Electronic Supplement Material). The ten environments were selected according to their classification in the World Reference Base for Soil Resources (IUSS Working Group WRB, 2015). A profile was examined at each site, according to the recommendations of Bockheim et al. (2006) and the necessary classification characteristics were acquired (depth, clarity and transition horizons, drainage, erosion, colour, coarse fractions, chemical properties and soil texture).

Due to the presence of permafrost, a cryogenic horizon or evidence of cryoturbation, all soils were classified as Cryosols. However, according to their principal qualifiers, the 10 pedoenvironments were classified differently (Table 1). For example, P1, P2, P5, P8, P9 and P10...
are Akroskeletic (they have ≥ 40% of the soil surface covered by fragments that have a greatest dimension ≥ 6 cm; stones, boulders or large boulders). However, other features make them different. P1 and P2 have similar qualifiers, such as Protosalic, Subaquetsic, Arenic and Protosodic, but differ from each other because P1 is Oligoeutric and P2 is Orthoetric and Akroturbic (Table 1).

### 2.3. Vegetation sampling

During the austral summer of 2017, 15 to 30 plots of 20 × 20 cm (Fig. A1.11) were established for the sampling of non-vascular plants (lichens, mosses and algae) in each selected pedoenvironment. A total of 206 plots across ten study pedoenvironments were sampled every five meters in four rows in the north–south direction and then returning south-north, adapted where necessary according to the size and shape of the vegetation patch. The survey was conducted using the Braun-Blanquet (1932) square method, adapted for Antarctic vegetation conditions, to measure the species coverage in each plot, as well as to calculate the total coverage of each plot. Most non-vascular plants were identified to species level within each plot by using the following keys: Putzke and Pereira (2001), Ochyra (1998) and Ochyra et al. (2008) for mosses, and Redon (1985), Øvstedal and Lewis-Smith (2001) and Olech (2004) for lichens.

### 2.4. Ecological significance index

The importance of the species in each pedoenvironment, the plant community’s classification and species association, was 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:

\[
\text{ESI} = F(1+C) \\
F = 100x/n \\
\text{where } F \text{ is the relative frequency of the species in the area or habitat and is generated by the number of occurrences } (x) \text{ divided by the total number of samples considered} (n); \text{ and } C \text{ is the average coverage of the species in the samples, calculated as:} \\
C = \Sigma (ci)x \\
\text{where } ci \text{ is the class of coverage and } x \text{ 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 codominant species or by restricted occurrence in more specific habitats (Longton, 1988; Poelking et al., 2015).}
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### 2.5. Soil collection

In order to measure the soil properties within each plot, a surface soil sample was taken (at 0–10 cm depth). Soil properties were measured following standard protocols (EMBRAPA, 1997). The following parameters were assessed: total N, available exchangeable P, K, Ca, Na, Mg, Fe, Cu, Mn, Zn, exchangeable acidity (H + Al), pH (H₂O), organic matter (OM), sum of exchangeable bases (SB), effective cation exchange capacity (t) and soil texture, classified as coarse sand (Sand_c), fine sand (Sand_f), clay and silt contents.

### 2.6. Data analysis

All analyses were carried out using R Environment (R Core Team, 2017). For all variables we tested normal distribution with Shapiro-Wilk test and by evaluating the Q-Q plot and we assessed homogeneity of variances by Bartlett’s test using the “dplyr” package (Crawley, 2013). To compare soil properties (non-normally distributed data), species richness, β-diversity components (Jsor, jsim, jsne), and coverage between pedoenvironment sites, we used Kruskal-Wallis’ test followed by a post hoc Dunn’s test performed with the ‘dunn.test’ (Dinno, 2017).

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 by using the adonis routine available within the “vegan” package (Oksanen et al., 2018).

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 bootstrap runs to estimate 95% confidence intervals (e.g. Rodrigues et al., 2019). Likewise, we considered whenever the 95% confidence intervals did not overlap among assemblages in each pedoenvironment, species numbers differed significantly at p < 0.05 (Colwell et al., 2012).

Soil variables were summarized using principal components analysis (PCA) to identify a possible pedoenvironmental gradient and to reduce the number of redundant soil properties (e.g. Qian et al., 2014; 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 fertility and texture properties and biotic (species) variables, a Canonical Correspondence Analysis (CCA) was used. CCA examines the 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 applying Monte Carlo randomizations (999 randomizations). The CCAs were performed using the ggdord and ordiplots 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; Rodrigues et al., 2019).

We evaluated the effect of potential predictors on species richness and species composition (e.g. extracting the scores on frequency-weighted NMDS axis 1; Dayananda et al., 2017; Oksanen et al., 2018; Villa et al., 2018) via linear mixed effect models (LMMs). To reduce any strong correlations among local environmental conditions (Table A3), we used the two axes of the PCA for soil fertility (PCA1t) 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 18 analysed parameters (see above), as well as further soil parameters such as sand, silt, clay, SB, OM and pH. Plant coverage is defined as proportion of plant community space occupied in each pedoenvironment (Ji et al., 2009); and therefore plant coverage is considered an important predictor with possible effect in plant diversity (Ji et al., 2009; Sanaei et al., 2018a,b).

Soil chemistry and texture were used as well as single soil parameters as explanatory variables for modelling, because single soil parameters also potentially show a direct effect on species richness and species composition (Villa et al., 2018a). For predictor selection, we assessed colinearity between selected predictor variables using Spearman correlation analysis; when two variables were strongly correlated (r ≥ 0.6) the most ecologically relevant predictors were selected, which were included in separate models (Fig. A.12). 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., 2018a). All models were fitted using the package ‘lme4’ (Bates et al., 2014) from the R platform (R- Core-Team, 2017); 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 one, but all models that differed less than four units from the best model were considered as equally good models (Burnham et al., 2011).

2.7. Beta diversity analysis

Dissimilarity in species composition between pedoenvironments was calculated using the taxonomic β-diversity decomposition approach proposed by Baselga (2010, 2012). For the β-diversity decomposition, three pairwise β-diversity metrics were calculated. First, βsor accounts for the total compositional variation between seedling assemblages (including both turnover and nestedness patterns) using Sørensen dissimilarity index (βsor). Second, βsim captures only compositional changes due to species turnover, using Simpson dissimilarity index (βsim). Third, βse represents nestedness-resultant dissimilarity, which measures how dissimilar the sites are due to a nested pattern (Baselga, 2010). βsne was calculated as the difference between βsor and βsim (e.g. Baselga, 2010, 2012; Villa et al., 2018b).

3. Results

3.1. Soil attributes pattern

Soils were generally moderately acid (5.68–6.52) and showed a high level of fertility (High Ca, CEC, P and Bases Sum; Table 2). Some pedoenvironments (P5, P6, P7 and P8) were clearly influenced by guano deposition (ornithogenesis), based on the amounts of available P, greater than 178 mg/dm³ and reaching 881 mg/dm³. The amount of Na was variable and high, particularly in P1, P2, P3 and P4, all influenced by salt spray carried by wind from marine sources. The amounts of OM were very low (Fig. A.13), except for soils with ornithogenic influence, where amounts reached 14.3 dag/kg (P7), representing exceptional figures. Soils were dominated by the sand fraction, with high values of coarse sand, but clay and silt was higher in samples P5-P10, closely associated with ornithogenesis.

3.2. Species composition and species richness pattern

We identified 20 species (representing 18% of the species described for Antarctica), 30 lichen species (8% of the species identified for the region, Table A1). The richest family was the Bryaceae with seven species, followed by the Amblystegiaceae with four species.

The NMDS revealed that species composition varied significantly between pedoenvironments but with a marked overlap among most groups (PERMANOVA: F2,195 = 12.17, p < 0.01; Fig. 2). Pedeoenvi- ronments P7 and P8 showed the highest species richness, both with 19 species. (Table 1; Fig. 3A). We observed similar richness patterns among pedoenvironments using sample-based rarefaction and extrapolation curves, but there are differences between pedoenvironments mainly due to the low number of species observed in P2, and P4 that does not overlap with other pedoenvironments according rarefaction. Rarefaction curves indicated sampling sufficiency as we noted an asymptote of the extrapolated curves. Between nine and 19 species occurred in each pedoenvironment (except P2, which presented only two species).

3.3. Ecological significance index

According to the growth pattern of the dominant species in the study area, the 10 pedoenvironments were classified as moss carpet communities, but their dominant species varied in seven distinct associations (Table 1). In P1 Sanionia georgicouncinata (ESI = 545) was the dominant species followed by Warnstorfia fontinaliopsis (242.25), other species were found at this pedoenvironment, but all with ESI < 50 (Table A2). Pedeoenvi ronments P2 and P8 had Sanionia uncinata as the dominant species, but in P8 this species was associated with Bryum argenteum. In P3 and P7, Warnstorfia sarmentosa was the dominant species, followed by S. georgicouncinata, but the other species found in these communities differed considerably (Table A2); thirteen species were identified in P3 (eight mosses and five lichens) and in P7, with the highest number of species, 12 lichens, six mosses and one alga were registered.

P4 and P5 were referred to as Sanionia spp. associations because they presented dominant species such as S. georgicouncinata (IES = 520) and S. uncinata (IES = 301.75), respectively and S. uncinita (IES = 242.50) and S. georgicouncinata (IES = 269.5) as co-dominant species. P6 presented a S. georgicouncinata-Hennediella heimii association, (Table A1), P9 had S. georgicouncinata as the dominant species (ESI = 308) followed by two co-dominant species, Syntrichia filaris (ESI = 159.25) and H. heimii (ESI = 104.5) forming an association distinct from the others found in this study. Finally, P10 was a pedoenvironment with exclusive dominance of S. georgicouncinata (ESI = 528.57) where none of the other 16 species occurred (ESI < 50).

3.4. Plant coverage pattern and species coverage distribution

Plant coverage varied significantly ($\chi^2 = 55, df = 9, p < 0.001$) along the pedoenvironmental gradient (Fig. 3B). The distribution of species coverage changed markedly along the pedoenvironment; the 10 most dominant species (along the species-rank axis), found in almost all pedoenvironments, accounted for 55% of the total proportional coverage (Fig. A.14). For instance, the two species of Sanionia were the most dominant along the pedoenvironmental gradient, being present in almost all plots and with the highest values of coverage. The species that presented the highest coverage value were S. georgicouncinata in pedoenvironments P1, P4, P6, P9 and P10, S. uncinata in pedoenviron- ments P2, P5 and P6 and W. sarmentosa in pedoenvironments P3 and P7 (Table A.2).
Table 2
Descriptive statistics of soil attributes for the ten sampled areas in the ice-free areas of Rip Point, Nelson Island, Maritime Antarctica.

<table>
<thead>
<tr>
<th></th>
<th>P1</th>
<th>P2</th>
<th>P3</th>
<th>P4</th>
<th>P5</th>
<th>P6</th>
<th>P7</th>
<th>P8</th>
<th>P9</th>
<th>P10</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>6.52 ± 0.20a</td>
<td>6.38 ± 0.15a</td>
<td>6.10 ± 0.21bc</td>
<td>6.38 ± 0.15ab</td>
<td>6.40 ± 0.17a</td>
<td>6.17 ± 0.76b</td>
<td>5.68 ± 0.50c</td>
<td>6.34 ± 0.17ab</td>
<td>6.40 ± 0.17ab</td>
<td>5.99 ± 0.15c</td>
</tr>
<tr>
<td>P</td>
<td>58.64 ± 8.30d</td>
<td>109.3 ± 40.73c</td>
<td>112.8 ± 64.92c</td>
<td>76.06 ± 32.87</td>
<td>178.36 ± 114.21c</td>
<td>455.9 ± 104.32b</td>
<td>881.6 ± 174.99a</td>
<td>263.1 ± 127.1c</td>
<td>68.7 ± 16.97d</td>
<td>40.78 ± 9.20e</td>
</tr>
<tr>
<td>K</td>
<td>209.2 ± 51.09a</td>
<td>269.6 ± 58.09a</td>
<td>154.0 ± 23.70</td>
<td>253.6 ± 52.60a</td>
<td>185.2 ± 25.40bc</td>
<td>169.6 ± 25.39c</td>
<td>163.6 ± 63.03c</td>
<td>148.8 ± 4.81c</td>
<td>116.8 ± 5.40d</td>
<td>124.0 ± 12.88d</td>
</tr>
<tr>
<td>Na</td>
<td>614.32 ± 186.18a</td>
<td>706.06 ± 217.08a</td>
<td>484.72 ± 156.9b</td>
<td>622.32 ± 201.37ab</td>
<td>394.96 ± 131.96b</td>
<td>323.1 ± 43.80bc</td>
<td>309.2 ± 117.83cd</td>
<td>287.2 ± 36.6cd</td>
<td>263.1 ± 127.1c</td>
<td>229.4 ± 27.66e</td>
</tr>
<tr>
<td>Ca²⁺</td>
<td>13.52 ± 2.76b</td>
<td>6.33 ± 0.95c</td>
<td>29.28 ± 5.54a</td>
<td>15.88 ± 3.04b</td>
<td>25.31 ± 4.56 a</td>
<td>30.14 ± 7.09 a</td>
<td>12.68 ± 7.76b</td>
<td>12.72 ± 2.39b</td>
<td>25.08 ± 5.96 a</td>
<td>16.86 ± 2.71b</td>
</tr>
<tr>
<td>Mg²⁺</td>
<td>10.37 ± 2.82b</td>
<td>6.94 ± 1.21d</td>
<td>19.68 ± 4.66a</td>
<td>11.60 ± 1.62b</td>
<td>15.54 ± 2.56a</td>
<td>13.19 ± 5.70bc</td>
<td>8.97 ± 5.17c</td>
<td>4.16 ± 0.40d</td>
<td>8.70 ± 1.2c</td>
<td>6.93 ± 1.54cd</td>
</tr>
<tr>
<td>H + Al</td>
<td>2.76 ± 1.06d</td>
<td>2.64 ± 0.51d</td>
<td>4.2 ± 0.69b</td>
<td>3.6 ± 0.34c</td>
<td>8.34 ± 6.72a</td>
<td>10.86 ± 5.37a</td>
<td>3.8 ± 0.95c</td>
<td>3.22 ± 0.57c</td>
<td>6.93 ± 1.54cd</td>
<td></td>
</tr>
<tr>
<td>SB</td>
<td>27.11 ± 6.10b</td>
<td>17.04 ± 1.88c</td>
<td>51.46 ± 6.35a</td>
<td>30.84 ± 2.80b</td>
<td>43.05 ± 6.32a</td>
<td>45.17 ± 5.70bc</td>
<td>23.42 ± 13.21bc</td>
<td>18.51 ± 2.65c</td>
<td>35.17 ± 7.17b</td>
<td>25.11 ± 4.03b</td>
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<tr>
<td>OM</td>
<td>0.36 ± 0.32d</td>
<td>0.70 ± 0.57d</td>
<td>1.35 ± 0.39b</td>
<td>1.2 ± 0.83c</td>
<td>1.93 ± 1.66c</td>
<td>2.45 ± 2.35bc</td>
<td>1.30 ± 0.94c</td>
<td>3.23 ± 1.91b</td>
<td>3.00 ± 1.27c</td>
<td>4.50 ± 0.91b</td>
</tr>
<tr>
<td>Cu</td>
<td>6.35 ± 2.20a</td>
<td>5.38 ± 0.74b</td>
<td>5.28 ± 1.58b</td>
<td>5.06 ± 0.92b</td>
<td>5.31 ± 3.55ab</td>
<td>4.18 ± 2.47bc</td>
<td>6.02 ± 1.61a</td>
<td>6.08 ± 2.32a</td>
<td>5.11 ± 0.66b</td>
<td></td>
</tr>
<tr>
<td>Mn</td>
<td>74.34 ± 19.51ab</td>
<td>34.7 ± 13.46b</td>
<td>69.54 ± 19.90ab</td>
<td>91.78 ± 33.22a</td>
<td>110.46 ± 15.47a</td>
<td>68.2 ± 51.63ab</td>
<td>43.7 ± 26.17b</td>
<td>46.5 ± 28.58b</td>
<td>62.58 ± 32.36b</td>
<td>53.42 ± 10.16b</td>
</tr>
<tr>
<td>Fe</td>
<td>237.0 ± 23.38ab</td>
<td>195.9 ± 34.58b</td>
<td>174.2 ± 47.09b</td>
<td>208.5 ± 47.59ab</td>
<td>170.7 ± 14.56b</td>
<td>187.9 ± 73.99b</td>
<td>277.3 ± 48.3a</td>
<td>238.8 ± 51.1a</td>
<td>216.32 ± 39.55b</td>
<td></td>
</tr>
<tr>
<td>Zn</td>
<td>0.86 ± 0.22c</td>
<td>0.96 ± 0.18c</td>
<td>1.33 ± 0.41b</td>
<td>1.48 ± 0.30b</td>
<td>1.30 ± 0.38b</td>
<td>1.08 ± 0.39b</td>
<td>3.00 ± 1.66a</td>
<td>2.30 ± 0.72a</td>
<td>1.38 ± 1.38b</td>
<td>1.59 ± 0.93b</td>
</tr>
<tr>
<td>N</td>
<td>0.032 ± 0.02d</td>
<td>0.063 ± 0.01d</td>
<td>0.122 ± 0.039d</td>
<td>0.085 ± 0.02d</td>
<td>0.138 ± 0.08c</td>
<td>0.193 ± 0.135c</td>
<td>0.682 ± 0.546a</td>
<td>0.274 ± 0.27bc</td>
<td>0.081 ± 0.016</td>
<td>0.183 ± 0.18c</td>
</tr>
<tr>
<td>Coarse sand (g/kg)</td>
<td>0.032 ± 0.02d</td>
<td>0.063 ± 0.01d</td>
<td>0.122 ± 0.039d</td>
<td>0.085 ± 0.02d</td>
<td>0.138 ± 0.08c</td>
<td>0.193 ± 0.135c</td>
<td>0.682 ± 0.546a</td>
<td>0.274 ± 0.27bc</td>
<td>0.081 ± 0.016</td>
<td>0.183 ± 0.18c</td>
</tr>
<tr>
<td>Fine sand (g/kg)</td>
<td>0.02 ± 0.009e</td>
<td>0.13 ± 0.10c</td>
<td>0.13 ± 0.01e</td>
<td>0.07 ± 0.03d</td>
<td>0.12 ± 0.06c</td>
<td>0.17 ± 0.04b</td>
<td>0.22 ± 0.04b</td>
<td>0.24 ± 0.08b</td>
<td>0.33 ± 0.07a</td>
<td>0.15 ± 0.04c</td>
</tr>
<tr>
<td>Clay (g/kg)</td>
<td>0.04 ± 0.02c</td>
<td>0.01 ± 0.003e</td>
<td>0.15 ± 0.06c</td>
<td>0.09 ± 0.01d</td>
<td>0.23 ± 0.08b</td>
<td>0.22 ± 0.04b</td>
<td>0.24 ± 0.08b</td>
<td>0.33 ± 0.07a</td>
<td>0.15 ± 0.04c</td>
<td>0.21 ± 0.07b</td>
</tr>
<tr>
<td>Texture</td>
<td>sand</td>
<td>sand</td>
<td>Clay loam</td>
<td>Sandy loam</td>
<td>Sandy loam</td>
<td>Sandy loam</td>
<td>Sandy loam</td>
<td>Sandy loam</td>
<td>Sandy loam</td>
<td>Sandy loam</td>
</tr>
</tbody>
</table>

**Notes:**
- pH: H₂O (relation (1):2:5)
- P: phosphor; K: potassium; Na: sodium (Mehlich extractor 1); Ca: calcium; Mg: magnesium; H + Al: acidity potential (calcium acetate extractor 0.5 mol L⁻¹ pH 7.0); SB: sum of exchangeable bases; t: effective cation exchange capacity; OM: organic matter; Cu: copper; Mn: manganese; Fe: iron; Zn: zinc. Different letters indicate significant differences at posteriori analyses (P < 0.05) between pedoenvironments with Dunn test.
3.5. Descriptors of soil fertility and texture

A higher level of variability in soil chemistry was observed along the pedoenvironmental gradient (Table 2, Fig. A.13). In general, most soils in the study area presented high values for nutrient variability, OM and sand content. The first two axes of the overall PCA explained 45% of the variation in the soil data (Fig. 4). The first axis explained 25.5% of variance and was positively correlated with silt (R = 0.74; p < 0.01), N (R = 0.73; p < 0.01), sand_t (R = 0.67) and OM (R = 0.61, p < 0.05) and was negatively correlated with sand_c (R = -0.80, p < 0.05) and Na (R = -0.66) (Table A3). Clay content was highly correlated with both PCA1 and PCA2. The second axis explained 19.5% of the variation in soil data and was positively correlated with the SB (R = 0.86, p < 0.05), effective cation exchange capacity (R = 0.81, p < 0.05) and clay (R = 0.61, p < 0.05) (Table A3).

3.6. Vegetation–soil properties relationships

The first axis of the CCA biplot explained 32.61% of the species composition with differences in soil properties, while the second axis explained 24.05% (Fig. 5). The CCA separated species along the pedoenvironmental gradient, which formed a continuum along a pH and OM gradient. However, Polytrichastrum alpinum, Chorisodontium aciphyllum and Cladonia rangiferina were linked to higher nutrient contents, effective cation exchange capacity and soil OM. On the other hand, species such as Andreaea regularis and W. fontinaliopsis were closely associated with pedoenvironments with greater pH and higher coarse sand content (Fig. 5A). Further, when considering the relationship between soil texture and vegetation, it was observed that the two axes explained more than 79% of the variability of species composition, maintaining the same physical properties distribution pattern along the pedoambiental gradient, in comparison to the CCA of overall soil properties (Fig. 5B).

3.7. Effects of soil properties on species richness and species composition

From the multi-model comparison, applied between pedoenvironments, we found that models including plant coverage, soil fertility, soil texture as well as single soil properties (clay, sand, silt, pH, OM, SB) had no significant effects on species richness and species composition, with either univariate or multivariate effects of variables (Fig. 6; Table A4). According to our best model, only clay influenced species composition positively (LMM: t = 0.24, p < 0.036), although further models fit species composition equally well without significant differences (Fig. 6; Table A4).

3.8. Taxonomic beta diversity pattern

Beta diversity components were significantly different between pedoenvironments (Fig. 7). Overall, the taxonomic turnover (Beta.sim) showed differences with the highest values in pedoenvironments; except P1, P2 and P4, which presented the lowest values (Fig. 7). Taxonomic β-diversity (Beta.SOR) ranged from 0.80 in pedoenvironments P3 to P10, but it was < 50 in P2. The taxonomic turnover and β-diversity were higher than the nestedness-resultant component (Beta.sne) in the study area, except for P2, where there was a higher degree of nestedness (Fig. 7).

4. Discussion

4.1. Changes in diversity and community structure.

Our results revealed significant differences in community diversity (species richness, species composition and beta diversity) and structure (plant coverage) along the pedoenvironmental gradient. However, these differences were not fully explained with the tested models. This finding demonstrates that environmental filters, mediated by soil properties and coverage, are not the primary determinant of species richness and composition, except for soil texture that positively affected species composition. We presume that other ecological drivers, beyond environmental filters, are probably also responsible for these differences (i.e., dispersal limitation, neutral theory and biotic interactions). These features were not evaluated in this study. We predicted a strong environmental filter effect on diversity, and there were overlaps in species composition (NMDS) between the pedoenvironments. Indeed, the results showed this diversity pattern, a finding that partially
supports our hypothesis. These changes in the soil properties along the pedoenvironmental gradient presumably also promoted high species turnover between pedoenvironments, similar to what was demonstrated with the variation in species composition (NMDS). We also detected that pedoenvironmental heterogeneity promoted different species associations (species level) that determined the different community types.

Environmental gradient effects on bryophyte species richness have been reported in previous studies (e.g. Baniya et al., 2012; Batista and Santos, 2016; Amorim et al., 2017; Peñaloza-Bojacá et al., 2018). However, such an effect was also observed for a surprisingly small number of species of bryophytes and higher plants, as regards the electrical conductivity and pH gradients (Granzow-de la Cerda et al., 2016). Other studies found that nutrient availability drove bryophyte diversity, showing that low nutrients constrain soils with high pH, supporting greater richness (Baniya et al., 2012; Batista and Santos, 2016). On the other hand, heterogeneity and availability of substrate (microhabitats) influenced species composition on ironstone outcrops (Amorim et al., 2017; Peñaloza-Bojacá et al., 2018). Likewise, Batista and Santos (2016), report environmental determinism (local filters, such as bark pH and rugosity) influenced epiphytic bryophyte composition.

The number of species was lower than that reported by Putzke et al. (1998), who recorded 33 species of bryophytes in the same area, may be due a larger sample effort. Probably interannual environmental variability (e.g. disturbance by retreating glaciers, microclimate variation) and dispersion and colonization processes cause these marked variations in species composition. In another study Putzke et al. (2015) recorded 18 species of bryophytes for Nelson Island. In both cases the family with greater richness was the Bryaceae. The species composition did not differ from that commonly found in the South Shetland Islands, where Sanionia is the dominant genus (S. georgicouncinata and S. uncinata) (Ochyra et al., 2008); it is the main genus of moss in all the Antarctic regions and is widely distributed over coastal areas (Lewis-
Sanionia does not seem to have any particular preference for soil nutrients or texture since it is present across the entire pedoenvironmental gradient, being found mainly as extensive carpets on hydromorphic soils (Pereira and Putzke, 2013; Thomazini et al., 2018). Victoria et al. (2009b) recorded its occurrence on pebbly or clayey soil and also on different terrace/beach levels (up to 20 m high), plateaus and hillsides around the Polish Station region.

### 4.2. Pedoenvironmental gradient analysis

In our study, PCA based on soil fertility and texture properties showed a marked influence of the clay gradient among the pedoenvironments. This gradient is determined by guano mineralization and neoformation of clay minerals in the ornithogenic soils, increasing clay content (Simas et al., 2007b). Previous studies on such soils in maritime Antarctica revealed a variable influence of guano, allowing soils to be distinguished as being under weak ‘ornithogenic influence’ or ‘ornithogenic soils’ (Simas et al., 2007a; Schaefer et al., 2008), depending on guano input. Furthermore, Thomazini et al. (2018) showed that clay is transported and accumulated in surrounding areas free from direct input of guano as a function of landscape redistribution by solifluxion. Although guano has a marked role in soil fertility in maritime Antarctica, the PCA clearly shows that soil fertilization (especially nitrogen and phosphorus) is associated with lower pH values and increasing soil acidification, consistent with the findings from Schaefer et al. (2008), Moura et al. (2012) and Thomazini et al. (2018). Conversely, some nutrients (e.g. Ca, Mg) are greatly reduced under ornithogenic influence (Michel et al., 2006; Simas et al., 2007b; Francelino et al., 2011; Moura et al., 2012), being up to two times lower than background figures, suggesting base leaching (Thomazini et al., 2018). Other factors, such as distance to the glacier, distance to the coast, altitude, the type of substrate and slope, may also be determinant in bryophyte assemblages (Favero-Longo et al., 2011; Rodriguez et al., 2018). However, in our case we selected sampling points with similar landscape characteristics, except for the varying physical and chemical properties of the soil, forming a clear soil gradient.

The direct gradient analysis (CCA, Fig. 5) showed non-vascular plant assemblages distribution along soil texture and chemical properties variability. The contents of clay, coarse sand and OM, as well as base saturation, were the main variables influencing changes in species composition along the gradient. However, based on tested models only clay had a significant effect on species composition. These results allow us to postulate that both methods can be complementary. First to determine changes in non-vascular species distribution along the pedoenvironmental gradient (i.e. direct gradient analysis). Second, tested the main effects of environmental filters on species composition at community level (i.e. linear models). However, it is still necessary to evaluate effects at species level, with emphasis on the species-soil relationship, fine-scale soil heterogeneity in resource availability (e.g. nutrients) and physical conditions (i.e. texture), that can also determine changes in species distribution along the pedoenvironmental gradient. Thus, we presumed that low nestedness is found along pedoenvironmental gradient, and assemblages are structured by spatial turnover processes probably linked to the specific conditions for some species growth.

Previous studies in maritime Antarctica have shown that in most areas where cover is patchy, vegetation occupies different landscapes with decreasing diversity and biomass from the coastal to inland areas, where sub-desert conditions prevail (Poelking et al., 2015). Plant coverage represents the proportion of the available physical space actually occupied by plants (Ji et al., 2009). It is therefore plausible that plant communities with high percentage cover are more likely to use environmental resources more efficiently than those with low coverage, with the result that plant coverage enhances diversity (Ji et al., 2009; Sanaei et al., 2018a,b). In the present study, however, plant coverage did not affect species richness or composition. This allows us to postulate that pedoenvironmental filtering is the main driver of community assemblage, because density-dependent processes are more important when environmental filters are less influential (Webb et al., 2002; Kraft et al., 2015). However, this does not rule out possible effects caused by temporal and spatial beta diversity that can simultaneously determine patterns at community scale, as well as types of associations between species.

### 4.3. Species associations and types of communities

Our results indicated that pedoenvironmental gradient not only determined diversity pattern at fine scale but also the type of community and species association. For example, the moss carpet S. georgica-W. fontinalis association (Longton, 1988) is commonly found in hydromorphic and poorly drained soils (e.g. P1) where melting water accumulates (Putzke and Pereira, 2001, Ochyra et al., 2008). On the other hand, the S. uncinata moss carpet community (e.g. P2) was closely associated with coarse sand and lower nutrient content (Fig. 2). The location where this S. uncinata moss carpet community developed
also experienced an anthropogenic impact, representing an area where the Chinese Refuge was located before its removal. Although we did not measure anthropogenic variables, it may well represent an additional factor promoting changes in bryophyte assembly communities. In this regard, Peñaloza-Bojacá et al. (2018) reported that moss assemblages in protected areas were very similar but differed when compared to areas with anthropogenic disturbance. On the other hand, the P4 pedoenvironment presented high richness with species growing on soils with high available Cu values, which may be associated with the presence of lichens *Lecania brialmontii* and *Physcia caesia*, which only occurred in this pedoenvironment. According to Olech (2004), these species have been reported as an association in sites influenced by bird guano or nesting areas. Indeed, nesting was not observed in points P1, P2 or P4 of pedoenvironmental gradient. In contrast, P3 and P5 were the pedoenvironments with the highest concentrations of Ca, Mg, Mn content (Table 2) and the lowest Fe and were associated with a *Sanionia* spp. community moss carpet. The *W. sarmentosa-Sanionia sp.* association moss carpet (P3), where *Pohlia cruda* and *Syntrichia* appeared with low values of ESI (both = 3.44, Table A2), suggested that these latter species are at an early stage of establishment.

The P6 pedoenvironment was a well-drained site located on a scree slope, ending at a giant-petrel nesting site (*Macronectes giganteus*),

![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 Zn, effective cation exchange capacity (t), exchangeable acidity (H + Al), pH, organic matter (OM), sum of exchangeable bases (SB); effective cation exchange capacity (t), and the soil texture as coarse sand (Sand_c), fine sand (Sand_t), clay and silt contents were included.](image)
which had moss carpet of *Sanionia* spp.-*Hennediella* association (Table 1). This pedoenvironment had a strong ornithogenic influence, due to the proximity of giant petrel, confirmed by the high levels of phosphorus detected (Table 2, Fig. A.12). Therefore, the richness and species composition of P7 and P8 pedoenvironments may be related to higher soil fertility caused by the ornithogenic input. There, *C. aciphyllum*, *Cladonia metacorallifera*, *C. rangiferina*, *Placopsis contortuplicata* and *Usnea aurantiaco-atra* were species that appeared to be related to high contents of P, N and OM (Table 2). Although birds are no longer nesting there, these abandoned penguin nesting areas are usually richer in P/N, long after the glacial-isostatic uplift. The P8 pedoenvironment was the area with the highest species richness, forming moss carpet of *Sanionia-Bryum* association. *Andreaea gainii*, *Cladonia* sp. and *Rhizocarpon geographicum* were only detected in this pedoenvironment and we consider that soil attributes represented a strong filter, due to high levels of Fe, acidity, OM and exchangeable aluminium, and represented an extreme of the gradient at fine scale. Finally, the P9 and P10 pedoenvironment was located on a similar waterlogged zone close to the drainage channel, forming a *Sanionia-Syntrichia-Hennediella* association and *S. georgicouncinata* community moss carpet respectively, where the lowest P and Na content were detected.

To attain a better understanding of the assembly rules of non-vascular plant communities in Antarctica, it is necessary to analyse ecological processes besides environmental filters, such as dispersal limitation and stochastic processes. In order to analyse these ecological processes, a functional trait approach must be sought allowing the evaluation of traits associated with dispersal mechanism and then by functional groups. Previous studies have showed that dispersal limitation was not related to the community organization of non-vascular plant assemblages, probably because they usually employ asexual

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**Fig. 6.** Effects of multiple predictors on species composition (A) and species richness (B) in Antarctic. Results are presented for the mean distributions. We show the averaged parameter estimates (standardized regression coefficients) of model predictors, the associated 95% confidence intervals and the relative importance of each factor, expressed as the percentage of explained variance. The p-value of each predictor is given as: (.), p < 0.1; *, p < 0.05; ** p greater than 0.01; *** p < 0.001.
strategies for dispersal (Benassi et al., 2011; Glime, 2015). On the other hand, different functional compositions indicate that moss species have different trait arrangements with environmental constraint, blurring the detection of ecological drivers of non-vascular plant community assembly (Silva et al., 2014). Finally, beta diversity patterns were attributed either to environmentally deterministic processes or dispersal limitation, but clear inferences about the involved processes are limited by species loss and replacement along environmental gradients (Baselga, 2010, 2012). These beta diversity component variations in Maritime Antarctica may also be due to different periglacial processes, degree of weathering, parental material and biological influence (especially by penguins and other birds) that should be further studied.

5. Conclusions

This study revealed that there were differences in non-vascular species richness, composition and plant coverage along a pedoenvironmental gradient in Maritime Antarctica. However, the different linear models used to test the main effects of pedoenvironmental filtering on diversity were not as marked as expected (except for texture that only affected species composition). Thus, clay content was the only soil variable with a significant effect on species composition (but not on species richness at the community level). High pedoenvironmental filtering apparently had no effect on species richness, but it determined differences in species composition. Therefore, we assume that pedoenvironmental filtering determined high beta diversity on this island from Maritime Antarctica. We found that non-vascular community assemblages tended to be more heterogeneous at the species level on the local scale, data that was mainly reflected by a higher turnover and lower nestedness among pedoenvironments. Therefore, turnover components explained most variations in the overall species beta diversity, and nestedness components contributed most variations only in the P2 with low species richness. This study revealed that fine-scale heterogeneity contributed to typical non-vascular species associations along the pedoenvironmental gradient. Furthermore, it determined species composition as well as community types.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105726.

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