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ECOSYSTEMS

Species composition, diversity and coverage pattern of associated communities of mosses-lichens along a pedoenvironmental gradient in Maritime Antarctica

DANIELA SCHMITZ, PEDRO MANUEL VILLA, ROBERTO F.M. MICHEL, JAIR PUTZKE, ANTÔNIO B. PEREIRA & CARLOS ERNESTO G.R. SCHAEFER

Abstract: Maritime Antarctica is one of the major terrestrial ecosystems dominated by lichens and mosses, which represent important ecological indicators. Thus, we aimed to evaluate the changes in associated communities of mosses-lichens diversity and coverage along a pedoenvironmental gradient on Half Moon Island, Maritime Antarctica. We focused on how patterns in associated communities of mosses-lichens species diversity (richness, species composition and beta diversity) and coverage are associated with soil properties using plant inventory data from 174 plots across 14 contrasting pedoenvironments. The results clearly show marked differences in soil properties along the pedoenvironmental gradient, which determine variations in species composition, richness and coverage. We presumed that these variations are common in Maritime Antarctica owing to varying periglacial processes, weathering degree, parent material and biological influence (especially by penguins and other birds). The community species richness and coverage along the pedoenvironmental gradient differ, nevertheless share common species present in most pedoenvironments, despite differences in coverage. We assume that most of the pedoenvironments are habitats to rare species that occur only under specific soil conditions, additionally promotes high β-diversity between pedoenvironments and low species similarity.

Key words: beta diversity, community composition, mosses, lichens, plant-soil relationships, soil filters.

INTRODUCTION

Understanding how soil gradients shape plant community diversity and structure represents an important question in ecology (Pekin et al. 2012, Hernández-Hernández et al. 2017). Plant-soil relationships have constituted an important approach in ecology studies to address diversity patterns at both large and fine spatial scales in different ecosystems worldwide (e.g. Pekin et al. 2012, Schmitz et al. 2020). Soil gradients may determine plant community assembly by selecting species from a regional species pool into a local habitat (e.g. Pekin et al. 2012, Villa et al. 2018). These patterns in plant community assembly reflected changes in species diversity (i.e. species richness, community composition), and structure (e.g. plant coverage) along soil properties gradients (i.e. soil fertility and depth filtering) based on multivariate analyses (e.g. Pekin et al. 2012, Villa et al. 2018, Schmitz et al. 2020). Thus, diversity patterns are highly scale-dependent, and particularly high species diversity often matches habitat patchiness and promotes high species turnover (e.g. beta diversity) along environmental gradients (e.g.

Hernández-Hernández et al. 2017, Schmitz et al. 2020).

Beta diversity (β-diversity) measures temporal and spatial variation in species composition (Baselga 2012). Taxonomic β-diversity corresponds to the percentage of dissimilarity in species composition between two distinct communities (Baselga 2010). For instance, a high β-diversity can result from a low proportion of shared species between two communities with a similar number of species, leading to a high contribution of the turnover (Baselga 2010, 2012). Most studies on β-diversity along environmental gradients have emphasised vascular plant communities in different ecosystems of the world. However, the relative importance of spatial dissimilarities in associated communities of mosses-lichens species composition (β-diversity) as ecological indicators along soil gradients remains poorly understood. In this context, changes in mosses-lichens species diversity along soil gradients can be significantly given ongoing climate change, affecting their response to rising global temperatures (e.g. Robinson et al. 2018).

Antarctica's main terrestrial ecosystems are dominated by lichens and mosses (Ochyra et al. 2008, Poelking et al. 2015, Rodriguez et al. 2018), and it is considered a key bioregion for the monitoring of environmental changes (Vieira et al. 2010, Michel et al. 2014). Antarctic vegetation is restricted to ice-free areas, such as the coastal zone, debris slopes or nunataks (Putzke & Pereira 2001, Ochyra et al. 2008). Relatedly, there are different community types, which can be dominated by mosses, forming carpets and turfs, or lichens with different life forms or forming mosses-lichens associations, modeled according to landforms and soil properties (Francelino et al. 2011, Poelking et al. 2015). However, differences in soil properties along the pedoenvironment gradient concerning to moss and lichen diversity and community structure remain poorly understood in Antarctica (Leishman & Wild 2001, Schmitz et al. 2020).

In this study, we aimed to evaluate the changes species composition, diversity and coverage in mosses-lichens communities along a pedoenvironmental gradient on Half Moon Island, Maritime Antarctica. We focused on how patterns in mosses-lichens species composition and richness, and coverage with soil properties using species inventory data from 174 plots across 14 contrasting pedoenvironments. In order to evaluate the community species diversity and coverage, we posed the following two research questions: 1) How do community species richness and coverage change along the pedoenvironmental gradient? 2) Do the community composition and β-diversity change across pedoenvironments? Based on the premise that soil filters shape mosses-lichens associated communities' distributions (e.g. soil chemistry, depth, elevation), we sought to determine the following hypotheses: 1) The pedoenvironmental conditions by soil properties determine differences in community species richness and coverage; 2) The community composition of mosses and lichens species diminishes in similarity with increased soil properties differences and depth vartion along the pedoenvironment gradient. These differences in community composition are driven by soil properties variables directly related to the pedoenvironment gradient; 3) Differences in soil properties along the pedoenvironment gradient promote high β-diversity.

MATERIALS AND METHODS

Study area

This study was performed on Half Moon island (62°35'42.94"S 59°55'8.41"W), one of the smallest of the South Shetland archipelago, Maritime Antarctica (Figure 1). Its total surface area is 171 hectares, of which 19.17% is covered by vegetation (Schmitz et al. 2018). There are three main hills on the island, Gabriel Hill (101 m.a.s.l) being the highest point (Schmitz et al. 2018) followed by

Xenia hill (≈ 90 m.a.s.l) and La Morenita Hill (≈ 85 m.a.s.l. behind Camara Base). Penguin rookeries are concentrated on Baliza Point and are frequently visited by tourists during the summer. The island was intensively studied during the 32^{nd} and 33^{rd} Brazilian Antarctic Expeditions in the austral summers of 2013/2014 and 2014/2015.

Selection of pedoenvironments

We selected 14 pedoenvironments with contrasting pedogenetic characteristics (Table I). We recognised that differents environmental processes (i.e. pedogenetic and landform processes) determine the 14 pedoenvironments along Half Moon island (Figure 2, Supplementary Material - Text S1 and Table SIa of Appendix). Given the marked differences between pedoenvironments, we considered the habitat filtering approach for soil-species relationship analysis (Poelking et al. 2015, Benavent-González et al. 2018, Schmitz et al. 2020). Thus, the possibility of a separating boundary between pedoenvironments provided an opportunity to study the effects of habitat filtering on species assemblages at a local scale in Maritime Antarctica (Poelking et al. 2015).

Soil properties collection

According to Bockheim et al. (2006) recommendations, each soil profile was dug and sampled, facilitating their classification using the World Reference Base for Soil Resources (IUSS Working Group WRB 2015). To measure the soil properties within each plot, a composite sample of the surface soil (0-10 cm) was collected. All soil samples were analysed at the Soil Laboratory of the Federal University of Viçosa, following international standard protocols (EMBRAPA 1997). The following parameters were assessed: available P; exchangeable K, Ca, Na, Mg, Fe, Cu, Mn, Zn; exchangeable acidity (H + Al); pH (H_2O); organic matter (OM); sum of exchangeable bases (BS); effective cation exchange capacity (t); potential effective cation exchange capacity (T); bases saturation percentage (V); Al saturation (m); and remaining phosphorus (Prem). Due to the limited sample size, physical analyses could not be performed for all environments, so they were not included in the statistical analyszes.

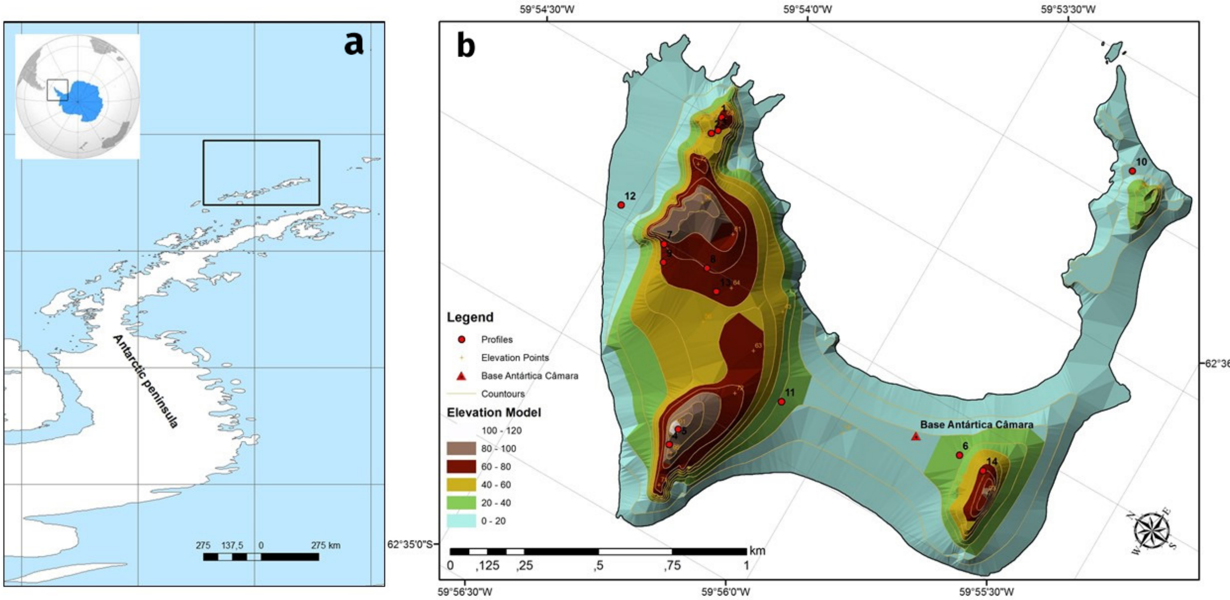

Figure 1. Localization of the study area in relation to Antarctica (a), Half Moon Island with the 14 pedoenvironments (b).

Table I. Description of the 14 sampling pedoenvironments (P).

P	Plots	Elevation (masl)	Number of species	depth of soil (cm)	Geographical coordinates	drainage level	Landform/ Geomorphology	Plant community	Soil
P1	11	83	18	20	62°35’3.30”S 59°54’28.90”W	moderately drained	Upper platforms and scarp	Moss carpet	Turbic Leptic Umbric Skeletic Cryosol (Arenic Humic Ornithic)
P2	12	71	17	20	62°35’3.17”S 59°54’33.23”W	poorly drained	Patterned ground	Moss carpet	Reductaquic Leptic Skeletic Cryosol (Arenic Humic Ornithic)
P3	5	76	10	20	62°35’3.65”S 59°54’31.92”W	little drained	Gelifluction lobes	Musciculous lichens	Turbic Leptic Umbric Skeletic Cryosol (Arenic Humic)
P4	14	100	29	20	62°35’15.78”S 59°55’39.78”W	well drained	crest, ridge	Moss carpet	Turbic Leptic Cryosol (Arenic, Humic)
P5	10	90	23	20	62°35’15.8”S 59°55’35.7” W	well drained	Upper plataforms and gelifluction lobes	Moss turf	Turbic Leptic Cryosol (Arenic Humic Ornithic)
P6	13	40	22	14	62°35’42.94”S 59°55’8.41”W	little drained	Debris slope and cone	Moss carpet	Turbic Leptic Umbric Cryosol (Arenic Humic)
P7	19	90	29	37	62°35’4.70”S 59°55’0.60”W	moderately drained	Middle platforms and scarps	Musciculous lichens	Turbic Leptic Umbric Cryosol (Arenic Humic)
P8	16	80	24	25	62°35’9.92”S 59°55’0.43”W	poorly drained	Upper platforms and scarp	Moss carpet	Turbic Reductaquic Leptic Mollic Cryosol (Arenic Humic)
P9	9	64	19	80	62°35’05.6” S 059°55’04.3”W	well drained	Scarp	Moss carpet	Turbic Cryosol (Dystric Arenic Ornithic)
P10	8	12	11	27	62°35’43.73”S 59°53’52.19”W	drained	Present day and Holocene beaches	Crustose lichens	Skeletic Leptosol (Arenic Gelic Ornithic)
P11	8	44	12	25	62°35’23.8”S 59°55’18.3”W	Moderately drained	Present day and Holocene beaches	Crustose lichens	Turbic Skeletic Cryosol (Arenic Eutric Patterned)
P12	21	3	6	25	62°34’58.70”S 59°54’57.80”W	well drained	Present day and Holocene beaches	Moss carpet	Eutric Leptosol (Siltic Gelic)
P13	18	67	30	37	62°35’12.0”S 59°55’04.0”W	moderately drained	Gelifluction lobes	Moss carpet	Turbic Umbric Cryosol (Arenic Ornithic)
P14	11	85	28	40	62°35’45.9”S 059°55’08.8”W	well drained	Middle platforms and scarps	Fruticose lichens	Turbic Leptic Umbric Skeletic Cryosol (Arenic Humic)

Figure 2. Barplots soil properties. For analysis, available: pH (H_2O), exchangeable acidity (H + Al), sum of exchangeable bases (SB), Ca^{2+}, Mg^{2+}, Na, P, K, organic matter (OM), Cu, Mn, Fe, potential cation exchange capacity (T), percentage of bases saturation (V), effective cation exchange capacity (t), Remaining phosphorus (P Rem), Al saturation (m) and Zn, were included.

Associated communities of mosses-lichens sampling

The pedoenvironments presented different mosses-lichens coverage areas; hence the number of plots was sufficient sampling representation in Half Moon. The number of plots ranged from five to 21 plots measuring 20×20 cm in differents pedoenvironments (Table I). A total of 174 plots across the 14 studied pedoenvironments were sampled using the Braun-Blanquet (1932) square method and adapted to Antarctic vegetation conditions to measure the coverage of species in each plot. Within each plot, the majority of mosses and lichens were identified to the species level. Moss species were identified using the taxonomy keys presented by Ochyra et al. (2008) and Putzke & Pereira (2001), and lichen species using the keys presented by Øvstedal & Lewis-Smith (2001) and Olech (2004). The species were deposited in the herbarium at the Universidade de Santa Cruz do Sul (HCB).

The types of plant communities were named according to Schmitz et al. (2018) and the landform classification provided by López-Martínez et al. (2012). Other characteristics such as elevation, depth and soil drainage levels and face of exposure were measured in the field (Table I).

Data analyses

All analyses were carried out in R Environment (R Core Team 2018). We tested normal distribution for all variables, using the Shapiro-Wilk test and evaluating the Q-Q plot, and the homogeneity of variances by Bartlett's test. In order to compare soil properties (non-normally distributed data), species richness and coverage between pedoenvironments sites, we used Kruskal-Wallis' test followed by a posterior Dunn's test performed with the 'dunn.test' package (Dinno 2017).

Soil variables were summarized using principal components analysis (PCA) to identify a possible pedoenvironmental gradient and to reduce the number of redundant soil properties; 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)

Species richness in the 14 contrasting pedoenvironments' sample areas was evaluated using both sample-based data to estimate rarefaction and extrapolation curves using the first Hill number (Chao et al. 2014). Extrapolations were made based on presence/absence in the plot data of species by pedoenvironment (e.g. Colwell et al. 2012). Sample-based rarefaction/extrapolations with 95% confidence intervals were computed using the 'iNEXT' package (Hsieh et al. 2016). Rarefaction was estimated as the mean of 100 replicate bootstrapping runs to estimate 95% confidence intervals. Whenever the 95% confidence intervals did not overlap, species numbers differed significantly at $P < 0.05$ (Colwell et al. 2012). These estimates were obtained using the "iNEXT" package (Hsieh et al. 2016).

We performed non-metric multidimensional scaling (NMDS) to analyse differences between pedoenvironments in terms of species composition using Euclidean distance, specifically the 'metaMDS' function of the "vegan" package (Oksanen et al. 2018). We used permutational multivariate analysis of variance (PERMANOVA, 9999 permutations) to determine differences in species composition by using the adonis routine available within the "vegan" package (Oksanen et al. 2018). We undertook two way cluster analyses using Sorensen measures dissimilarity based on presence/absence data to identify pattern dissimilarity in species between pedoenvironments.

We used the multivariate homogeneity analysis to assess β-diversity along pedoenvironments (Anderson 2006). We calculated β-diversity as distance to group centroid based on Euclidean distance by using the R function betadisper in 'vegan' (Monte-Carlo, 999 permutations). We tested for differences in β-diversity between pedoenvironments for each site using the permutation test of homogeneity of multivariate dispersion (PERMDISP), which avoids problems of lack of independence among pairwise site comparisons (Anderson 2006). We subsequently used TukeyHSD.betadisper to create a set of confidence intervals on the differences between the mean distance-to-centroid of the levels of the grouping factor (Anderson 2006). We used the vegdist function to calculate Euclidean distance, and the betadisper and permutest functions to test for homogeneity of multivariate dispersion in the vegan package in R software 3.4.2. (Oksanen et al. 2018, R Development Core Team 2018).

RESULTS

Soil fertility descriptors

The first two axes of the soil fertility PCA explained 52.7 % of the data variance (Figure 3). The biplot scores of the soil fertility descriptors were significantly correlated with the first axis (PCA1) and explained 34.3 % of the variance. The first axis was positively correlated (Figure S1 of Appendix) with pH ($R = 0.70$ $p < 0.05$), the percentage of base saturation ($R = 0.48$, $p < 0.05$) and nutrients such as Mn ($R = 0.60$, $p < 0.05$), and Mg ($R = 0.58$, $p < 0.05$), distinguishing different pedoenvironments. Conversely, the PCA_1 was negatively correlated with organic matter ($R = -0.87$, $p < 0.05$), Al saturation ($R = -0.63$, $p < 0.05$) and potential cation exchange capacity (R =

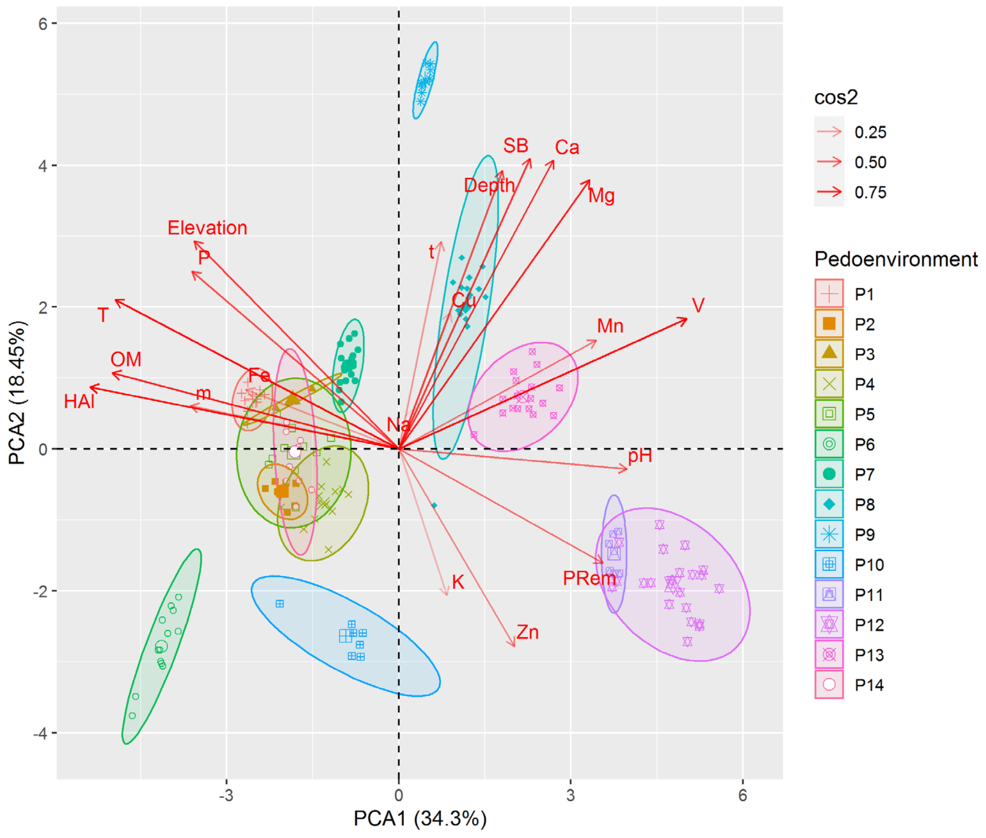

Figure 3. Principal Component Analysis (PCA) for the soil parameters of different types of pedoenvironment sites. For analysis, chemical properties available: P, K, Ca, Na, Mg, Fe, Cu, Mn, Zn, exchangeable acidity (H + Al), pH (H_2O), organic matter (OM), sum of exchangeable bases (SB); effective cation exchange capacity (t), potential cation exchange capacity (T), Al saturation (m), percentage of bases saturation (V); soil depth and elevation were included.

-0.86, $p < 0.05$). The second axis explained 18.4% of the variation and was negatively correlated with soil depth ($R = 0.88$, $p < 0.05$), elevation ($R = 0.70$, $p < 0.05$) and phosphorus ($R = 0.67$, $p < 0.05$) along the pedoenvironmental gradient.

Species richness and plant coverage pattern

Twenty-one bryophyte species (20 mosses and one liverwort), 42 lichen species and one macroscopic algae (*Prasiola crispa* (Lightfoot) Kützing) were identified in the 14 pedoenvironments of Half Moon Island (Table SIb). The number of sampled plots reached the asymptote in most pedoenvironments, i.e. the extrapolation did not differ significantly from the interpolation (Figure 4a). The exceptions were P2, P5 and P6, suggesting that these environments could have presented more species with a greater sampling effort. Given that plots were set along transects over the vegetation patches, in some cases sampling was limited. The pedoenvironments revealed

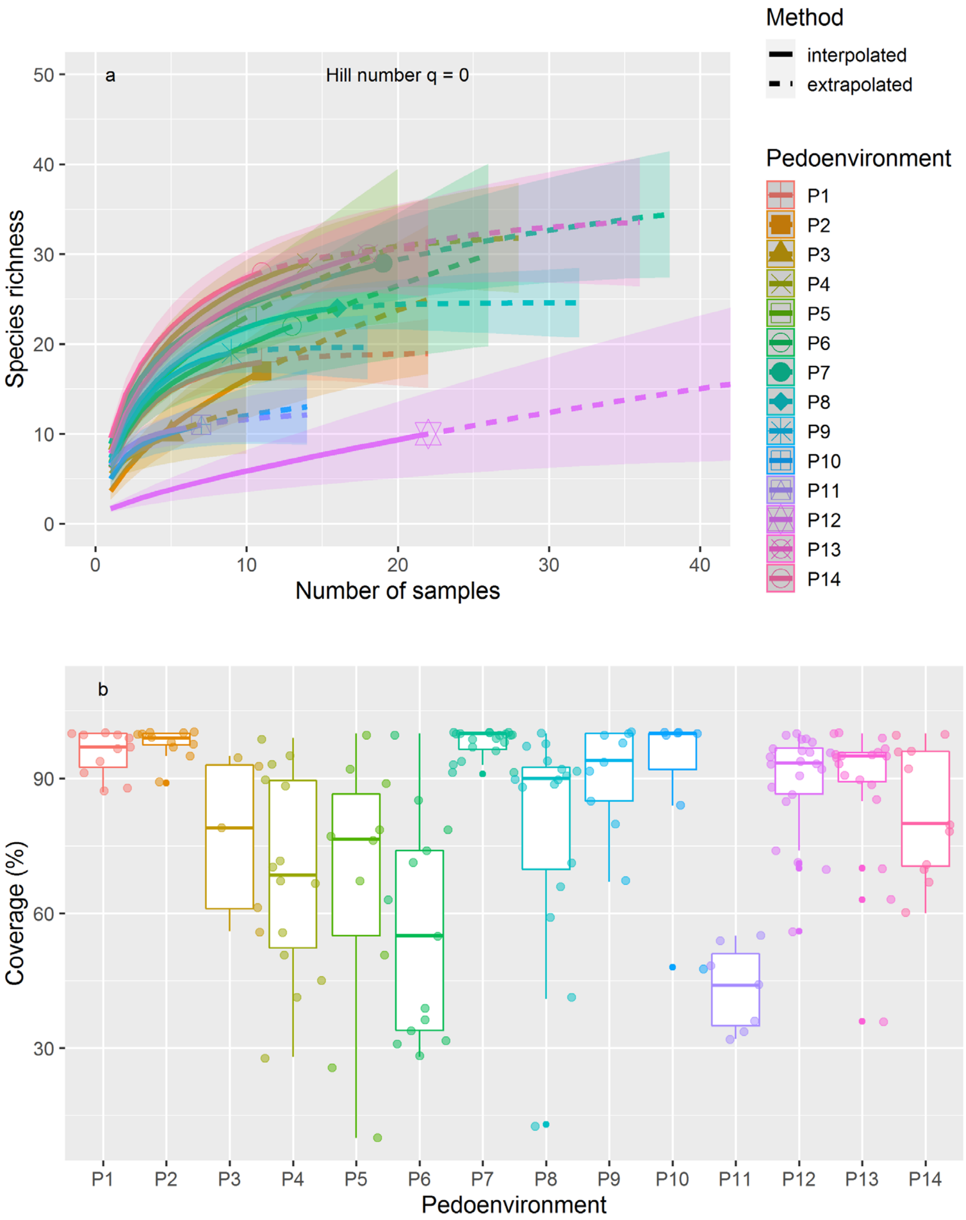

Figure 4. Sampled-based rarefaction (solid lines) and extrapolation curves (dashed lines) of bryophyte species diversity based on the first Hill numbers ($q = 0$) for the sampled pedoenvironment and differences in species richness (a), and coverage (b) between sampled pedoenvironment. Rarefaction and extrapolation curves present the lines that represent the mean values and the bands the standard deviation with 95% confidence intervals.

similar patterns of richness, but with different species. P12 had the lowest number of species (six), while P1, P2, P3, P9, P10 and P11 had similar numbers (ranging from 10 to 20 species) (Table I). The highest numbers were recorded for P4, P5, P6, P7, P8, P13 and P14 (22 to 30 species). The community coverage also presented significant differences (chi-squared = 79.53, df = 13, p-value = 0.001) among pedoenvironments (Figure 4b).

Community composition and beta diversity pattern

The pedoenvironments differed significantly in their species composition, forming 14 groups on the first and second axis (Figure 5). Although some species were present in various pedoenvironments, their spatial distribution was concentrated in pedoenvironments such as P4, P6, P8, P9 and P13 (Figure 6). Others were restricted to specific environments with particular soil conditions, such as *Buellia racovitzae* CW rodeio and *B. russa* (Hue) Darb. in P4; *Ceratodon purpureus* (Hedw.) Brid. in P5; *Bartramia patens* Brid., *Bryum* sp., *Bacidia* sp. in P6; *Physconia muscigena* (Ach.) Poelt and *Pohlia nutans* (Hedw.) Lindb. in P7; *Candelaria murrayi* Poelt, *Lecania brialmontii* (Vain). Zahlbr., *Ramalina terebrata* Hook. f. & Taylor, *Syntrichia magellanica* (Mont.) RH Zander and *Xantoria elegans* (Link) Th. Fr. in P10; *Bryum nivale* Müll. Hal. in P12; *Bryum dichotomum* Hedw. and *Scapania* sp in P13; and *Sanionia* spp, despite its absence in P10, was dominant in the other pedoenvironments. Differences in β-diversity among pedoenvironments (PERMDISP: $F_{13,173} = 8.12$, $p < 0.001$) were observed (Figure 7). β-diversity, measured as the distance to the group centroid, was higher in the P13 and P14 pedoenvironments than in the P11 and P12 pedoenvironments.

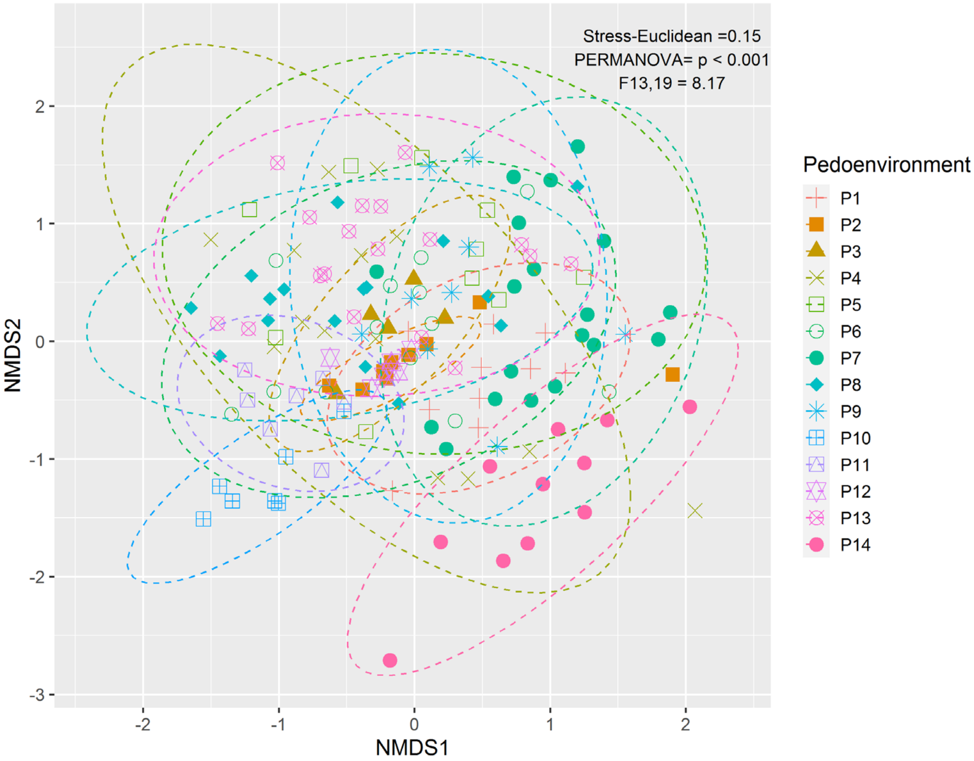

Figure 5. Non metric multidimensional scaling (NMDS) based on species composition from different pedoenvironments.

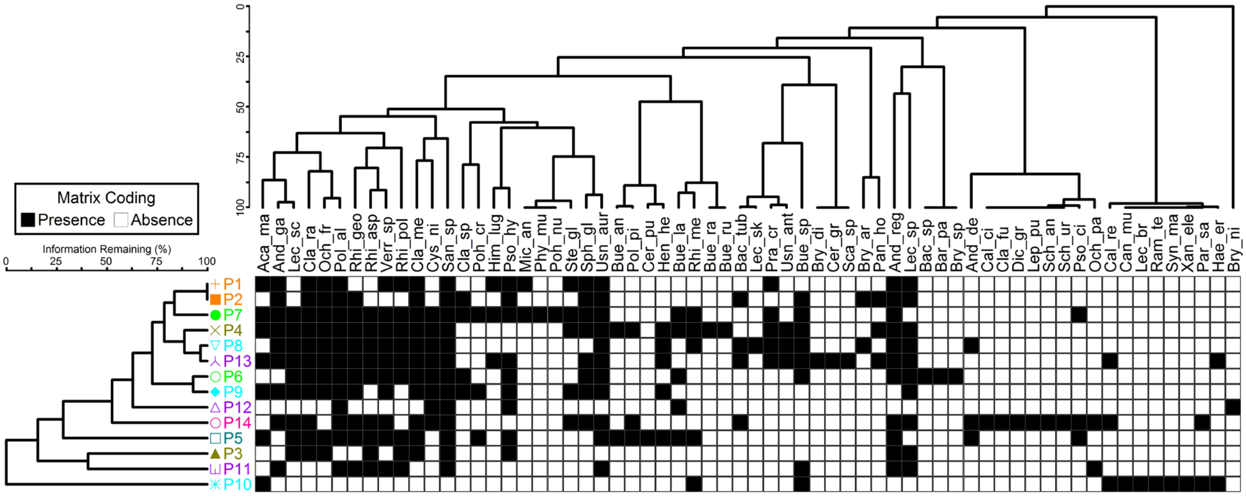

Figure 6. Distribution of 64 species within 174 samples plots installed along a pedoenvironmental gradient by a two way cluster dendrogram based on Euclidian distance. See full names of the species in Table SIb from ESM.

DISCUSSIONS

Our study area clearly presented marked differences in soil properties along the pedoenvironmental gradient. These variations are common in Maritime Antarctica (Thomazini et al. 2018) due to varying periglacial processes, weathering degree, parent material and biological influence (especially by penguins and other birds) (Simas et al. 2007, Schaefer et al. 2008). On Half Moon Island, the discontinuous permafrost affects sites located above the marine terraces, where landforms are mainly periglacial and include till. Many different landforms occur on this tiny island, such as patterned ground, stone stripes, gelifluction sheets, gelifluction lobes, debris slopes and debris cones (López-Martínez et al. 2012).

This study showed marked differences in species richness and coverage due to differences in soil properties along the pedoenvironmental gradient, corroborating our first hypothesis. Accordingly, we note that community similarity decreases as differences in soil properties between pedoenvironments increases, supporting our second hypothesis. These changes in soil properties along the pedoenvironmental gradient promote a high degree of species turnover between pedoenvironments (β-diversity) despite a fine spatial scale, confirming our third hypothesis. Therefore, differences observed in β-diversity can be related to differences in the soil properties evaluated through a direct gradient analysis.

Direct gradient analysis: community diversity and coverage pattern

The 14 pedoenvironments are distributed throughout the entire length of Half Moon Island and show substantial soil variability. The different pedoenvironments studied probably have different levels of ornithogenic influence, where the formation and variability of soil chemical properties are shaped by penguins' activity (Simas et al. 2007). Penguins incorporate organic matter into the soil through their excreta (known as guano), which is dependent on the long-term permanence of penguins at each specific pedoenvironment, thereby altering the nutrient cycling process at a fine scale (Zhu et al. 2014). In this way, we assume that most differences in soil properties between pedoenvironments owe to the temporal and spatial variation of

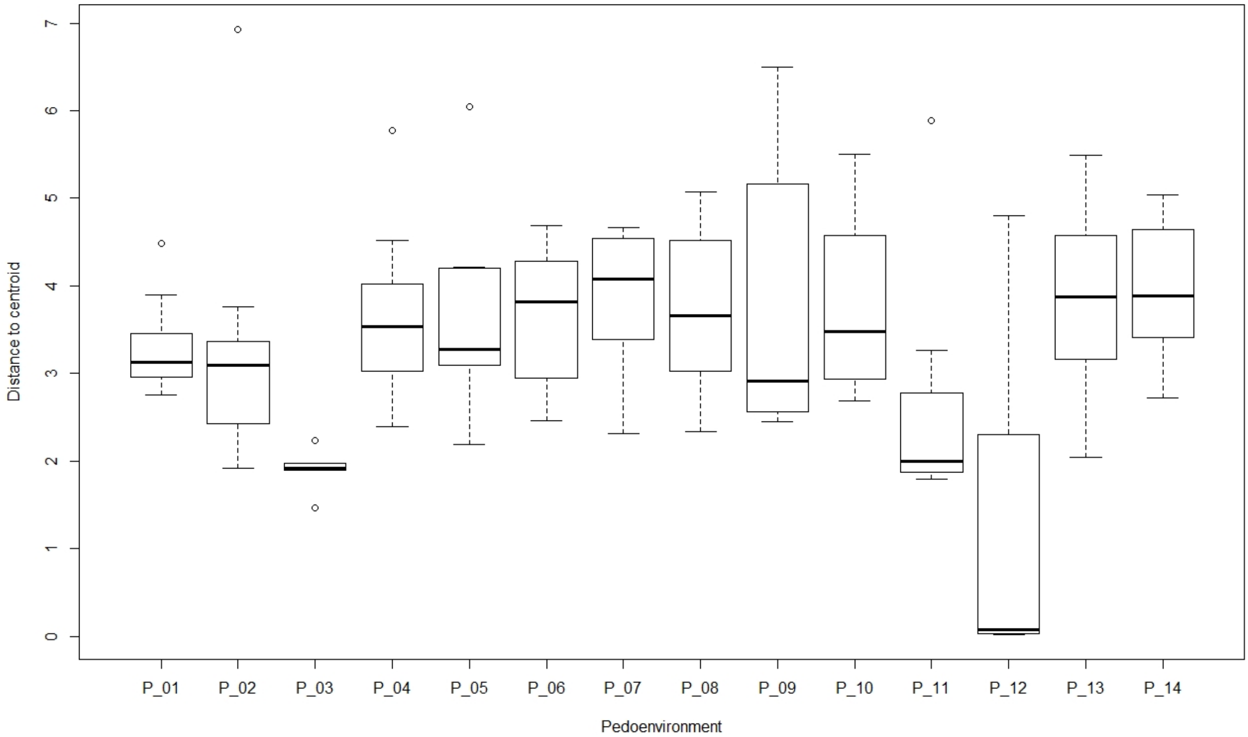

Figure 7. Differences in β-diversity measured as distance to group centroid along the pedoenvironmental gradient. Average pairwise dissimilarity is presented. Beta diversity differs significantly between the pedoenvironments.

penguin activity in the study area, resulting in contrasting values of available P and acidity (pH and H + Al) in the different pedoenvironments (Tatur 1989, Tatur & Myrcha 1989, Tatur & Keck 1990, Tatur et al. 1997, Michel et al. 2006, Simas et al. 2007). According to Simas et al. (2007), guano is initially alkaline, but rapid progressive acidification occurs with greater microbial degradation of organic matter. Ornithogenic soils are well-known in the Maritime Antarctic region, where phosphatisation is the main soil formation process (Michel et al. 2006, Simas et al. 2007, Pereira et al. 2013, Daher et al. 2019).

Despite their proximity, some pedoenvironments showed differences in species composition, associated with large variations in soil properties at a fine scale. For example, even though the adjacent P1 and P2 areas located on the eastern side of Xenia Hill were covered by a similar moss carpet in terms of species composition, they exhibited large differences in soil chemical properties. In this example, P2 presented soils with low acidity (pH 6.5) and P, K and Ca values twice as high as P1, whereas P1 showed the highest content of Na (1551.41 cmol/dm^3, Table SIb) due to its exposure to marine saline sprays and local aridity (Michel et al. 2006). This finding can be corroborated by the presence of *Verrucaria* sp., which is associated with saline environments and wind exposure (Olech 2004). Although we mainly focused here on the species distribution patterns and types of communities along with a complex pedoenvironmental gradient system, presumably other environmental factors (e.g. sea spray, drainage and biotic interactions) may also influence plant community diversity and structure. On the other hand, P2 is located in a poorly drained and small depression pedoenvironment where a high water table and substantial organic matter content favor the growth of a thick moss carpet. However, along with P3, these two pedoenvironments exhibited the highest organic matter content associated with abundant available P, suggesting that a former penguin colony inhabited the area (Michel et al. 2006) and created a phosphatized environment (Simas et al. 2007).

Soils P3 and P7 have a muscicolous lichen community, and both showed similar soil patterns, only differing significantly to OM and Mn. These soils are well-developed, with lichens growing on moribund or living mosses, confirming their advanced succession and favorable status for the coexistence of some species, as suggested for similar soils from King George Island (Tatur & Myrcha 1993). However, P7 has higher species richness (29 species), and P3 only 10, nine of which share (Figure 6).

P4 (moss carpet community) and P5 (moss turf community) are located at Gabriel Hill, at more elevated sites. They followed similar soil fertility patterns, except for micronutrients (Fe and Zn), but presented different plant compositions. However, these pedoenvironments exhibited different textural classes (Table SIa), P4 being sandy-loam and P5 sandy, i.e. P4 has a higher percentage of clay, probably there is a significant effect on species composition (e.g. Schmitz et al. 2020).

In P9, high phosphorus (P), calcium (Ca) and magnesium (Mg) content combined with high effective cation exchange capacity levels, and greater depth characterize an ornithogenic cryosol (Michel et al. 2006), indicating a former penguin rookery. Located on an elevation escarpment (64 m a.s.l.) with a moss carpet cover, it is certainly an abandoned penguin colony that with glacio-isostatic uplift migrated to lower parts of the island. There is ample evidence that due to deglaciation and resultant glacio-isostatic uplift during the Holocene (Fretwell et al. 2010), a large number of penguin rookeries moved from upland areas to newly exposed marine terraces (Rodrigues et al. 2019), closer to the emerging coast and into adjacent rock outcrops (Michel et al. 2006, Daher et al. 2019). These highland areas thus became inaccessible for penguins, while the newly emerged land became occupied by new populations (Daher et al. 2019, Rodrigues et al. 2019), resulting in pedoenvironments with higher plant coverage, such as P9 (Figure 4b).

This is consistent with known glacio-isostatic uplift rates, between 16 and 20 m (Fretwell et al. 2010) with the highest beach ridge is located 16.8 m above the present-day beach (P12). Contemporary periglacial processes in a warming scenario seem less intense, corroborating the widespread presence of lichens over debris slopes and patterned ground, like P11 (López-Martínez et al. 2012). P11 is a high marine terrace in the Holocene, at an elevation of 20 m.a.s.l. (Table I) and located in the central tombolo formed by marine graves connecting the northern and southern parts of the island. It presented the lowest P and OM amounts recorded in the study, with sparse coverage of crustose lichens on cobbles and gravels at the soil surface, under similar areas from the South Shetland Islands (Kim et al. 2007, Simas et al. 2008, Rodrigues et al. 2019). Despite the intermediary species richness observed (Figure 4a, Table I), this pedoenvironment showed the lowest community coverage (Figure 4b) due to its recent exposure and relative lack of local bird activity.

P10 is located in the extreme south of the island, in an area called Baliza Point near an active penguin colony, and can be classified as a crustose lichens community (Schmitz et al. 2018). Some rare species, such as *C. murrayi*, *R. terebrata* and *X. elegans*, which only occur in this pedoenvironment, are ornitocoprophilous

(Olech 2004), capable of surviving under the high phosphorus and nitrogen levels present in penguin guano. As it is a dry and stony pedoenvironment, it was the only one where *Sanionia* spp. was not detected, even though this is a genus of wide distribution on this island and elsewhere in Maritime Antarctica. It is usually absent in dry habitats dominated by crustose lichens (Ochyra et al. 2008, Schmitz et al. 2018).

P12 is located on current beaches on the northern side of Half Moon Island that receives meltwater from the highest parts. Scattered bone and egg shell fragments, nest remains and bird droppings indicate nesting activity by skuas, with weak ornithogenic influence (Simas et al. 2007). A discontinuous vegetation community composed of moss carpet *Sanionia* ssp is present (Table I), and only six species were identified, the lowest level of richness (Figure 4a). The moss *Bryum nivale* is a rare species that only occurred in this pedoenvironment, which is often flooded or covered by snow, and recorded the highest values of V, P Rem and Mn. The *B. nivale* record for the South Shetland Islands is rare and recent, indicating that this species may currently be colonizing areas after glacier retreat, as postulated by Wierzgoń et al. (2018).

P6 and P14 are located at La Morenita Hill, at different elevations (40 and 85 m.a.s.l., respectively), although some of their soil properties followed similar patterns (Figure 2, Table SIa). Indeed, they showed plant coverage with distinct communities: whereas P6 has a moss carpet, P14 has a fruticose lichen community (Table I). Both are closely related to drainage and landform, as P6 is a flat area in the lower part of La Morenita Hill, classified as a debris slope and cone (López-Martínez et al. 2012), whereas P14 at the top of the hill is classified as a middle platform. Some rare species were found in P6 (*B. patens*, *Bacidia* sp. and *Bryum* sp.) that did not occur in any other pedoenvironment of this study, and may be related to water logging and high Fe content. Species such as *Caloplaca cinericola* (Hue) Darb., *Cladonia furcata* (Huds.) Schrad., *Dicranoweisia* (*Hymenoloma*) *grimmiacea* (Müll. Hal.) Broth, *Leptogium puberulum* Hue, *Schistidium antarctici* (Card.) L.I. Savicz & Smirnova and *Schistidium urnulaceum* (Müll. Hal.) BG Sino were only recorded in P14 (Figure 6), where the highest levels of Cu were noted (Figure 2). According to Schaefer et al. (2004), the presence of *Usnea* spp as common fruticose lichen (P14) generally indicates a more stable, rocky and drained landscape. This species has a tendency to occur in locations with greater exposure, less snow cover and high altitude (Kim et al. 2007). On the other hand, bryophytes, which are positively associated with higher water content and waterlogging (Leishman & Wild 2001), are found in moister, more sheltered habitats (Kim et al. 2007). This was the case of *Sanionia* spp., which often occurs in hydromorphic soils (Thomazini et al. 2018), probably regardless of their chemical attributes.

P8 is located at a slightly higher landscape position than P13, and both have moss carpet communities. The soil fertility patterns and species composition of these pedoenvironments are very similar, but the number of species in P13 is much higher, reaching 30 species, the most in this study. The species that appeared in P13 but were absent in P8 were mostly fruticose lichens (*Himantormia lugubris* (Hue) Cordeiro IM, *Sphaerophorus globosus* (Huds.) Vain.) and crustose lichens (*Acarospora macrocyclos* Vain., *Haematomma eryhtromma* (Nyl.) Zahlbr.) with a preference for growing on pebbles and boulders (Kim et al. 2007), in places of better soil drainage, such a stable Felsenmeer surfaces, and platforms with high wind exposure and desiccation (Francelino et al. 2011). Despite P13's ornithogenic influence, it showed a neutral/alkaline pH (7.2) and lower values of Fe, which is associated with the presence of *Scapania* sp., *Bryum dichotomum* and *Ceratodon grossiretis* Cardot, indicating that these mosses are limited by soil acidity. This pattern is consistent with previous reports that bryophyte diversity increases with soil pH (e.g. Stephenson et al. 1995). Hence, this environment with higher soil fertility also presented higher β-diversity, probably because favorable soil conditions and considerable availability of resources enable greater species coexistence (Laliberté et al. 2014), while environmental filtering has less importance than in other pedoenvironments with lower fertility.

We found higher β-diversity in P13 and P14, where higher pH and Mg^{2+} respectively occur. Lower β-diversity was recorded in P12 and P11, with CEC, P and OM contents. We predicted that the β-diversity pattern was also influenced by changes in species richness along the pedoenvironmental gradient. For example, where higher β-diversity was observed, higher richness was also found, and vice-versa (P12) with lower species richness. However, there is limited information available regarding the abiotic and biotic processes and drivers to explain how resource availability (i.e. nutrients) in these pedoenvironments directly influence β-diversity in non-vascular communities in Maritime Antarctica.

A similar β-diversity pattern has been observed in numerous studies from other locations where the plant coverage of dryland vegetation is discontinuous by forming a patchy mosaic of grasses and shrubs in a more or less bare soil matrix (Rietkerk & van de Koppel 2008). This patchy mosaic is assumed to be the result of close feedback on the availability of resources (nutrients and water) and associated communities of mosses-lichens dynamics (Rietkerk & van de Koppel 2008). On the other hand, species coexistence in these patchy mosaics may be crucial to increasing species richness by facilitation (Molina-Montenegro et al. 2016). Thus, we presumed that different community types and plant coverage levels between different soil conditions reported for Maritime Antarctica (i.e. Schmitz et al. 2018) can also promote higher species turnover along the pedoenvironmental gradient. Previous studies have shown that high vegetation density produces a niche differentiation, and promotes species coexistence and niche facilitation processes between rare and common species (e.g. Sanaei et al. 2018).

CONCLUSIONS

1. Our study has revealed differences in environmental conditions (elevation, depth and chemical soil properties) between 14 contrasting pedoenvironments of Half Moon Island, a small island in Maritime Antarctica.

2. Newly exposed pedoenvironments (P10, P11 and P12) have lower species richness and coverage. Thus, species richness and coverage along the pedoenvironmental gradient differed, yet some species were present in the majority of the pedoenvironments. Nevertheless, most pedoenvironments recorded rare species that occurred only under specific soil conditions, thereby contributing to the high species turnover between pedoenvironments and low floristic similarity, which promoted high β-diversity.

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SUPPLEMENTARY MATERIAL

Appendix.
Table SIa.
Table SIb.
Figure S1.

How to cite

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DANIELA SCHMITZ[1]
https://orcid.org/0000-0002-3162-2430

PEDRO MANUEL VILLA[1]
https://orcid.org/0000-0003-4826-3187

ROBERTO F.M. MICHEL[2]
https://orcid.org/0000-0001-5951-4610

JAIR PUTZKE[3]
https://orcid.org/0000-0002-9018-9024

ANTÔNIO B. PEREIRA[3]
https://orcid.org/0000-0003-0368-4594

CARLOS ERNESTO G.R. SCHAEFER[4]
https://orcid.org/0000-0001-7060-1598

[1] Universidade Federal de Viçosa, Departamento de Biologia Vegetal, Av. PH Rolfs, s/n, 36570-900 Viçosa, MG, Brazil

[2] Universidade Estadual de Santa Cruz (UESC), Departamento de Ciências Agrárias e Ambientais, Rodovia Jorge Amado, km 16, Salobrinho, 45662-900 Ilhéus, BA, Brazil

[3] Núcleo de Estudos da Vegetação Antártica (NEVA), Universidade Federal do Pampa, 97300-000 São Gabriel, RS, Brazil

[4] Campus Universitário, Núcleo TERRANTAR, Departamento de Solos, Universidade Federal de Viçosa, Av. PH Rolfs, s/n, 36570-900 Viçosa, MG, Brazil

Correspondence to: **Daniela Schmitz**
E-mail address: danni_schmitz@hotmail.com

Author contributions

CEGRS and ABP designed the study. DS, JP, ABP and RFMM carried out the fieldwork. DS, JP and ABP sampled the vegetation and identified the species. RFMM collected and classified the soils. DS and PMV wrote the manuscript with contributions from all co-authors.